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BASE CATION IMMOBILIZATION IN THE STEM OF SOME HARDWOODS OF SOUTHERN QUÉBEC

by

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A thesis submitted to the Faculty of Graduate Studies and Research

in partial fulfilment of the requirements for the

degree of Master of Science

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ABSTRACT

The objective of this study was to investigate K, Ca, and Mg immobilization in the stem of species typical of the hardwood forest of southern Québec. The species examined included American basswood, sugar maple, and white ash from a rich site, and American beech, red oak, and red maple from a poor site. Firstly, rates of immobilization were evaluated over a time span of 40 years. Higher rates of immobilization in the wood only were generally observed on the rich site. Sugar maple immobilized Ca at an elevated rate during 1978-1997, in comparison to the other species on site. In the case of Ca for white ash, and Ca and Mg for red oak, a low wood element concentration and a high rate of growth was associated with a low rate of immobilization. Mean annual immobilization rates on a whole stem basis were also determined for the life of the tree. These results suggest that American basswood and red oak immobilize significant amounts of Mg and Ca in their bark, respectively.

In a second study, concentrations of K, Ca, and Mg across the radial section of the stem (heartwood, transitional, sapwood, and bark) were determined. In a majority of cases, the bark was highest in concentration of base cations. Whereas, for the woody portion of the stem, concentrations were generally highest in the heartwood.

Short Title:

Base cation immobilization in the stem of some hardwoods

RÉSUMÉ

L'objectif de cette étude était d'étudier l'immobilisation de K, Ca, et Mg dans la tige d'espèces caractéristiques de la forêt feuillue du sud du Québec. Les espèces étudiées incluaient le tilleul, l'érable à sucre et le frêne d'Amérique sur un site riche, et le hêtre, le chêne rouge et l'érable rouge sur un site pauvre. Dans un premier temps, les taux d'immobilisation dans le bois seulement ont été évalués sur une période de 40 ans. Des taux plus rapides d'immobilisation avec le temps ont généralement été observés sur le site riche. L'érable à sucre a immobilisé plus rapidement le Ca de 1978 à 1997 que les autres espèces à ce site. Dans le cas du Ca pour le frêne et du Ca et Mg pour le chêne rouge, des concentrations basses dans le bois et une croissance rapide étaient associées avec une immobilisation lente. Les taux d'immobilisation pour le bois et l'écorce ont également été déterminés pour la durée totale de vie des arbres. Ces résultats suggèrent que le tilleul et le chêne rouge immobilisent des quantités significatives de Mg et Ca dans leur écorce, respectivement.

Dans une deuxième étude, les concentrations de K, Ca et Mg le long de la section radiale de la tige (bois de coeur, zone de transition, aubier et écorce) ont été déterminées. Dans la majorité des cas, l'écorce avait les concentrations les plus élevées alors que pour le bois, le bois de coeur était généralement le plus élevé.

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GENERAL INTRODUCTION

It has long been established that any site which serves as the medium of growth for a tree will be indefinitely altered as a consequence of the trees' presence. A trees' influence is most often directly linked to species specific characteristics, which exert a strong effect upon processes of nutrient cycling in the ecosystem. A wealth of scientific research in this area has now focused on establishing clear relationships between tree species characteristics and patterns of nutrient cycling between the tree and the immediate soil environment (Witkamp & van der Drif, 1961; Alban, 1982; Beniamino et al., 1991; Raulund-Rasmussen & Vejre, 1995).

The influence of a tree in altering a forest site has predominantly been examined with respect to selected processes of nutrient cycling. Changes in the chemical and to a lesser extent the physical environment in the immediate vicinity of the tree are commonly linked to processes of decomposition, mineralization, and crown leaching (Attiwill, 1967; Gosz et al., 1973; Aber et al., 1990; Côté & Fyles, 1994b, Côté & Ouimet, 1996; Crockford et al., 1996). It must however be kept in mind that, in the complex cycling of nutrients in a typical forest stand, these processes do not exclusively contribute to observed soil characteristics on site. In order to begin to fully understand the influence a tree has on its immediate environment, research with respect to nutrient cycling must be expanded.

As nutrients are cycled from the tree to the soil, consideration of the processes by which nutrients are stored within the tree and not immediately returned to the soil have not been a focus of attention. The accumulation or immobilization of elements within the wood and bark tissues of a tree is a process which must, however, be taken into account when evaluating the influence of a particular species upon observed properties and characteristics of the site. Despite a lack of research in this area, preliminary results have suggested that interspecific differences with respect to base cation immobilization do exist, and may be said to directly influence soil nutrient availability and fertility (Rennie, 1955; Miller, 1963; Johnson et al., 1982; Chatarpaul et al., 1985; Houde, 1995).

The actual mechanism by which nutrients are immobilized within the tissues of a tree has not been investigated in great detail in the literature, but is generally believed to be a complex process. The elements available for immobilization in xylem tissues are primarily derived from the xylem sap (Lepp & Dollard, 1974; Baker, 1983; Reeves, 1993). These nutrients are said to enter the xylem through three main pathways: a) through the root:soil interface, b) through foliage after direct deposition, and c) through the stem following deposition on the bark (primarily occurring through imperfections in the bark) (Burton, 1985; Donnelly et al., 1990). The major pathway for the movement of nutrients into the xylem is however at the root:soil interface (Burton, 1985).

Elements retranslocated within the tree, from regions of source to sink, may additionally serve as a source of nutrients available for immobilization. This retranslocation of nutrients primarily occurs as a result of the event of leaf abscission or heartwood formation, wherein nutrient ions other that those irretrievably bound in structural tissues are liable to be retranslocated back into living tissue (Wardell & Hart, 1973; Bamber & Fukazawa, 1985; Hendrickson, 1987; Bockheim & Leide, 1990; Myre & Camiré, 1994; Marschner, 1995). As a result of this process and depending upon the element and the stem component, various reserves of nutrients may be identified within the tree. For a majority of hardwood species, a high concentration of mobile elements (N, P, K) are found in the external part of the xylem or sapwood, while concentrations of immobile or intermediately mobile elements (Mg, Ca) are found to be highest in the internal xylem or heartwood (Bamber & Fukazawa, 1985; Myre & Camiré, 1994; Rochon et al., 1998). Scientific evidence in support of these claims is however weak as only a limited number of studies have sought to investigate different distribution zones of nutrients in the stem.

In overview of the body of literature which has investigated this process, it is clear that research in this area has only been narrowly focused. One area of research where investigation of trends of cation accumulation in trees has been ongoing is with respect to the practice of intensive harvesting. The outcome of such research typically documents elemental concentrations for different component parts of selected tree species, most notably the stemwood and bark (Rennie, 1955; Comeford & Leaf, 1982; Messina, et al., 1983; Chatarpaul, et al., 1985). Determination of element concentrations is usually based upon various physical measurements of the tree. Data of this sort is highly useful from a harvesting standpoint, in beginning to establish relationships between tree dimensions and nutrient content for various species.

Another area of forestry which focuses on elemental immobilization in the perennial tissues of trees, specifically the annual rings, is dendroecology. Dendroecology, a subfield of dendrochronology, utilizes dated tree rings to study ecological and environmental problems (Reeves, 1993). Dendroecological analysis has been commonly used to construct records of climate, document heavy metal pollution, and study the relation between growth and air pollution (Baes III & McLaughlin, 1984; Innes & Cook, 1989; McClenahen et al., 1989; Cutter & Guyette, 1993; Côté & Camiré, 1995). The interpretation of changes in elemental composition of tree rings has been met with some difficulty however, primarily relating to known translocation and redistribution of elements within the tree (Arp & Manasc, 1988; McClenahen et al., 1989; Cutter & Guyette, 1993; Momoshima et al., 1995).

Despite the work which has been conducted in these two areas with respect to immobilization processes, it may still be concluded that this is a topic which has only been explored in a very limited sense. For the most part, immobilization has only been indirectly investigated from research of such topics relating to intensive harvesting or environmental monitoring. Such existing research has however highlighted the fact that information concerning the actual process of immobilization and the rate at which trees accumulate nutrients is lacking and insufficient. As stated previously, from the limited research conducted thus far, differential rates of immobilization may be said to significantly influence the nutrient status of the site, as well as the future productivity of the stand (Rennie, 1955; Johnson et al., 1982; Chatarpaul et al., 1985; Houde, 1995). With this in mind, the need for additional research in this specific area may be emphasized.

The general objective of this study is twofold: to calculate the rate at which certain essential nutrients (K, Ca, Mg) are immobilized in selected tree species, and to determine the concentration (mg/g) of these base cations in the radial zones of the woody component of the stem, including the bark, for the same species.

Rates of immobilization of these elements for the hardwood species studied, were evaluated using two separate approaches. Firstly, rates of immobilization ($mg/m^2/yr$) were determined for the wood only on a ground area basis over a defined time scale, spanning the period of 1958-1997. In addition, a second equation was employed to determine rates of immobilization ($g/m^2/yr$) for the whole stem of the tree, including both the wood and bark. Cation concentrations (mg/g) across the transverse section of the stem in the heartwood, transitional, and sapwood zones and bark were also determined.

A natural forest stand typical of the hardwood forest of southern Québec was selected in order to meet the preceding objectives. The species studied were chosen from a rich and poor site, and included American basswood (*Tilia americana* L.), sugar maple (*Acer saccharum* Marsh.), white ash (*Fraxinus americana* L.), American beech (*Fagus grandifolia* Ehrh.), red oak (*Quercus rubra* L.), and red maple (*Acer rubrum* L.).

CHAPTER 1

COMPARISON OF RATES OF NUTRIENT IMMOBILIZATION IN THE STEMWOOD AND BARK OF SELECTED HARDWOOD SPECIES

1.1 INTRODUCTION

The potential effects of tree species on the immediate environment is a subject which has been explored extensively in the literature. Findings from such research generally indicates that trees do differ in their effects on selected soil characteristics (Melin, 1930; Samoylova, 1962; Gosz et al., 1973; Melillo et al., 1982; Boerner, 1984; Aber et al., 1990; Côté & Fyles, 1994b). Alban (1982) and Binkley and Valentine (1991) found that many species change soil pH and cation concentrations, especially in the surface horizons. Binkley and Valentine (1991) found more acidic soils under white pine (*Pinus strobus* L.) and Norway spruce [Picea abies (L.) karsten] than under green ash (*Fraxinus pennsylvanica* Marshall var. *pennsylvanica*). Alban (1982) on the other hand, found that the acidifying effect of aspen (*Populus tremuloides* Michaux) was greater than red pine (*Pinus resinosa* Aiton) or jack pine (*Pinus banksiana* Lambert) and about equal to white spruce [*Picea glauca* (Moench)]. These findings are among numerous references in the literature of the effects of different species on soil properties. Overall, it may generally be noted that soil properties such as pH, exchangeable nutrients, and forest floor characteristics are much more likely to be altered by species, within 40 years, than are such properties as particle size distribution, bulk density, and horizon thickness or sequence (Alban, 1982).

The effect of species on soils should be expected due, in part, to differences in observed processes of nutrient cycling. In the transfer of nutrients within the tree and between the tree and soil, the means by which a tree may acquire and accumulate nutrients is representative of one such process. Existing research has established that interspecific differences in rates of nutrient immobilization in the stemwood and bark specifically can influence soil nutrient availability and fertility (Rennie, 1955; Cole et al., 1967; Whittaker et al., 1979; Houde, 1995).

Variability in the rate at which a particular tree accumulates elements is based primarily upon differences with respect to species and site characteristics. Related research on this topic has provided proof that the concentration of nutrients observed in the various components of a tree is dependent upon the soil nutrient status of the site (Ovington, 1959; McClenahen et al., 1989; Momoshima & Bondietti, 1990; Morrison, 1990; Cutter & Guyette, 1993). In the Hubbard Brook Ecosystem Study, the relatively low nutrient concentration of the study trees were thought to reflect the acid and infertile soil of the study site (Whittaker et al., 1979). In connection, Morrison (1990) noted that elements accumulated in the phytomass of a sugar maple (*Acer saccharum* Marsh.) stand were in rough proportion to their abundance in the soil. From such studies, it has been concluded that the chemical make-up of the annual woody increment at least partially reflects the chemistry of the environment in which it was formed (Amoto, 1988). Conflicting evidence in the literature does however exist on this point. Selected studies have documented that the correlation between the nutrient content of the wood and soil is weak, suggesting that trees do in fact maintain some independence from the surrounding environment (Osonoubi et al., 1988; Glavac et al., 1990; Côté & Camiré, 1995).

Site characteristics as influenced by interactions between the tree and soil may have a notable effect upon the availability of nutrients for uptake and immobilization. These interactions are primarily defined with respect to characteristic patterns of litterfall, humus accumulation, and decomposition (Melin, 1930; Samoylova, 1962; Olson, 1963; Gosz et al., 1973; Melillo et al., 1982; Aber et al., 1990; Côté & Fyles, 1994a). Thus, knowing in general how a particular species cycles nutrients as based upon the above processes, inferences concerning immobilization may be made. This reflects the approach adopted in this study when hypothesizing the rate at which a particular species may accumulate base cations.

Species of maple for example, may be assumed to immobilize nutrients at a fast rate, based upon evidence of a high rate of nutrient transfer within the tree and a slow rate of transfer between the tree and soil. An observed high element concentration in the woody tissue

(Chatarpaul et al., 1995; Houde, 1995), and a low soil nutrient content (Kipkech, 1995), for selected elements, may support a hypothesized high rate of accumulation. Kipkech (1995) documented that exchangeable soil K^+ decreased with an increase in proportion of sugar maple. Accompanying species of maple, American basswood (*Tilia americana* L.) and white ash (*Fraxinus americana* L.), may in contrast show different patterns of nutrient cycling and accumulation. Relative to maple and other deciduous broadleaved species, the leaf litters of *Tilia* and *Fraxinus* have been found to decompose most rapidly (Melin, 1930; Chandler, 1941; Samoylova, 1962; Melillo et al., 1982; Côté & Fyles, 1994a). This may undoubtedly play a role in the enrichment of the soil, increasing the availability of nutrients at the level of the forest floor. Such conditions may allow for a rapid rate of nutrient transfer between the tree and soil and a slow rate of transfer within the tree for these species. As a result, it is hypothesized that American basswood and white ash will accumulate nutrients at a low rate within their perennial tissues.

It is also important to acknowledge that processes of nutrient cycling in the forest ecosystem have been drastically altered in recent decades because of changes associated with climate. These changes primarily relate to acid deposition, elevated N-input and increased atmospheric CO_2 concentrations (Miller et al., 1979; Ulrich et al., 1980; Arp & Manasc, 1988; Johnson et al., 1988; McClenahen & Vimmerstedt, 1989; Hüttl & Schaaf, 1995). Acid and elevated N deposition into forest ecosystems can result in a reduction of soil alkalinity that may reduce the supply of nutrients such as Mg^{2+}, Ca^{2+} and K^+ (Huttl & Schaaf, 1995). Zoettl et al., (1989) showed that acid deposition induced nutrient deficiencies in some soils and was thus seen to be a contributing factor to observed forest decline in Europe. Increasing atmospheric concentrations of greenhouse gases, mainly CO_2, may also affect forest nutrient cycling, as a result of changes in the biochemical processes of trees (Sandenburgh et al., 1987). These include changes in the rate of photosynthesis, change in water-use efficiency, and increasing nitrogen fixation (Kramer & Sionit, 1987). Overall, these climatic changes may directly alter trends of elemental cycling, including processes of immobilization.

Patterns of elemental uptake and accumulation in the tree are also strongly dependent upon the age and stage of development of the forest stand (Foster & Morrison, 1976; Arp & Manasc, 1988; Majumdar et al., 1991; Knoepp & Swank, 1994; Colin-Belgrand et al., 1996). In general, it may be said that in early stages of development, rates of growth and uptake are at a maximum (Lutz & Chandler, 1955). A second stage of growth as defined by Attiwill & Leeper (1987) is characterized by the development of heartwood as a support structure for the organs of growth. In subsequent stages, as the forest approaches maturity, the rate of increase in mass of the tree declines and most of the annual net primary production of the tree is shed as litter. At this stage, it may be assumed that growth processes of the forest are maintained by the cycling of nutrients in litterfall (Attiwill & Leeper, 1987).

In accordance with the previously mentioned factors and reflecting the complexity of nutrient cycling in a forest stand, variations in the process by which a tree may accumulate nutrients do exist. Evaluation of these differences on a species basis is essential as elemental immobilization in a tree has been shown to influence levels of available nutrients in the soil, which may in turn impact the future productivity of the site (Rennie, 1955; Johnson & Todd, 1987; Johnson et al., 1988; Frelich et al., 1989; Johnson & Todd, 1990).

The main aim of this study was to evaluate interspecific differences in rates of immobilization in tree stems for selected species typical of the hardwood forest of southern Québec. Rates of immobilization were determined using two different approaches in order to meet specific objectives.

The first approach was devised to evaluate the evolution in time of rates of immobilization over the last 40 years. A second approach was used to determine mean annual rates of immobilization for the entire life of the tree. Based upon information of overall patterns of nutrient cycling for the species examined here, it was hypothesized that American basswood and white ash on the rich site and red oak (*Quercus rubra* L.) on the poor site would immobilize base cations in the stemwood at a slower rate than the maples or American beech (*Fagus grandifolia* Ehrh.).

1.2 MATERIALS AND METHODS

1.2.1 Site description

The study sites are located in the Morgan Arboretum of McGill University on the West Island of Montréal, Québec (45 25'N, 73 57'W; 30 m above sea level). The majority of the Arboretum is composed of natural forest stands that range from pioneer to climax forests typical of the Great Lakes-St. Lawrence forest (Rowe, 1972). Two sites within the Arboretum were selected in order to evaluate differences with respect to tree species. The first site was composed of a mixed stand of American basswood, sugar maple, and white ash. The soils of this site have properties of a loamy till and are classified as Sombric Brunisol of the Saint-Bernard series (Lajoie & Stobbe, 1951). The second site was composed of a mixed stand of red maple (*Acer rubrum* L.), American beech, and red oak. The soils on this site have developed on a fluvial sand deposit and are classified as Ferro-Humic Podzols (Millette, 1948). These sampling sites have been generally categorized as rich and poor respectively, based primarily upon soil type, site index, and leaf nutrient concentration (Table 1.1).

1.2.2 Sampling and increment cores

Tree selection was based upon a number of criteria including size, crown class, stem form, and live crown ratio (percentage of the length of the stem with live branches) (Kozlowski et al., 1991). Tree size was measured in terms of stem diameter, at 1.3 m aboveground (DBH). Trees chosen for sampling were between 20-40 cm in DBH, of the dominant or co-dominant class, had a single, relatively straight stem and a live crown ratio greater than 30%. Approximately 25 trees per species were sampled.

As part of sampling procedures, one core sample was extracted from each of the selected trees using an increment borer at DBH. To minimize surface contamination, the increment borer was rinsed with methyl alcohol in between sampling of the different tree species. In the field, each of the cores was placed in a plastic straw and was later frozen in the laboratory until further analysis could be carried out.

In order to facilitate analysis, the increment cores were mounted and a very small slice of wood (approximately 1/3 of the diameter of the core) was removed with a Teflon-coated

Table 1.1. Species, number of trees sampled, soil type, site index, and leaf nutrient concentration for the rich and poor sites.

Site	Species	Nb. of Trees Sampled	Soil Type	Site Index	Leaf Nutrient Concentration (mg/g)[1]				
					N	P	K	Ca	Mg
rich	white ash	25	Sombric Brunisol	28	8.6 ± 0.7	1.6 ± 0.2	9.6 ± 0.1	22.5 ± 1.1	3.3 ± 0.2
	sugar maple	25			6.6 ± 0.3	1.1 ± 0.1	3.8 ± 0.3	18.5 ± 0.4	2.7 ± 0.07
	A. basswood	25			11.2 ± 0.4	1.3 ± 0.08	7.7 ± 0.8	33.8 ± 0.9	4.8 ± 0.09
poor	A.beech	25	Ferro-Humic Podzols	21	7.2 ± 0.2	0.43 ± 0.08	1.4 ± 0.2	9.6 ± 0.3	2.4 ± 0.1
	red oak	25			7.2 ± 0.2	0.78 ± 0.02	2.4 ± 0.1	11.6 ± 0.4	2.4 ± 0.03
	red maple	25			6.5 ± 0.5	0.60 ± 0.1	2.4 ± 0.5	9.8 ± 0.4	2.1 ± 0.04

[1] Data from Côté & Fyles (1994b).

razor blade. A scanned image of each of the cores was then obtained using the Win/Mac DENDRO™ software program for Apple Macintosh Computer (Regent Instrument Inc., 1993). Using this software, the width and the total number of tree rings were recorded for each increment core.

1.2.3 Immobilization rates

1.2.3.1 *Wood only*

Immobilization rates on a ground area basis, were determined for the wood only for four observed decades of growth spanning the period from 1958-1997. As an exception, only the most recent two decades could be observed for white ash because it was found to exist as a younger species in the stand. It is important to note that these values represent the trees' rate of immobilization of base cations at a single point in the stem (DBH) from which the sample was taken. The rates calculated may similarly apply to subsequent heights along the stem however, as results from a preliminary study on the effect of height on nutrient concentration did not show any significant trends. The equation used to determine these rates of immobilization ($mg/m^2/yr$) is as follows:

$$NC * D * BA * T * CA^{-1} * P^{-1}$$

where NC is nutrient concentration for the period (mg/g), D is wood density (g/cm^3), BA is basal area growth for the period (cm^2), T is a constant representing the thickness of the core (assumed to be 1 cm), CA is crown area (m^2), and P is also a constant representing period (10 years).

In order to determine the concentration (mg/g) of K, Ca, and Mg for the specific periods, the increment cores were cut into 10 year segments prior to chemical analysis. Each of the wood segments was cut into smaller pieces using a pair of hand clippers; the clippers of which were cleaned with distilled water in between samples to prevent cross contamination. The samples were then digested according to the procedure of Thomas et al. (1967), and the digests were analyzed for K, Ca, and Mg by atomic absorption spectrometry.

In calculating the wood density of the cores, measurements of the length, radius and mass of the cores, without the bark were recorded. The total volume of wood (cm^3) was then determined using the following formula:

$$\pi R^2 * L$$

where R is the radius and L is the length measured for each of the cores. The density of the wood (g/cm^3) was then calculated by dividing the weight of the sample (g) by its total volume (cm^3). Using this technique, the density of the wood was assumed to be uniform along the entire length of the core.

The basal area determined for each of the different time periods was calculated on an area basis from the cross section of the stem. The area of each of the individual annual rings was first calculated as a series of concentric circles. From summation of these individual areas on a decade basis, a basal area value could be given for the observed time periods.

Rates of immobilization for the wood only were determined on a ground area basis (m^2) for each tree. Ground area simply defines the physical space which the tree is estimated to occupy in the stand. In this study, the areal extent of the tree crowns was used as a measure of ground area. Crown area was determined in the field by measuring the ground distance between three or four points, corresponding to the extent of the main branches of the tree. For certain trees, crown area could not be measured in the field because in the time period after initial sampling, the tree stems had broken or split. In such cases, an area measurement was determined through regression analysis. Linear regressions between tree age and crown area were determined on an individual species basis. A majority of the trees damaged, for which an area measurement was determined through regression analysis, were species of white ash. The coefficient of determination (R^2) value computed from the regression for this species was 0.2294. Initial crown area measurements from the field (or from regression analysis) were also adjusted for each of the observed decades. The diameter of the tree at breast height (DBH) was calculated for the periods ending, from which a measurement of crown area could be derived, using again, linear regression.

1.2.3.2 *Wood and bark*

Immobilization rates were calculated for the same trees that were used in the previous approach. The values obtained for these rates of immobilization ($g/m^2/yr$) were determined using the following equation:

$$NCt * CA^{-1} * A^{-1}$$

where NCt is tree cation content (g), CA is crown area (m^2), and A is the age of the tree (yr).

In this study, three trees for each of the species, with the exception of four trees for American basswood, were felled. The selected trees were cut at the base and a cross sectional disc or "cookie" was cut at the base and subsequent three metre intervals along the entire length of the stem. The height of the tree thus determines the number of discs obtained for each tree (Figure 1.1).

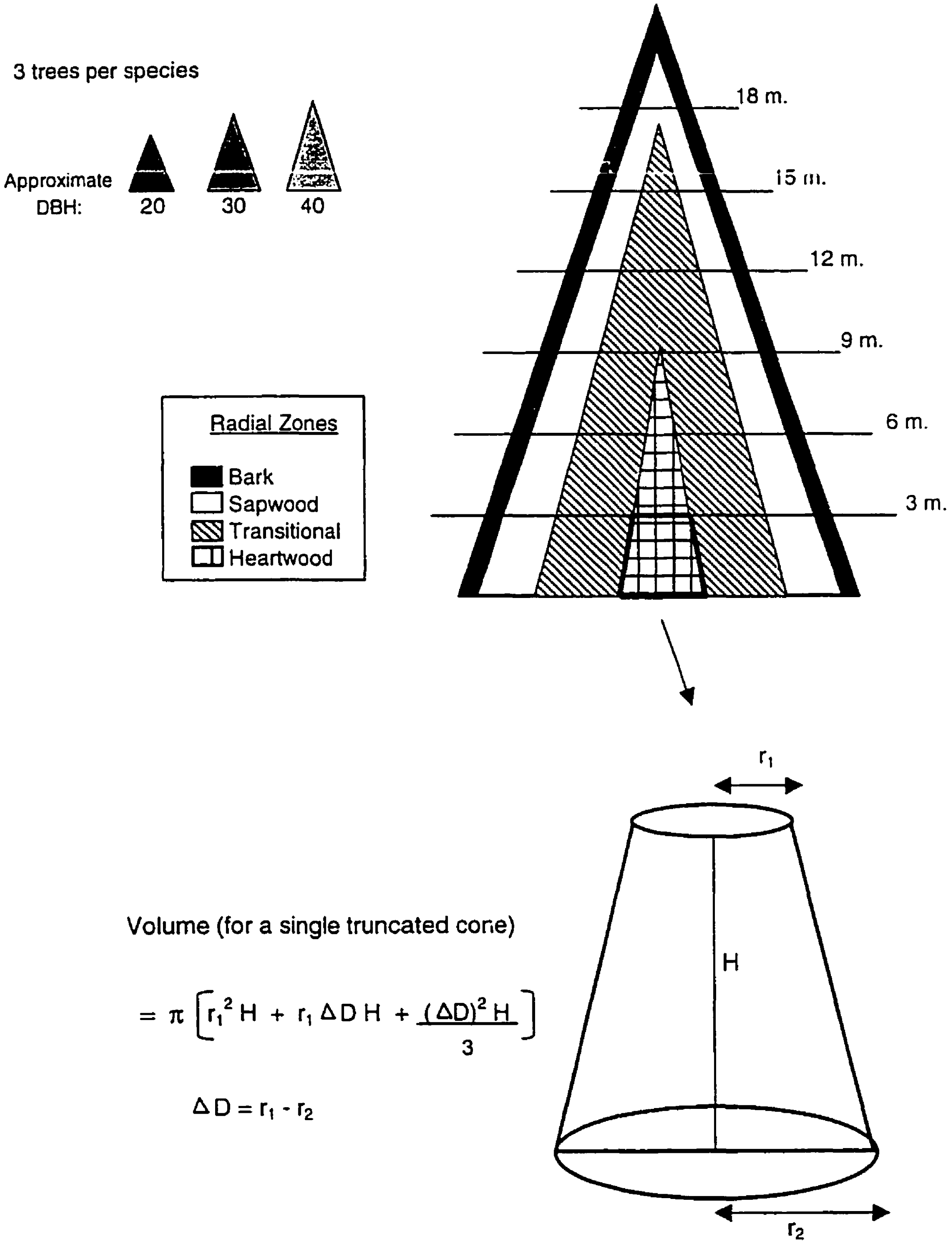
The cation content (mg) of each of the discs was calculated using the following formula:

$$D * NC * V$$

where D is wood density (g/cm^3), NC is nutrient concentration (mg/g), and V is volume (cm^3).

Using a sample taken from each of the discs at the specified heights, the volume (cm^3) of the piece was determined by water displacement. The density (g/cm^3) was then calculated by dividing the dry weight of the sample (g) by its total volume (cm^3). The density of the wood was assumed to be uniform across the radial section of the stem. In order to calculate the density of the bark, the physical dimensions of a cubical sample were recorded. (No

Fig. 1.1. Sampling procedures for determination of tree volume



$$= \pi \left[r_1^2 H + r_1 \Delta D H + \frac{(\Delta D)^2 H}{3} \right]$$

$$\Delta D = r_1 - r_2$$

differentiation was made between dead bark (cork) and living bark (phloem and cambium)). The density of the bark was then determined for each tree, however an average value for each species was used to calculate the total cation content of the sample trees.

The concentration of base cations (K, Ca, Mg) was determined separately for each of the different radial sections of the tree. The total volume of the heartwood, transitional and sapwood zones and bark for the stem of each of the trees was also determined. The summation of the total cation concentration (g) by volume for each of these sections may then provide a measure of the total nutrient content of the tree.

Before calculating the total volume of these radial zones, their precise location in the annual rings of the cross section of the stem was determined. Identification of the heartwood and bark is relatively simple but becomes difficult in the case of the transitional and sapwood zones. For the purposes of this study, the sapwood was defined to be comprised of the first five annual rings, while the transitional zone was located in the section of the stem from the sixth ring until the start of the heartwood. The delineation of the transitional and sapwood zones in this manner was based upon the results of a study wherein distributional zones of nutrients for European larch (*Larix decidua* (Mill.)) and tamarack (*Larix laricina* [K. Koch (Du Roi)] were determined (Myre & Camiré, 1994).

Measurement of the width or diameter of the heartwood, transitional and sapwood zones, as well as the bark for each of the discs, was a starting point in determining their total volume in the tree. By means of extrapolation from these measurements at the different heights at which the discs were cut, the total volume of these areas on a stem basis was estimated. The premise by which this extrapolation was performed can be said to be based upon several assumptions. It was first assumed that the volume of the tree stem was comprised of a series of vertically stacked truncated cones. Within each cone, the volume of the heartwood, transitional and sapwood zones, and bark was thought to be represented by a series of superimposed truncated cones (Figure 1.1).

It may be further assumed that each disc cut at a point along the stem is representative of a certain area of the tree. Thus, with measurements of the diameter of the heartwood, transitional and sapwood zones and bark at each of the cookies, and the distance between which each disc was cut, the total volume of each of the zones for each vertically stacked cone was determined using the formula given in Figure 1.1. Knowing these volumes, the total cation content of the 19 sample trees could then be calculated.

Using this data and the applications of regression analysis, the total cation content of the trees which were cored may be determined. Regressions between DBH and total nutrient content for each of the elements on a species basis were determined. Depending upon the particular species and element, one of a linear, polynomial, or exponential equation was used to estimate the total cation content of the stem, including both the wood and bark.

1.2.4 Statistical analyses

The experimental design used for analysis of the immobilization rates in wood only across the four observed decades of growth is as follows. For each element, a repeated measures analysis of variance was performed on the four observed decades (two decades in some cases) for the species on site, to assess (1) the main effects of species (SPECIES), averaged over the decades (between-subject effects), (2) the main effects of the individual sample trees nested within the species (TREE (SPECIES)), averaged over the decades (between-subject effects), and (3) the main effects of time (TIME) and its interaction with species (TIME*SPECIES), and tree within the species (TIME*TREE (SPECIES)) (within-subject effects). Mean rates of immobilization for each of the species for the different time periods was also determined for comparison purposes, using the Student-Newman-Keuls (SNK) multiple range test.

For the data in which rates of immobilization were determined for the wood and bark of the stem, the experimental design adopted was a complete randomized design, wherein the treatments were the different tree species on their respective sites. The main effects of the different species were tested for on an element basis for the rich and poor sites. The SNK test was again employed in order to compare mean rates of immobilization of K, Ca, and Mg for each of the species. Statistics were performed using the Statistical Analysis System (SAS Institute Inc., 1987) at a probability level of 5%.

The homogeneity of the treatment variances was tested using Bartlett's test in Statistix (Analytical Software, 1996). In a majority of cases, the variances were significantly different at the 0.05 probability level and thus could not be considered homogeneous. In these cases, a log transformation was used. The data is presented in retransformed form.

1.3 RESULTS

1.3.1 Immobilization by decade - *Wood only*

1.3.1.1 Rich site

In a majority of cases, the main effect of species, tree (species), time and the interaction between time and species and tree (species) were found to be highly significant when sugar maple and American basswood were analyzed together (Table 1.2). Two exceptions were however noted. With analysis of the between-subject effects, the main effect of species for K and Mg was not found to be significant. Wood only immobilization rates of K, Ca, and Mg for the period of 1958-1997 for sugar maple and American basswood are presented in Figure 1.2. When analyzing trends of immobilization over time for sugar maple and American basswood, rates of immobilization of K, Ca, and Mg were observed to be increasing with time. For K, mean rates of immobilization of sugar maple and American basswood were only found to differ significantly in the period of 1978-1987, and were thus observed to be statistically similar at the other time periods. For Ca, mean rates of immobilization for these two species were found to differ significantly at all but the 1968-1977 time period. For this element, in the most recent two decades, sugar maple was found to have a statistically higher rate of immobilization in comparison to American basswood, but the opposite trend was noted for the earliest decade. For Mg, in the first and last observed time periods, mean rates for sugar maple and American basswood were not found to be statistically different. However, for the period of 1968-1987, sugar maple was found to have a higher rate of immobilization.

Rates of accumulation for all three species on the rich site, including white ash, sugar maple, and American basswood were analyzed for the two most recent decades. The main

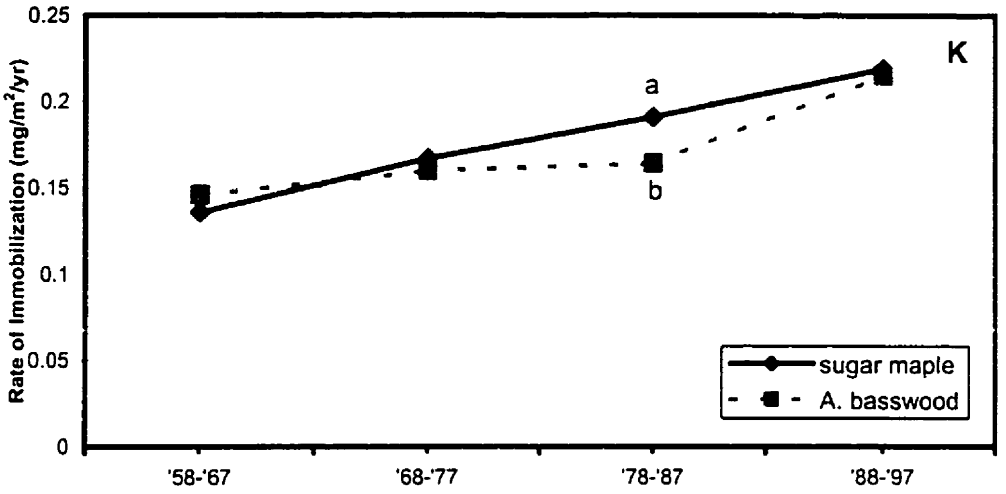
Table 1.2. Repeated measures analysis of variance for the period of 1958-1997 for sugar maple and American basswood: Results in terms of significance probabilities P > F.

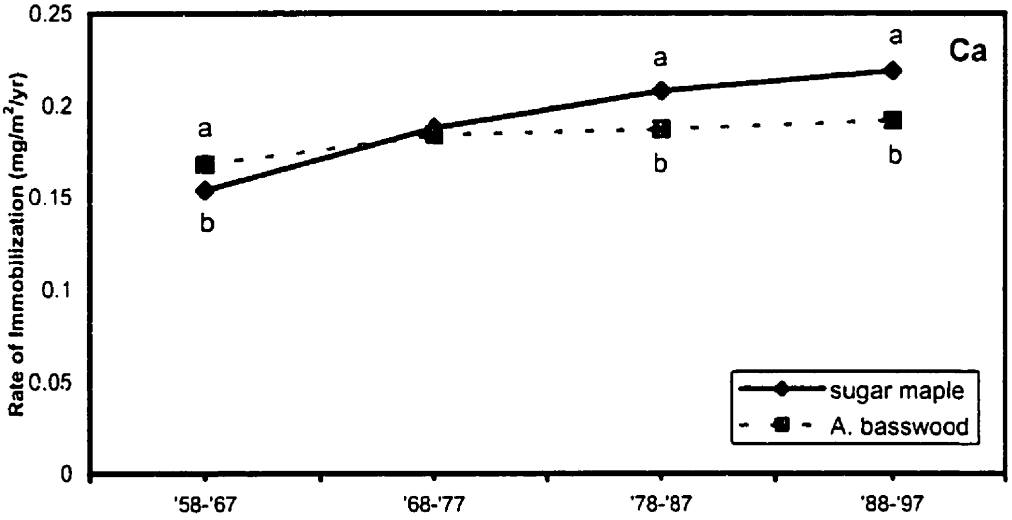
	ANOVA[1]	Modified ANOVA[2]	
		G-G	H-F
K			
SPECIES	0.8599		
TREE (SPECIES)	0.0001		
TIME		0.0001	0.0001
TIME*SPECIES		0.0001	0.0001
TIME*TREE (SPECIES)		0.0001	0.0001
Ca			
SPECIES	0.0001		
TREE (SPECIES)	0.0001		
TIME		0.0001	0.0001
TIME*SPECIES		0.0001	0.0001
TIME*TREE (SPECIES)		0.0001	0.0001
Mg			
SPECIES	0.4279		
TREE (SPECIES)	0.0001		
TIME		0.0001	0.0001
TIME*SPECIES		0.0001	0.0001
TIME*TREE (SPECIES)		0.0001	0.0001

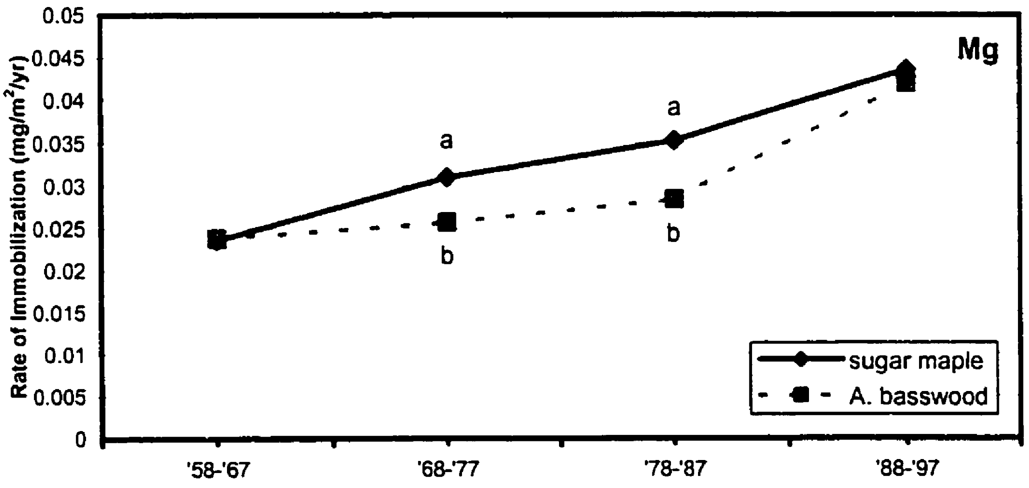
[1] The between-subject effects (i.e.: species and tree (species) main effects) are tested in the univariate ANOVA.

[2] The within-subject effects (i.e.: time main effects, time-by-species interaction, and time-by-tree (species) interaction) are tested in the modified ANOVA. In this modified testing procedure, the probabilities of significance P > F are adjusted by using Greenhouse and Geisser's (1959) and Huynh and Feldt's (1976) estimates of Box's (1954a,b) epsilon correction factor. The corresponding adjusted probabilities are denoted G-G and H-F respectively.

Fig. 1.2. Wood only immobilization rates of K, Ca, and Mg for the period of 1958-1997 for sugar maple and American basswood on the rich site. Means for each element and time period having different letters are significantly different using SNK and p =0.05.


K
Rate of Immobilization (mg/m²/yr)
0.25
0.2
0.15
0.1
0.05
0
'58-'67
'68-'77
'78-'87
'88-'97
a
b
sugar maple
A. basswood


Ca
Rate of Immobilization (mg/m²/yr)
0.25
0.2
0.15
0.1
0.05
0
'58-'67
'68-'77
'78-'87
'88-'97
a
b
a
b
a
b
sugar maple
A. basswood


Mg
Rate of Immobilization (mg/m²/yr)
0.05
0.045
0.04
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
'58-'67
'68-'77
'78-'87
'88-'97
a
b
a
b
sugar maple
A. basswood

effect of species, tree (species), time and the interaction between time and species and tree (species) were found to be either significant or highly significant (Table 1.3). Immobilization rates of K, Ca, and Mg for the period of 1978-1997 for white ash, sugar maple, and American basswood are presented in Figure 1.3. For K and Mg, white ash consistently recorded immobilization rates which were significantly high in comparison to the other species on site. Sugar maple however immobilized Ca at a rate which was statistically higher than that recorded for white ash and American basswood. Again, with the exception of K for white ash, elevated rates of immobilization were documented with time.

Additional data for wood density, wood nutrient concentration and basal area growth for the species on the rich site are presented in Table 1.4. For the period of 1958-1997, American basswood in comparison to sugar maple had a lower wood density, a generally higher element concentration in the woody tissue and a lower rate of growth for the period. When comparing all three species for the period of 1978-1997, American basswood again had the lowest wood density. The concentration of K in the wood was highest for white ash, followed by American basswood and sugar maple. Wood concentrations of Ca and Mg were highest for American basswood, lower for sugar maple and lowest for white ash. The concentration of Mg in the wood of sugar maple was however only slightly higher than that of white ash. Basal area growth was similarly high for both white ash and sugar maple, in comparison to lower values for American basswood.

1.3.1.2 Poor site

In most instances, the main effects of species, tree (species), time and the interaction between time and species and tree (species) were found to be highly significant (Table 1.5). As an exception, the within-subject effects of time for K and Ca were not found to be significant.

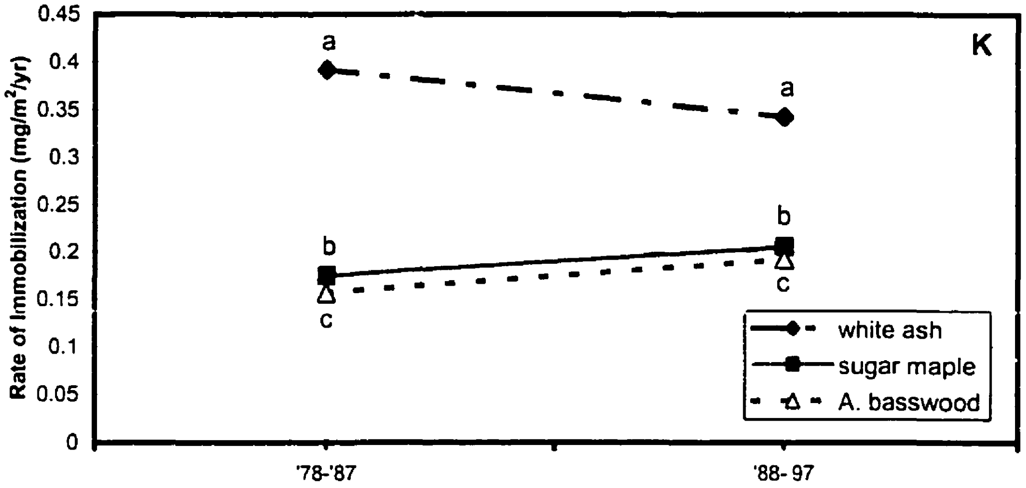
When comparing the species on site, red maple was found to have the lowest rate of K immobilization (Figure 1.4). Mean rates of immobilization of K in the most recent two decades were highest for red oak. In the two earlier decades however, the mean rates computed for American beech and red oak did not differ significantly. For Ca and Mg, with the exception of the most recent decade (1988-1997), red oak had the lowest rate of immobilization in

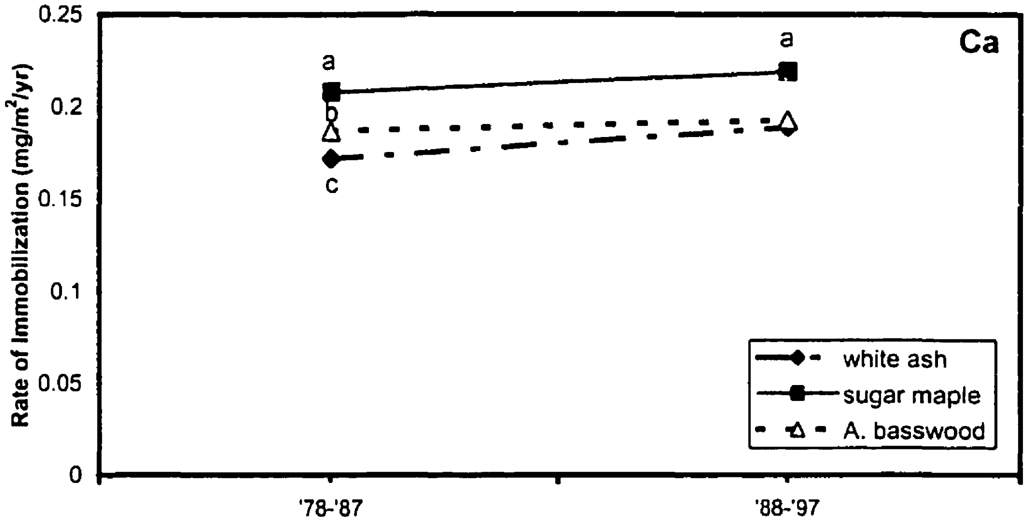
Table 1.3. Repeated measures analysis of variance for the period of 1978-1997 for white ash, sugar maple, and American basswood: Results in terms of significance probabilities P > F.

	ANOVA[1]
K	
SPECIES	0.0001
TREE (SPECIES)	0.0001
TIME	0.0211
TIME*SPECIES	0.0002
TIME*TREE (SPECIES)	0.0001
Ca	
SPECIES	0.0001
TREE (SPECIES)	0.0001
TIME	0.0441
TIME*SPECIES	0.0001
TIME*TREE (SPECIES)	0.0001
Mg	
SPECIES	0.0001
TREE (SPECIES)	0.0001
TIME	0.0001
TIME*SPECIES	0.0001
TIME*TREE (SPECIES)	0.0001

[1] The between-subject effects (i.e.: species and tree (species) main effects) effects) and within-subject effects (i.e.: time main effects, time-by-species interaction, and time-by-tree (species) interaction) are tested in the univariate ANOVA.

Fig. 1.3. Wood only immobilization rates of K, Ca, and Mg for the period of 1978-1997 for white ash, sugar maple, and American basswood on the rich site. Means for each element and time period having different letters are significantly different using SNK and p=0.05.


K
Rate of Immobilization (mg/m²/yr)
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
a
a
b
b
c
c
'78-'87
'88- 97
white ash
sugar maple
A. basswood


Ca
Rate of Immobilization (mg/m²/yr)
0.25
0.2
0.15
0.1
0.05
0
a
a
b
c
'78-'87
'88-'97
white ash
sugar maple
A. basswood

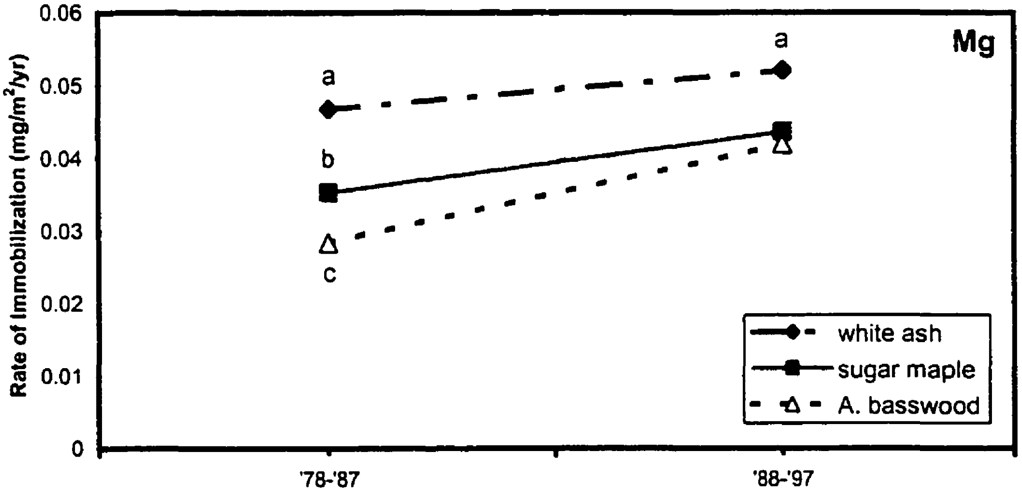

Mg
Rate of Immobilization (mg/m²/yr)
0.06
0.05
0.04
0.03
0.02
0.01
0
a
a
b
c
'78-'87
'88-'97
white ash
sugar maple
A. basswood

Table 1.4. Mean wood density, wood nutrient concentration, and basal area growth by period for the species on the rich and poor sites.

Site	Species	Period	Wood Density	K	Ca	Mg	Basal Area
			(g/cm^3)		(mg/g)		(cm^2/10 yr. period)
rich	sugar maple	1958-1997	0.841	0.542	0.636	0.119	166.355
	A. basswood		0.558	0.721	0.844	0.140	121.286
	white ash	1978-1997	0.746	0.911	0.428	0.123	216.216
	sugar maple		0.840	0.555	0.620	0.129	196.082
	A. basswood		0.556	0.768	0.827	0.154	131.762
poor	A. beech	1958-1997	0.831	0.599	0.592	0.144	77.109
	red maple		0.708	0.512	0.479	0.109	62.400
	red oak		0.941	0.511	0.248	0.030	146.712

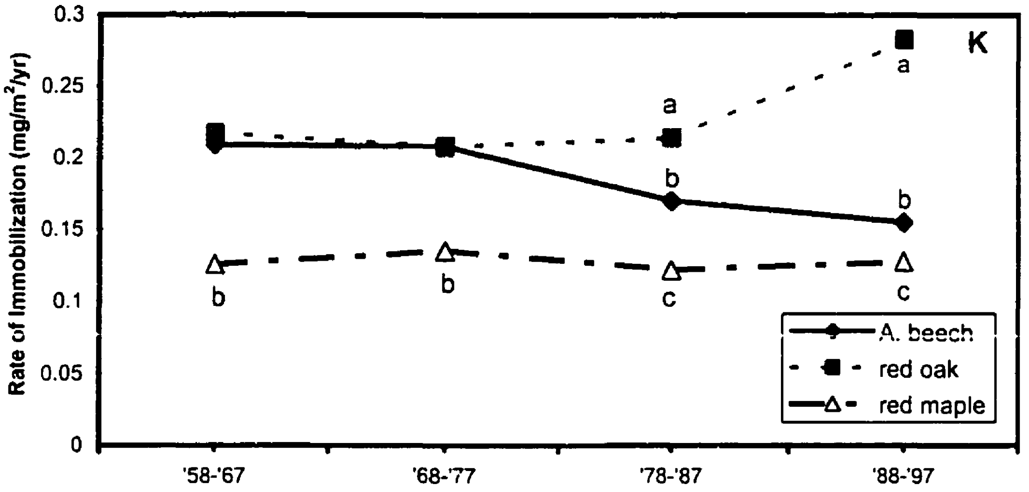
Table 1.5. Repeated measures analysis of variance for the period of 1958-1997 for American beech, red maple, and red oak: Results in terms of significance probabilities P > F.

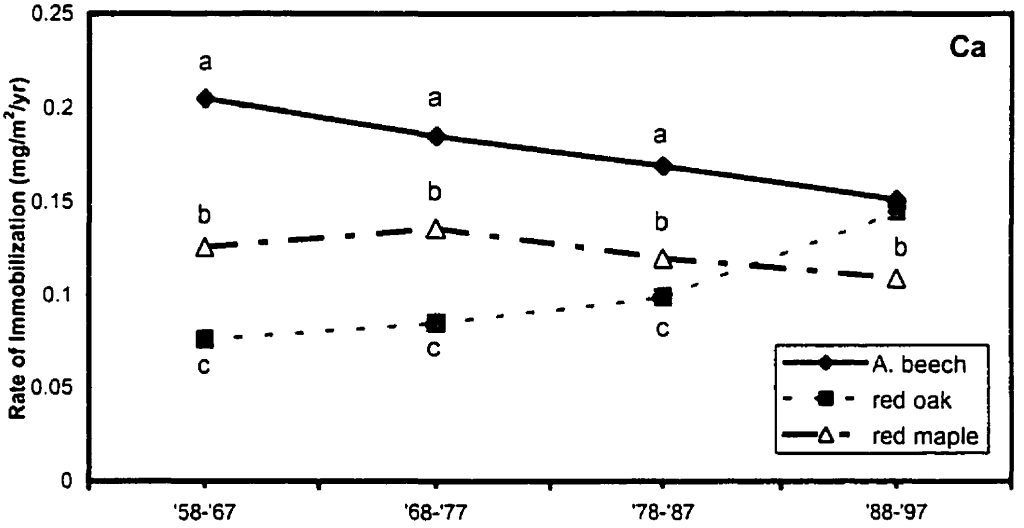
	ANOVA[1]	Modified ANOVA[2]	
		G-G	H-F
K			
SPECIES	0.0001		
TREE (SPECIES)	0.0001		
TIME		0.0582	0.0502
TIME*SPECIES		0.0001	0.0001
TIME*TREE (SPECIES)		0.0001	0.0001
Ca			
SPECIES	0.0001		
TREE (SPECIES)	0.0001		
TIME		0.6296	0.6460
TIME*SPECIES		0.0001	0.0001
TIME*TREE (SPECIES)		0.0001	0.0001
Mg			
SPECIES	0.0001		
TREE (SPECIES)	0.0001		
TIME		0.0001	0.0001
TIME*SPECIES		0.0001	0.0001
TIME*TREE (SPECIES)		0.0001	0.0001

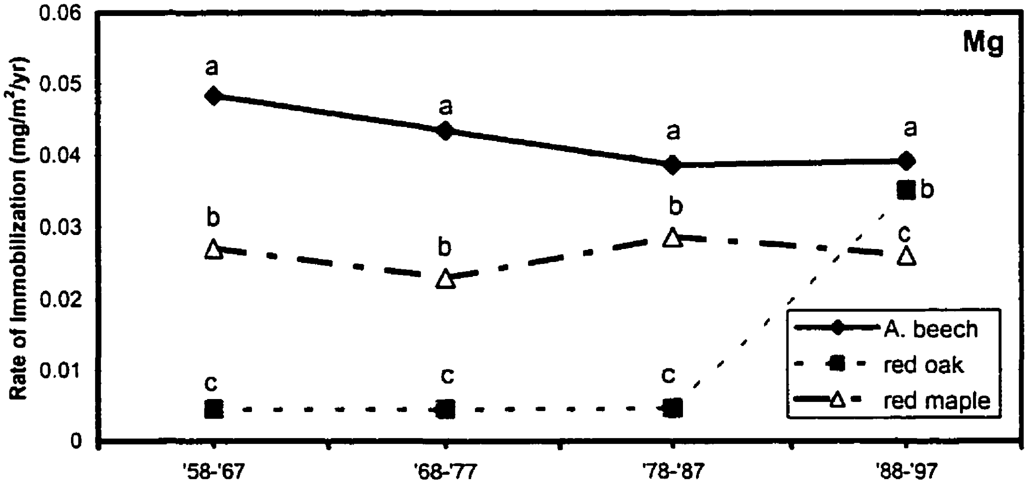
[1] The between-subject effects (i.e.: species and tree (species) main effects) are tested in the univariate ANOVA.

[2] The within-subject effects (i.e.: time main effects, time-by-species interaction, and time-by-tree (species) interaction) are tested in the modified ANOVA. In this modified testing procedure, the probabilities of significance P > F are adjusted by using Greenhouse and Geisser's (1959) and Huynh and Feldt's (1976) estimates of Box's (1954a,b) epsilon correction factor. The corresponding adjusted probabilities are denoted G-G and H-F respectively.

Fig. 1.4. Wood only immobilization rates of K, Ca, and Mg for the period of 1958-1997 for American beech, red oak, and red maple on the poor site. Means for each element and time period having different letters are significantly different using SNK and $p = 0.05$.


K
Rate of Immobilization (mg/m²/yr)
0.3
0.25
0.2
0.15
0.1
0.05
0
'58-'67
'68-'77
'78-'87
'88-'97
a
a
b
b
b
b
c
c
A. beech
red oak
red maple


Ca
Rate of Immobilization (mg/m²/yr)
0.25
0.2
0.15
0.1
0.05
0
'58-'67
'68-'77
'78-'87
'88-'97
a
a
a
b
b
b
b
c
c
c
A. beech
red oak
red maple


Mg
Rate of Immobilization (mg/m²/yr)
0.06
0.05
0.04
0.03
0.02
0.01
0
'58-'67
'68-'77
'78-'87
'88-'97
a
a
a
a
b
b
b
b
c
c
c
c
A. beech
red oak
red maple

comparison to red maple and American beech. It is also significant to note that for these two elements, American beech consistently had a significantly higher mean rate of immobilization across the four observed decades; only in the case of Ca for the period of 1988-1997 was this rate comparable to that of red oak. In contrast to the rich site, patterns of immobilization over time for these species did not show any consistent trends.

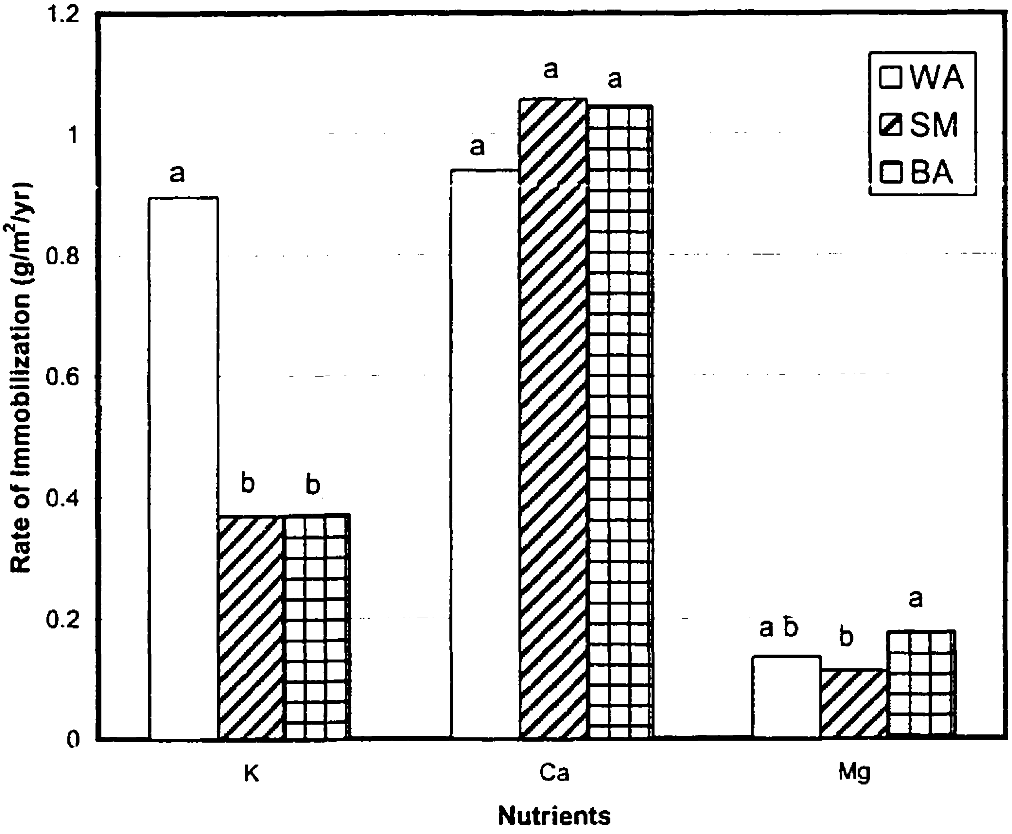
Data with regards to wood density, wood nutrient concentration and basal area growth for the species on the poor site are also given in Table 1.4. Wood density was highest for red maple followed by American beech and red oak. The concentration of K in the woody tissue was found to be within a similar range for all species on site. Wood concentration of Ca and Mg was highest for American beech, followed by red maple and red oak. Basal area growth was noticeably higher for red oak in comparison to similar but lower values for American beech and red maple.

1.3.2 Mean annual rate of immobilization - *Wood and bark*

On the rich site, the main effect of species was found to be highly significant for K and Mg, but not significant for Ca. For K, mean rates of immobilization for white ash were significantly higher than sugar maple and American basswood (Figure 1.5). For Ca, mean rates of immobilization did not reveal any significant differences for the three species. In the case of Mg, the mean values calculated for white ash and American basswood were statistically similar; the rate determined for sugar maple was significantly lower in comparison to American basswood but was ranked similarly to that of white ash.

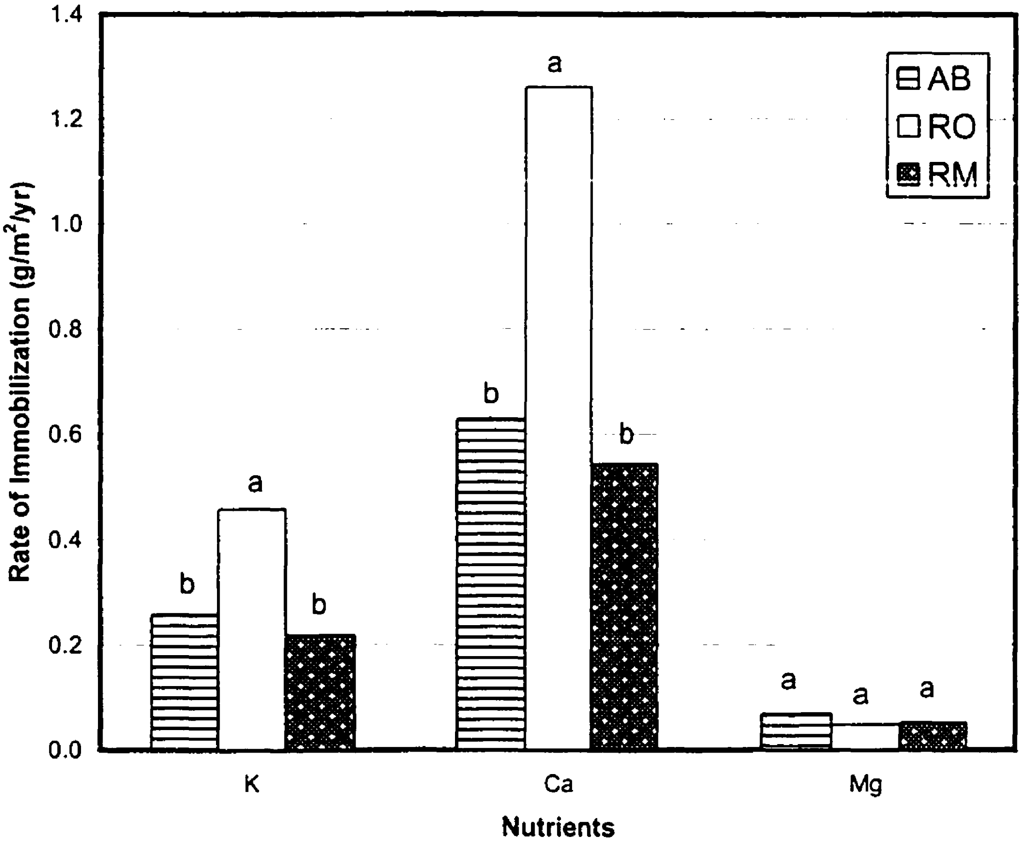
For the poor site, species was found to be highly significant for K and Ca, but not significant for Mg. Mean rates of immobilization of K and Ca were significantly high for red oak, while American beech and red maple had similarly lower rates of immobilization for these elements (Figure 1.6).

Figure 1.5. Wood and bark immobilization rates for white ash (WA), sugar maple (SM), and American basswood (BA) on the rich site.



Note: Means for each element having different letters are significantly different using SNK and p =0.05.

Figure 1.6. Wood and bark immobilization rates for American beech (AB), red oak (RO), and red maple (RM) on the poor site.



Note: Means for each element having different letters are significantly different using SNK and $p = 0.05$.

1.4 DISCUSSION

1.4.1 Rates of immobilization - *Wood only*

On the rich site, rates of immobilization observed for sugar maple and American basswood in the period of 1958-1997 were generally variable. Sugar maple was however noted to be immobilizing Ca at an elevated rate in the last two decades, from 1978-1997. This is in agreement to an earlier hypothesis, which suggested that sugar maple would immobilize base cations at a higher rate in comparison to the other species on the site. This hypothesis was based upon information suggesting that there is a higher rate of nutrient transfer within the tree and a slower rate between the tree and soil for this species. Evidence of a high element concentration in the woody tissue (Chatarpaul et al., 1995; Houde, 1995) and a low soil nutrient content (Kipkech, 1995), for selected elements, may support this hypothesized high rate of accumulation of nutrients in the stem of sugar maple. Trends of immobilization documented for sugar maple for Ca may be used to lend support to an initial hypothesis of this study.

In analysis of these research findings, it may be of some significance to note the connection between observed rates of accumulation and wood density data, cation concentrations in the wood, and the rate of growth for the species. When comparing rates of immobilization for all three species on the rich site, white ash is noted to be immobilizing Ca at a lower rate in comparison to sugar maple and American basswood. Reasons to begin to account for this lower rate of accumulation may relate to an observed low concentration of Ca in the stemwood that compensates for a high rate of growth for this species, as evident from the high basal area values. For white ash, it may thus be assumed that a low element concentration and a high rate of growth are reflective of a low rate of immobilization.

In further explanation of this low rate of accumulation of Ca, it must be kept in mind that white ash has generally been found to exist as a younger species in the stand. Calcium, a relatively immobile element, tends to accumulate in the older organs of tree stems, namely the heartwood (Wright & Will, 1958; Wardell & Hart, 1973; Myre & Camiré, 1994). The younger white ash species may be assumed to contain a proportionally smaller amount of heartwood in the bole, in comparison to the other species on site. The lack or immature formation of a heartwood in the stem of this species may account for the low rate of accumulation of Ca (Turner & Lambert, 1983).

Similarly, red oak on the poor site immobilized Ca and Mg at a low rate in accordance with a low concentration of these elements in the woody tissue and an observed high rate of growth. The low rate of accumulation of Ca and Mg in the woody tissue is in agreement to an earlier hypothesis, which stated that red oak would immobilize base cations at a slower rate than red maple or American beech. Overall, differences in rates of immobilization on a species basis may provide evidence to suggest that such species differ in their processes of nutrient cycling.

1.4.2 Rates of immobilization with time

An increased rate of immobilization of base cations with time was generally observed for the species on the rich site. This specifically relates to trends of immobilization documented for American basswood and sugar maple for the period of 1958-1997. In contrast, for American beech and red maple on the poor site, no consistent trends of an increasing or decreasing rate of immobilization over time was evident. These findings may indicate that the nutrient supply at the rich site is increasing, relative to that of the poor site. Previous research has documented that an increased availability of nutrients at the level of the forest floor may in turn allow for elevated rates of uptake by the species on site (Pritchett, 1979; Bowen & Nambiar, 1984; Morrison, 1990). The nutrients taken up may be utilized for growth processes, allowing for continued biomass expansion, or they may be stored within the tissues of the tree for use in periods of inadequate nutrient supply (Myre & Camiré, 1994).

An increased nutrient supply at the rich site may reflect changing levels of nutrients in the soil, as influenced by the impacts of air pollution, particularly acid deposition or "acid rain". Though there is still much uncertainty regarding the effects of acid deposition on forest ecosystems, it has been suggested that there may actually be a beneficial effect during the early stages of deposition (Wood & Bormann, 1977; Bondietti et al., 1990; Momoshima & Bondietti, 1990; Momoshima et al., 1995). Acid deposition may be seen to initially benefit forests, through some fertilizing effect associated with its nitrate (NO_3^-) or even sulphate

(SO_4^{2-}) content (Tamm, 1976; Wood & Bormann, 1977; Morrison, 1984; Backiel & Hunt, 1986). In a study by Wood and Bormann (1977), using stimulated acid rain, a slight positive effect on tree seedlings was noted. Foliar nitrogen concentrations indicated that fertilization with NO_3^{-1}, added to the rain as HNO_3, might have caused the growth increase (Wood & Bormann, 1977). Bondietti et al., (1990) reported that an increase in divalent cations present in the wood of red spruce (*Picea rubens* Sarg.), was linked to both rapid increases in SO_x and NO_x deposition and increases in radial growth increment. Over the long term, it is strongly believed that acid deposition will adversely affect forest ecosystems through extensive leaching of nutrients from the soil, or by increasing the concentration in solution and on exchangeable complex of aluminum (Smith, 1991). As soil acidity rises, aluminum increases to toxic levels and can displace beneficial nutrients, inhibit their uptake and damage fine root hairs, leading to nutrient and moisture stress (Backiel & Hunt, 1986).

Another factor to be taken into account when evaluating patterns of accumulation over time is the stage of development of the stand. Distinct patterns of nutrient accumulation over time for the species on the sample sites could indicate that these stands are in fact at different phases of development. Elevated rates of immobilization over time on the rich site may suggest continued growth and biomass expansion of the species on site. In general, it may be said that average rates of nutrient accumulation in biomass are greatest in the early stages of stand development and less marked as stands age (Foster & Morrison, 1976; Attiwill & Leeper, 1987; Wang et al., 1996). For the species on the rich site however, rates of cation accumulation are steadily increasing over time with age. These findings are in agreement with that reported in a study by Morrison (1990), wherein it was concluded that processes associated with growth, particularly element uptake, may still be substantial despite the advanced age of the stand.

1.4.3 Rates of immobilization - *Wood and bark*

Similarities in the species ranking for the rates of immobilization computed for the wood at DBH and for the wood and bark of the whole stem may be noted. In both cases, rates of immobilization of K for white ash were significantly higher in comparison to sugar maple and American basswood on the rich site. These findings are likely due to the fact that there is a proportionally greater mass of wood in the stem of a tree in comparison to the bark. In the Hubbard Brook Ecosystem Study, it was found that despite the higher nutrient concentrations in the bark than in the wood, uptake into stemwood exceeded that into the bark by 1.4 to 4 x for most elements (Whittaker et al., 1979). Thus, in the case of K for white ash, it may be assumed that patterns of immobilization in the woody tissue component of the stem will parallel those observed for the whole stem, including both the wood and bark. White ash was also found to be immobilizing Ca at a lower rate in both the woody tissue at DBH and on a whole stem basis. In the latter approach however, differences in rates of immobilization among the species were not statistically significant. In this particular case, element concentrations in the bark can be seen to compensate for the differences among species with respect to the wood only rates of immobilization.

Specific findings from the study may however be used to support a claim that nutrients accumulated in the bark can significantly contribute to overall patterns of elemental immobilization for the wood and bark component of the stem. On the rich site, elevated rates of immobilization of Mg for American basswood for the wood and bark component of the stem may be analyzed in contrast to the low accumulation rates observed in only the woody portion of the stem at DBH. This trend of a high accumulation rate of an element on a stem basis in comparison to low rates in the woody tissue was also evident for red oak on the poor site, in the case of Ca. These findings indicate that the bark of American basswood and red oak contains a high content of Mg and Ca respectively (Appendix 1). A high content of one or several elements within the tree may be related to the process by which a species may selectively absorb and accumulate mineral elements, as related to their nutritional needs (Gerloff et al., 1966; Beadle & White, 1968; Clarke, 1983; Chapin III, 1988; Johnson et al., 1988). In addition, it may also be of some importance to note that the bark of American basswood and red oak is proportionally thicker on a stem basis in comparison with the other species on site (Elias, 1980), which may further account for the elevated cation content observed.

Immediate implications of differential rates of nutrient immobilization in the stemwood and bark relate to the availability of soil nutrients for cycling in the forest stand. From a management perspective, it is significant to recognize that selected soil properties can be changed through the floristic composition of the forest stand (Rennie, 1955). Alban (1982), for example, provides convincing evidence that species differences in Ca accumulation in both live and dead wood have caused changes in the forest floor and soil Ca^{2+}. These results are in agreement with those of Johnson et al., (1982), Johnson & Todd (1987) and Gessel et al., (1990). Information of rates of uptake and accumulation on a species basis may have obvious applications when evaluating the impacts of various harvesting systems.

Results from this study show that sugar maple on the rich site immobilized Ca at an elevated rate in the most recent two decades. On the poor site, American beech in a majority of cases immobilized Ca and Mg at a significantly high rate in comparison to the other species on site. Furthermore, it was found that red oak and American basswood immobilized significant amounts of Mg and Ca in their bark, respectively. These species may be seen to play an important role in sequestering nutrients within the perennial tissues of their wood and bark. Identification of such species with a tendency towards increased immobilization may be significant when assessing the impacts of intensive harvesting practices. A vital issue in this regards centres upon whether or not the soil processes the ability to replenish the nutrients being removed via the stem. Upon nutrient rich soils, nutrient removal via the stem may be of little significance, but upon many nutrient poor soils, this may be an important factor leading to soil degradation and declining fertility (Rennie, 1955). Interpretation of the impact of harvesting on the overall productivity of the site is however difficult, related to the variability in nutrient cycling and accumulation known to exist on a stand basis (Chatarpaul et al., 1985).

1.5 CONCLUSION

Over time, progressively higher rates of immobilization in the woody tissue were observed in a majority of cases for the species on the rich site. Sugar maple was documented to be accumulating Ca at an elevated rate in the most recent two decades, in comparison to the other species on the site. Certain parallels with respect to selected species characteristics and observed rates of immobilization may be identified. In the case of Ca for white ash, and Ca and Mg for red oak, a low wood element concentration and a high rate of growth was assumed to reflect a low rate of immobilization.

When comparing the two approaches used in estimation of immobilization rates for the sampled trees, in some instances it was found that rates of immobilization observed at DBH (wood only) were similar to the rates observed for the entire bole, including the bark. In the cases in which these accumulation rates were not comparable, the bark of these species was found to contain elevated amounts of selected base cations. This was observed in the case of American basswood and red oak for Mg and Ca, respectively.

CHAPTER 2

DISTRIBUTION OF NUTRIENTS IN TRANSVERSE SECTIONS OF STEMS OF SELECTED HARDWOOD SPECIES

2.1 INTRODUCTION

It is well known that the different components of a tree, the leaves, stem, bark and branches can accumulate and store nutrients. In specifically investigating the element content of these components in connection with forest nutrient cycling, it is clear that much of the research conducted has been only narrowly focused. A wealth of research has centred on evaluating the nutrient content in the foliage and leaf litter of selected hardwood species (Chandler, 1941; Samoylova, 1962; Melillo et al., 1982; Howard & Howard, 1990; Côté & Fyles, 1994a), while the nutrient composition of their wood and bark has received only limited attention (Rennie, 1955; Morrison, 1990; Houde, 1995). From the research conducted thus far, the distribution of nutrients in the wood and bark component of the stem may be said to vary primarily according to the element, species and site (Hillis, 1987). Despite the influence of these factors in contributing to differential patterns of immobilization in the bole, some general trends may be noted. The following section will serve to briefly discuss typical patterns of elemental concentrations in the defined radial sections of a stem, the sapwood, transitional zone, heartwood and bark.

The physiological importance of the sapwood in the overall nutrition of the tree cannot be underestimated, as this section of the stem is believed to contain a significant proportion of the trees' nutrient reserve. From previous research, it may generally be said that the concentration of mobile nutrients (N, P, K) is highest in the sapwood relative to the other woody sections of the stem (Wardell & Hart, 1973; Attiwill, 1980; De Visser, 1992; Myre & Camiré, 1994; Colin-Belgrand et al., 1996). Reasons to begin to account for these high concentrations relate to the fact that "this zone is most susceptible to store nutrient reserves from retranslocation (during foliar senescence or formation of heartwood), or through uptake during the growing season" (Myre & Camiré, 1994). In a study conducted by Myre & Camiré (1994), wherein *Larix decidua* (Mill.) (European larch) and *Larix laricina* [K. Koch (Du Roi)] (tamarack) were examined, the external zone of the xylem was characterized by high concentrations of P and K. These results were in agreement to findings of similar studies which reported high nutrient concentrations in the sapwood for different tree species (Hampp & Höll, 1974: Tout et al., 1977: Arp & Manasc. 1988).

The presence of a distinct transition or intermediate zone between the sapwood and heartwood has been identified in the cross section of many trees (Kramer & Kozlowski, 1979). The delineation of this transitional zone is however difficult due to the subjective nature of the limits of each radial zone. Nevertheless, an increase or reduction in element concentrations in this area are often noted with relatively constant levels observed in both the sapwood and heartwood zones (Wardell & Hart, 1973; Tout et al., 1977; McClenahen et al., 1989; Myre & Camiré, 1994). A change in concentration is thought to be the result of the transportation of elements within the tree, across a horizontal plane. Studies have found that movement of nutrients not only occurs out of the sapwood and into the heartwood as suggested by the mechanism of disposal of waste substances, but also out of the heartwood and into the sapwood, as selected nutrients are retranslocated to more active tissues within the tree (Tout et al., 1977).

In terms of nutrient content, the heartwood itself has been characterized by a group of immobile or elements of intermediate mobility (Ca, Mn, Mg, Zn) (Attiwill & Leeper, 1987; Momoshima & Bondietti, 1990; Myre & Camiré, 1994). The presence of such elements in this zone may be directly related to the process by which sapwood is converted to heartwood. As part of this transition, elements such as those mentioned above are retained in the heartwood as immobile elements, while mobile nutrients, such as P and K are exported to the sapwood (Likens & Bormann 1970; Wardell & Hart, 1973; Frelich et al., 1989). An observed low concentration of mobile elements in the heartwood supports this theory of retranslocation during heartwood formation (Bowen 1984; van den Driessche 1984; Lims & Cousens 1986; Helmisaari & Siltala 1989).

Lastly, for a majority of hardwood species, the bark is seen as an important site for the storage of many essential nutrients, most notably calcium (Rennie, 1955; van den Driessche, 1984; Chatarpaul et al., 1985). This generalization is well supported by studies wherein element concentrations in the bark of selected species have been determined. It is significant to note that this research has predominantly focused on the implications of various harvesting practices in relation to base cation exports (Johnson et al., 1982; Chatarpaul et al., 1985; Johnson & Todd, 1987; Johnson et al., 1988; Federer et al., 1989). With this narrow focus, it is difficult to account for high element concentrations in the bark. Continued research in the area of forest nutrient cycling, has however begun to note the importance of nutrients stored in the inner bark, as these may be utilized for growth processes, primarily during spring flush (Siminovitch & Chater, 1958; van den Driessche, 1984; Hendrickson, 1987; Wetzel et al., 1989).

As mentioned previously, the distribution of nutrients observed across the transverse section of a stem for a particular species may vary according to the element, species and site (Hillis, 1987). The literary findings presented here only represent a generalized outline of typical patterns of elemental concentrations in the radial section of a stem. Whether or not these specific patterns can be considered valid, despite differences of species and site characteristics is dependent upon continued research.

The objective of this study was to determine the concentration (mg/g) of selected base cations across the radial section of the stem in the sapwood, transitional zone, heartwood (if present in the bole sample), and bark. The concentration of K, Ca, and Mg in these defined zones was compared for each of the hardwood species investigated in this study. It was hypothesized that cation concentrations would be highest in the bark. For the woody component, concentrations of mobile nutrients are thought to be highest in the sapwood, while concentrations of immobile or intermediately mobile elements are assumed to be highest in the heartwood. The transitional zone was thought to be characterized by a noticeable change in element concentration in comparison to the sapwood and heartwood.

2.2 MATERIALS AND METHODS

2.2.1 Site description

The study sites are located in the Morgan Arboretum of McGill University on the West Island of Montréal, Québec (45 25'N, 73 57'W; 30 m above sea level). The majority of the Arboretum is composed of natural forest stands that range from pioneer to climax forests typical of the Great Lakes-St. Lawrence forest (Rowe, 1972). Two sites within the Arboretum were selected in order to evaluate differences with respect to tree species. The first site was composed of a mixed stand of American basswood (*Tilia americana* L.), sugar maple (*Acer saccharum* Marsh.), and white ash (*Fraxinus americana* L.). The soils of this site have properties of a loamy till and are classified as Sombric Brunisol of the Saint-Bernard series (Lajoie & Stobbe, 1951). The second site was composed of a mixed stand of red maple (*Acer rubrum* L.), American beech (*Fagus grandifolia* Ehrh.), and red oak (*Quercus rubra* L.). The soils on site have developed on a fluvial sand deposit and are classified as Ferro-Humic Podzols (Millette, 1948). These sampling sites have been generally categorized as rich and poor respectively, based primarily upon soil type, site index and leaf nutrient concentration (Table 2.1.).

2.2.2 Field sampling and stem discs

The concentration of nutrients in the stem of the designated species, was investigated from observation of selected trees chosen from each of the sample sites. A total of 19 trees, representing three trees for each of the six identified species, with the exception of four trees for basswood, were cut between November and December 1997.

Tree selection was based upon a number of criteria including size, crown class, stem form, and live crown ratio (percentage of the length of the stem with live branches) (Kozlowski et al., 1991). Tree size was measured in terms of stem diameter at 1.3 m aboveground (DBH). Trees chosen for sampling were between 20-40 cm in DBH, were of the dominant or co-dominant class, had a single, relatively straight stem and a live crown ratio greater than 30%.

As part of sampling procedures, the selected trees were cut at the base and a cross sectional disc or "cookie" was cut at the base and subsequent three metre intervals along the

Table 2.1. Species, number of trees sampled, soil type, site index, and leaf nutrient concentration for the rich and poor sites.

Site	Species	Nb. of Trees Sampled	Soil Type	Site Index	Leaf Nutrient Concentration (mg/g)[1]				
					N	P	K	Ca	Mg
rich	white ash	3	Sombric Brunisol	28	8.6 ± 0.7	1.6 ± 0.2	9.6 ± 0.1	22.5 ± 1.1	3.3 ± 0.2
	sugar maple	3			6.6 ± 0.3	1.1 ± 0.1	3.8 ± 0.3	18.5 ± 0.4	2.7 ± 0.07
	A. basswood	4			11.2 ± 0.4	1.3 ± 0.08	7.7 ± 0.8	33.8 ± 0.9	4.8 ± 0.09
poor	A.beech	3	Ferro-Humic Podzols	21	7.2 ± 0.2	0.43 ± 0.08	1.4 ± 0.2	9.6 ± 0.3	2.4 ± 0.1
	red oak	3			7.2 ± 0.2	0.78 ± 0.02	2.4 ± 0.1	11.6 ± 0.4	2.4 ± 0.03
	red maple	3			6.5 ± 0.5	0.60 ± 0.1	2.4 ± 0.5	9.8 ± 0.4	2.1 ± 0.04

[1] Data from Côté & Fyles (1994b).

entire length of the stem. The height of the tree thus determines the number of discs obtained for each tree. From the discs cut, the precise location of the radial zones in the annual rings of the cross section of the stem was then determined.

One of the most readably distinguishable characteristics of heartwood is its darker colour (due to the presence of extractives) (Carrodus, 1971). Caution must however be used when identifying heartwood in the stem on the basis of colour alone. For selected species, such as maple, there is only a very gradual colour change making it difficult to distinguish heartwood from sapwood, or indeed to know whether such trees have true heartwood (Good et al., 1955). A central core of discolouration in the stem may also be the result of processes associated with injury (Shigo & Hillis, 1973). Despite the similarity in colour, there appears to be some important differences between normal heartwood, formed from internal stimuli associated with aging, and the discolouration of sapwood brought on by injury (Kramer & Kozlowski, 1979). In this study, no attempt was made to distinguish between these two types of tissues; the term heartwood has been generally used in this paper to describe this discoloured core.

For the purposes of this study, the sapwood was defined as the first five annual rings, while the transitional zone was located in the section of the stem from the sixth ring until the start of the heartwood. The delineation of the transitional and sapwood zones in this manner was based upon the results of a study wherein distributional zones of nutrients for European larch and tamarack were determined (Myre & Camiré 1994). No differentiation was made between the outer bark (cork) and the inner bark (phloem and cambium).

2.2.3 Sampling and chemical analysis

After the discs had been cut in the field, they were then labelled accordingly before being put in a cold storage in order to reduce moisture lost. From each of the discs, a longitudinal section (approximately three inches wide) encompassing the pith of the tree was cut; samples were then taken from the remaining pieces of the disc for determination of wood nutrient concentrations. Wood tissue samples for the heartwood, transitional and sapwood zones, and bark, were obtained by randomly drilling approximately 10-15 holes in each of the different zones. For each tree cut, samples were taken from two or three discs (randomly selected) and pooled for analysis. This sampling procedure may be justified as results from a preliminary study on the effect of height on nutrient concentration did not show any significant trends. The material produced by drilling was then carefully collected and stored until chemical analysis could begin. In between sampling, the drill bit was cleaned with distilled water to prevent cross contamination among samples. The material produced by drilling was digested according to the procedure of Thomas et al. (1967), and the digests were analyzed for K, Ca, and Mg by atomic absorption spectrometry.

2.2.4 Statistical analyses

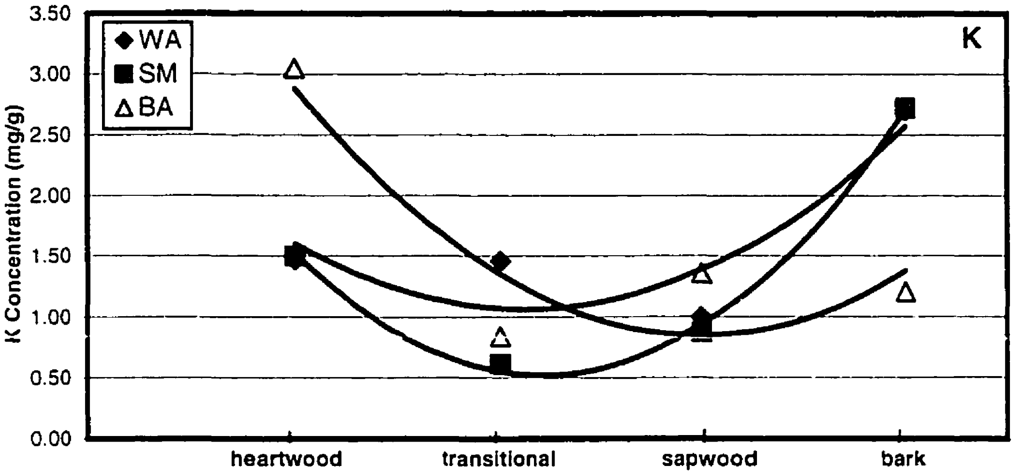
The experimental design used for analysis was a randomized complete block design, wherein the blocks and treatments included the different tree species and radial zones respectively. The main effects of the defined zones were tested for on an individual species and element basis. The TUKEY option was employed in order to compare mean concentrations of K, Ca, and Mg in the different zones for each of the six hardwood species. This option specifically allows for comparison of all main effect means for a data set where there are unequal cell sizes. Statistics were performed using the Statistical Analysis System (SAS Institute Inc., 1987) at a probability level of 5%.

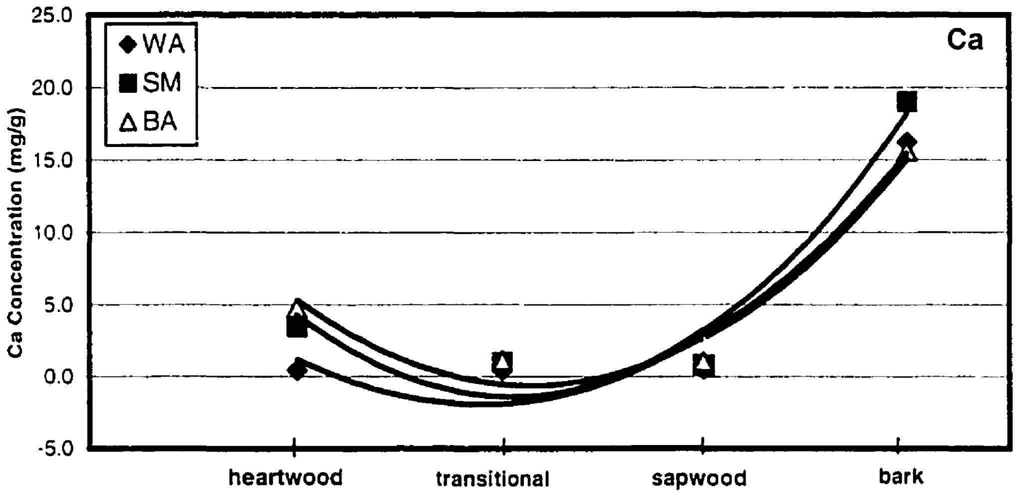
The homogeneity of the treatment variances was tested using Bartlett's test in Statistix (Analytical Software, 1996). In a majority of cases, the treatment variances were significantly different at the 0.05 probability level and thus could not be considered homogeneous. Subsequently, on an individual case basis, various log transformations were used. For a particular element and species, either a log, log+1, log(log+1), or log(log(log+1)+1) transformation was applied. The data is presented in retransformed form.

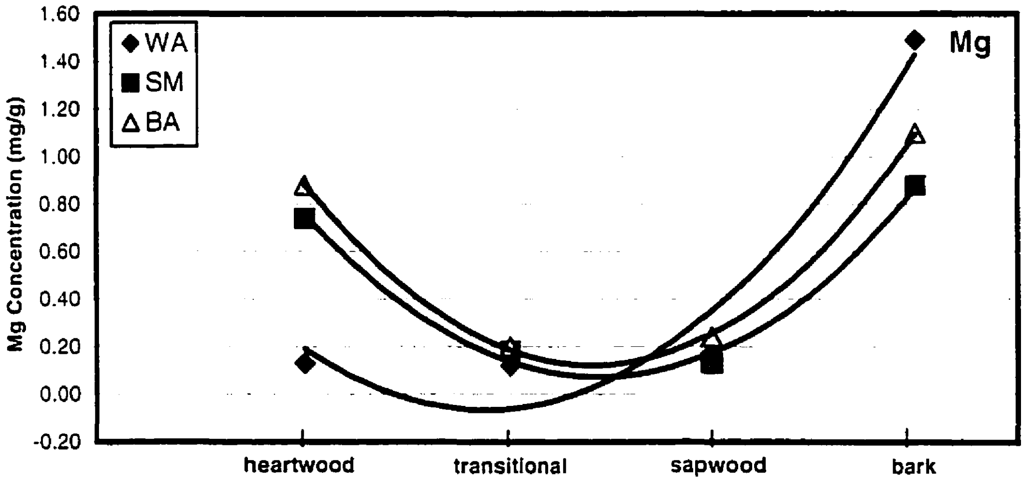
2.3 RESULTS

For each element and hardwood species studied, the main effect of zone on cation concentrations (mg/g) was found to be highly significant. The concentration of K, Ca, and Mg in the defined radial zones for the species on the rich and poor site are presented in Figures 2.1

Fig. 2.1. Radial concentration of K, Ca, and Mg by zone for white ash (WA), sugar maple (SM), and American basswood (BA) on the rich site.


K
◆ WA
■ SM
△ BA
K Concentration (mg/g)
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
heartwood
transitional
sapwood
bark


Ca
◆ WA
■ SM
△ BA
Ca Concentration (mg/g)
25.0
20.0
15.0
10.0
5.0
0.0
-5.0
heartwood
transitional
sapwood
bark


Mg
◆ WA
■ SM
△ BA
Mg Concentration (mg/g)
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
-0.20
heartwood
transitional
sapwood
bark

and 2.2 respectively. In all cases, a second order polynomial trendline was fit in order to visualise distributional patterns of element concentration across the radial section of the stem.

2.3.1 Rich site

In most instances, mean cation concentrations were significantly higher in the bark. Exceptions were for K and Mg in American basswood and Mg in sugar maple. For the zones comprising the woody portion of the stem, a generalized pattern of distribution may be observed for all species on site. Next to observed high cation concentrations in the bark, concentrations in the heartwood were elevated, while comparably lower concentrations in the transitional and sapwood zones were documented. Levels of K observed for American basswood across this section seemed to deviate from this trend. For this species, concentrations of K were highest in the heartwood, with intermediate levels in the sapwood and bark and low element concentrations in the transitional zone. For white ash, which was found to exist as a younger species on the site, generally lower element concentrations of Ca and Mg in the woody tissue (especially the heartwood) were observed in comparison to the other species.

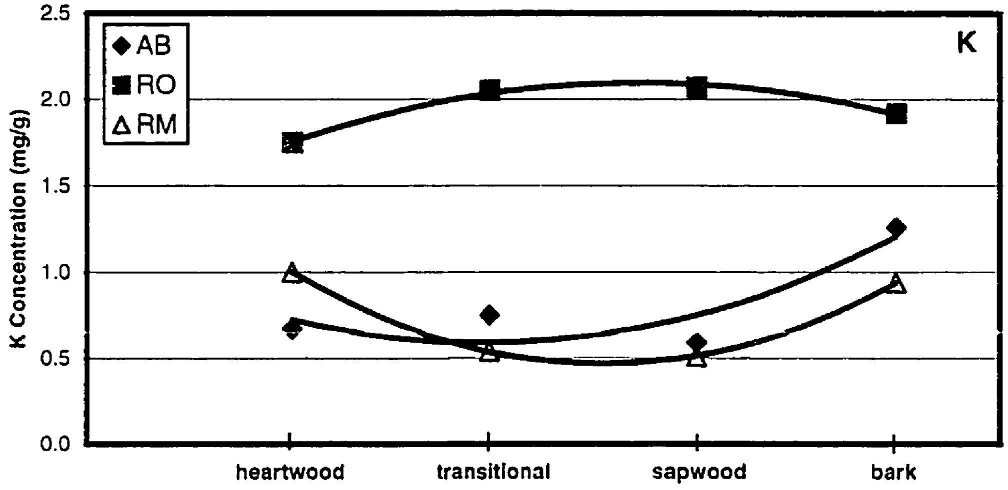
2.3.2 Poor site

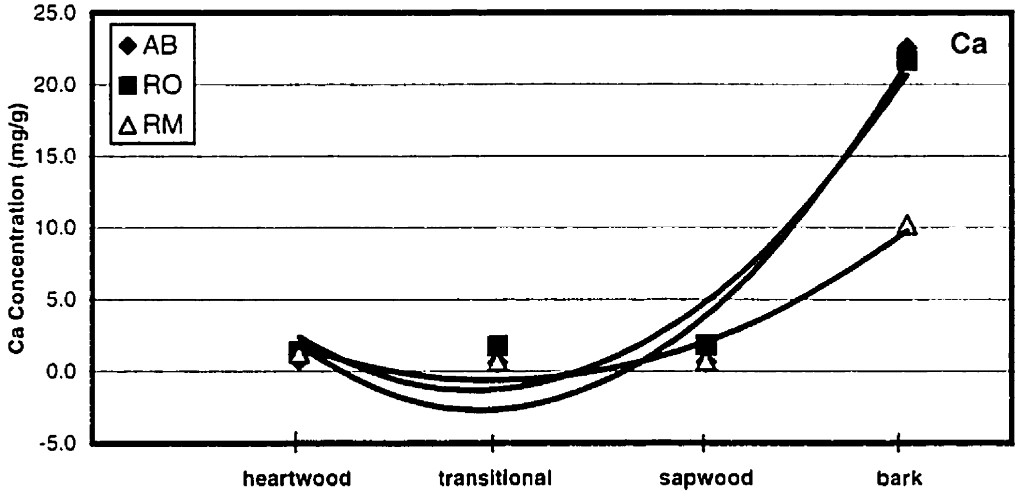
For the species on the poor site, with the exception of K for red oak and red maple, mean concentrations of K, Ca, and Mg were significantly higher in the bark. The general trend noted above for the species on the rich site, with respect to distributional patterns of base cations in the woody tissue was similarly observed for these species. An opposite trend was however noted for red oak for K as elevated concentrations were documented in the sapwood and transitional zones. The distribution of Mg observed for red oak also deviated from this trend, as low element concentrations were evident in the heartwood.

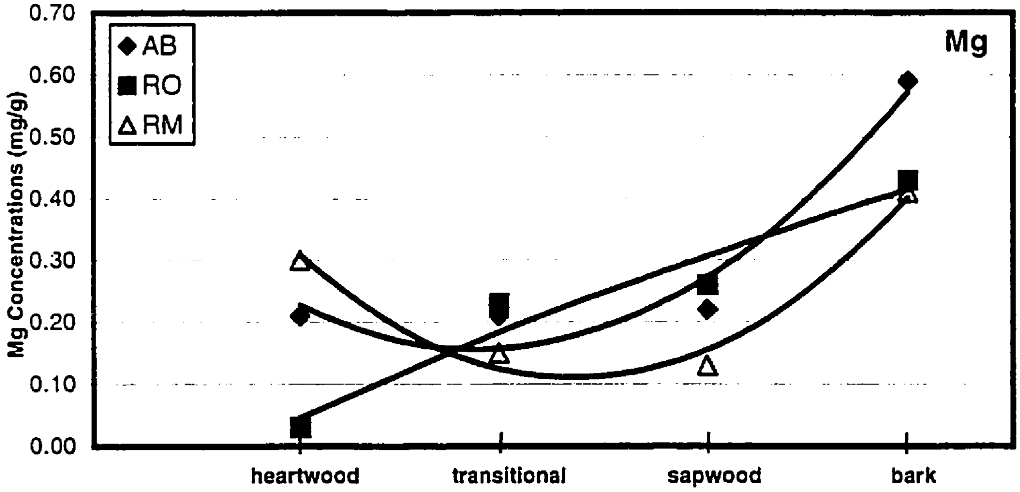
2.4 DISCUSSION

The distribution of base cations across the radial section of the stem for the six species examined here seemed to show a single, generalized pattern. Elevated concentrations of K, Ca, and Mg were observed in the heartwood, compared to a decline in concentration in the

Fig. 2.2. Radial concentration of K, Ca, and Mg by zone for American beech (AB), red oak (RO), and red maple (RM) on the poor site.


K
◆ AB
■ RO
Δ RM
K Concentration (mg/g)
2.5
2.0
1.5
1.0
0.5
0.0
heartwood
transitional
sapwood
bark


Ca
◆ AB
■ RO
Δ RM
Ca Concentration (mg/g)
25.0
20.0
15.0
10.0
5.0
0.0
-5.0
heartwood
transitional
sapwood
bark


Mg
◆ AB
■ RO
Δ RM
Mg Concentrations (mg/g)
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
heartwood
transitional
sapwood
bark

transitional and sapwood zones, while highest concentrations were present in the bark. Reasons to account for this observed pattern may be discussed in connection with trends documented in the literature.

Despite limited published work in this area, research findings support a general claim that the radial distribution of nutrients in the bole does not follow a linear pattern. Rather, evidence of nonlinear patterns of horizontal variation in nutrient concentrations in tree boles have been obtained in several studies (Clément & Janin, 1976; Bamber & Fukasawa, 1985; Colin-Belgrand et al., 1993; Myre & Camiré, 1994). According to Bamber & Fukasawa (1985), the distribution of mobile nutrients in the stem is generally thought to be a result of retranslocation from older tissues toward the cambial zone.

As a result of internal retranslocation, a high concentration of mobile and intermediately mobile elements are typically evident in the external part of the xylem or sapwood (Wardell & Hart, 1973; Attiwill, 1980; De Visser, 1992; Myre & Camiré, 1994; Colin-Belgrand et al., 1996). These nutrients appear to be concentrated in the most physiologically active tissues, near the cambial zone (Colin-Belgrand et al., 1996). A decline in concentration of these elements in the interior of the stem is believed to be associated with the death of parenchyma cells. These non-living cells commonly have a lower concentration of nutrients because, as the cells die, nutrients in their cytoplasm are apparently retrieved for possible reuse elsewhere in the tree (Merrill & Cowling, 1966). This concentration gradient across the transverse section of the stem has been well documented in the literature; hence, an absence of an increased concentration of K and Mg in the external xylem for the species of this study is difficult to account for.

Seasonal variations in nutrient concentrations in the stem may however be used in explanation of these findings. Reports on seasonal variability in the mineral composition of woody tree components are however limited (Jones & Smith, 1978). Nevertheless, it has been suggested that for estimating nutrient concentrations, the most suitable time to sample perennial tissues is during the leafless period (Messina et al., 1983; Alban, 1985; Hendrickson, 1987). At this time, nutrient concentrations remain relatively constant and short-term fluctuations due to translocation or environmental conditions are minimized (Alban, 1985). Subsequently, element concentrations of the external xylem documented during the dormant period, as in the case of this study, may not be directly comparable to the fluctuating and often high concentrations observed during the growing season.

In further analysis of this data, cation concentrations observed in the transitional and sapwood zones may be compared. In a majority of cases, for the species on the rich site, these zones were found to have statistically different levels of base cation concentrations; no consistent trends indicated a higher concentration in either of the zones however. On the poor site, in all cases, the sapwood and transitional zones did not differ significantly in their base cation concentrations. These results do not support the initial hypothesis of this study, wherein a noticeable change in element concentration was thought to occur in the transitional zone. These findings may suggest that active retranslocation of these elements is not taking place between the heartwood and sapwood, otherwise a change in concentration in the transitional zone would be evident (Wardell & Hart, 1973; Tout et al., 1977; McClenahen et al., 1989; Myre & Camiré, 1994). More likely however, discrepancy of these findings with those of the literature may be directly related to the delineation of the area of the radial section of the stem where these zones are believed to be located. Due to a lack of research in this area, the identification of the transitional and sapwood zones in this study was only based upon the results of a single experiment (Myre & Camiré, 1994). These findings may thus reinforce the need for additional research in description of the transverse sections present in a tree stem, on a species specific basis.

An elevated concentration of Ca and Mg in the heartwood samples analyzed for the species of this study are in agreement with the initial hypothesis of this study. These results were also consistent with previous findings from the literature. Elevated element concentrations in this particular region may be related to an increase in the number of exchange sites present for cation binding, arising as a result of changes associated with the formation of heartwood (Ferguson & Bollard, 1976; Myre & Camiré, 1994; Momoshima et al., 1995). For example, a higher number of exchange sites may be linked to changes in pH values, the translocation of elements towards the pith area, and/or an increased deposition of lignin in this region (Ferguson & Bollard, 1976; Baqui et al., 1979; Myre & Camiré, 1994). In a study by Momoshima & Bondietti (1990), it was noted that the concentration of cation binding sites decreased in a predictable manner from the pith towards the cambium in red spruce (*Picea rubens* Sarg.) as a function of radius, not chronological age. A decline in the number of divalent cation binding sites with radius may help explain why trees store Ca and Mg in often high concentrations in the interior of the stem.

Elevated concentrations of Ca and Mg documented in the interior of the stem for the species studied here may be seen as a consequence of processes associated with heartwood formation. This may provide some indirect evidence to suggest that the samples analyzed here are representative of true heartwood, as opposed to discoloured wood, induced by injury.

Mean cation concentrations observed for the bark were highest in comparison with the other radial zones; this was true in a majority of cases for the species on the rich and poor sites. These results may be expected, as it was hypothesized that cation concentrations would be highest in the bark. These findings are comparable to previous research wherein elemental concentrations were determined for the different component parts of selected tree species, including the bark (Rennie, 1955; Wright & Will, 1958; van den Driessche, 1984; Chatapaul et al., 1985). Such existing research has only been primarily directed towards estimating base cation exports in connection with various harvesting practices. As a result, information to account for high cation concentrations in the bark is weak, except to suggest that the "living bark" (phloem and cambium) may exist as a plentiful nutrient reserve (Siminovitch & Chater, 1958; van den Driessche, 1984; Hendrickson, 1987; Wetzel et al., 1989). During the process of leaf abscission and senescence, selected nutrients may be withdrawn before the leaves are shed and stored in woody branch tips, particularly the bark (Hendrickson & Richardson, 1993). It was also noted by Wetzel et al. (1989), that high levels of specific proteins in inner bark tissues and the presence of protein bodies within the parenchyma cells indicate that the living cells of the bark act as a nutrient reserve. A tree may be highly dependent upon such reserves as in periods of inadequate nutrient supply, the elements stored can be retrieved and recycled by the tree in order to sustain growth processes.

In comparison to the living bark, a high concentration of base cations in the outer bark is not as easily accounted for in the literature. There may naturally be a connection between a high element concentration and the role of the external bark in the overall protection of the tree. Research findings in support of such a claim are for the most part absent. Results from studies on the chemical composition of the outer bark may however provide evidence of this protective function. In a study conducted by Kelsey & Harmon (1989), the outer bark of Pacific silver fir (*Abies amabilis* Dougl. ex Forbs), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and western red cedar (*Thuja plicata* D. Don) was in most cases, found to contain elevated concentrations of total phenols and tannins. A high concentration of these compounds in the outer bark is consistent with their function in chemical defenses (Kelsey & Harmon, 1989). For example, phenolic compounds in the outer, as well as the inner bark of beech, have been found to play an important role in combating infections (Dübeler et al., 1997). In general, the significance of the bark as a nutrient reserve and as a component for protection of the tree has been well established.

Despite the general trends noted above, distinct patterns of distribution on a species basis for selected elements may be observed (Table 2.2.). On the rich site, for white ash, relatively uniform element concentrations in the radial sections of the woody component of the stem may be observed in comparison to a peak in concentration in the bark. This generalized pattern of distribution may also be observed for American beech on the poor site. For sugar maple and American basswood, a similar radial distribution of nutrients may be identified. Concentrations of Ca and Mg for these species were high in the heartwood, similarly lower in the transitional and sapwood zones, while highest concentrations were present in the bark. This pattern may also apply to red maple on the poor site. Red oak displayed a distinct distributional pattern of nutrients in the stem. For this species, concentrations of Ca and Mg were highest in the bark; concentrations then decreased in the transitional and sapwood zones, while lowest concentrations were present in the heartwood.

Similar studies have also provided proof that individual tree species may possess a characteristic pattern of elemental concentrations among the tissues (Rennie, 1955; Beadle &

Table 2.2. Mean nutrient concentration by species.

Species	heartwood	transitional	sapwood	bark
		K		
white ash	1.530 (0.119)	1.544 (0.109)	1.022 (0.047)	2.898 (0.214)
sugar maple	1.782 (0.304)	0.654 (0.053)	0.891 (0.028)	2.839 (0.155)
A. basswood	4.150 (0.983)	0.874 (0.043)	1.408 (0.066)	1.576 (0.194)
American beech	0.665 (0.067)	0.748 (0.066)	0.591 (0.037)	1.255 (0.058)
red oak	0.761 (0.038)	1.069 (0.108)	1.085 (0.050)	0.950 (0.072)
red maple	1.107 (0.146)	0.571 (0.041)	0.537 (0.037)	1.040 (0.099)
		Ca		
white ash	0.438 (0.021)	0.449 (0.019)	0.525 (0.014)	16.66 (0.778)
sugar maple	4.468 (0.803)	1.007 (0.025)	0.859 (0.043)	20.208 (1.255)
A. basswood	5.466 (0.828)	1.121 (0.019)	1.206 (0.129)	16.308 (0.836)
American beech	0.787 (0.046)	0.576 (0.019)	0.647 (0.061)	22.123 (1.049)
red oak	0.391 (0.043)	0.764 (0.091)	0.855 (0.091)	20.986 (0.770)
red maple	1.279 (0.061)	0.684 (0.022)	0.807 (0.121)	10.468 (0.562)
		Mg		
white ash	0.134 (0.009)	0.121 (0.005)	0.178 (0.009)	1.508 (0.055)
sugar maple	0.901 (0.139)	0.187 (0.012)	0.141 (0.009)	0.923 (0.053)
A. basswood	1.047 (0.189)	0.200 (0.007)	0.225 (0.009)	1.165 (0.061)
American beech	0.226 (0.021)	0.228 (0.022)	0.229 (0.015)	0.619 (0.045)
red oak	0.028 (0.020)	0.239 (0.106)	0.263 (0.096)	0.431 (0.107)
red maple	0.329 (0.041)	0.159 (0.009)	0.131 (0.007)	0.423 (0.025)

Note: Standard errors of the means are given in parentheses.

White, 1968; Wardell & Hart, 1973; Chatarpaul et al., 1985). Trees of different species growing in the same stand do not necessarily show similar nutrient contents or similar concentrations in corresponding tissues or similar distribution patterns (Beadle & White, 1968; Alban, 1982; Perela & Alban, 1982; Hillis, 1987). Interpretation of differential trends of elemental distribution is however difficult, beyond the suggestion that elemental use, storage and/or redistribution is controlled primarily by genetic differences between species.

Recognition of distinct trends in the distribution of nutrients in the stem is however important when estimating the nutrient content of the bole for a particular species. Improved models for estimation of stem nutrient content have attempted to account for the variability in nutrient concentrations across the radial section of a stem (Rochon et al., 1998). Information in this respect may be significant in evaluation of the implications of various harvesting methods for a particular stand. Evidence of varying levels of elemental concentrations within the stem may also be used to assess the importance of the internal cycling of elements inside the bole. In latter stages of stand development, nutrient cycling in forest trees can be seen as an efficient strategy, which may render the tree somewhat independent of soil nutrient reserves (Vitousek, 1982; Hendrickson, 1987; Colin-Belgrand et al., 1996; Mitchell et al., 1996). Elements contained within the various tree components cannot be overlooked as a contributing factor to the nutrition of the tree and the overall productivity of the stand.

2.5 CONCLUSION

Notwithstanding differences on an element, species and site basis, similar distributional zones of nutrients could be delimited. In complement to previous findings, the bark in a majority of cases was found to contain the highest concentration of all base cations measured. Next to the bark, concentrations of K, Ca, and Mg were generally highest in the heartwood. Elements such as Ca and Mg may be documented to accumulate in elevated concentrations here, as part of elemental redistribution during heartwood formation (Likens & Bormann, 1970; Wardell & Hart, 1973; Frelich et al., 1989; Myre & Camiré, 1994). With regards to elemental concentrations in the transitional and sapwood zones, findings presented here may be considered inconclusive. The sampling procedures employed in the identification and delineation of these zones may serve as a significant source of error in analysis of cation concentrations observed in these radial sections. This generalized pattern of distribution has been recognized, despite noted exceptions of distinct trends of distribution on a species basis.

GENERAL CONCLUSIONS

Research conducted with regard to nutrient immobilization within the perennial tissues of trees is lacking in existing forestry literature. This study has aimed at expanding current scientific knowledge in this area through investigation of trends of base cation immobilization in the stem of selected hardwood species.

Rates of immobilization were evaluated primarily in connection with observed base cation concentrations in the wood and bark, as well as species' rates of growth. In the case of Ca for white ash, and Ca and Mg for red oak, it was assumed that a low element concentration and a high rate of growth was reflective of a low rate of immobilization. As well, elevated concentrations of Mg and Ca in the bark of American basswood and red oak were found to significantly contribute to overall patterns of immobilization for the wood and bark component of the stem. Analysis of such rates on a species basis is significant as previous studies have suggested that differential rates of immobilization may influence the availability of nutrients on site (Rennie, 1955; Miller, 1963; Johnson et al., 1982; Chatarpaul et al., 1985).

Across the radial section of the stem, a similar pattern of distribution of nutrients was observed for the hardwood species investigated. In general, it was found that concentrations of base cations (K, Ca, Mg) decreased in the order of bark > heartwood > transitional zone = sapwood. The significance of the bark as an essential nutrient reserve within the tree has been clearly established here. Identification of such reserves in the woody proportion of the stem is more difficult however, because of the variability relating to the delimination of the radial zones in the cross section of the stem. This may be again reflective of the fact that information as a result of research conducted is sparse with respect to this process.

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Appendix 1. Ratios of wood and bark nutrient content determined from regression analysis using a DBH of 20, 30, and 40 cm.

Rich site

Species	DBH	K	Ca (g)	Mg
white ash	20	7.20:1	1.41:1	2.61:1
	30	9.52:1	1.35:1	2.13:1
	40	10.48:1	1.60:1	2.32:1
sugar maple	20	4.76:1	1.48:1	4.00:1
	30	3.91:1	1.68:1	3.43:1
	40	4.90:1	1.70:1	4.21:1
American basswood	20	11.79:1	2.11:1	2.27:1
	30	7.13:1	1.69:1	1.94:1
	40	4.31:1	1.35:1	1.65:1

Poor site

Species	DBH	K	Ca (g)	Mg
American beech	20	8.45:1	1.57:1	8.28:1
	30	15.51:1	1.99:1	12.17:1
	40	28.46:1	2.51:1	17.89:1
red oak	20	5.10:1	1.14:1	1.83:1
	30	10.37:1	1.21:1	2.25:1
	40	11.61:1	1.22:1	2.31:1
red maple	20	4.54:1	1.63:1	3.20:1
	30	7.53:1	1.72:1	5.58:1
	40	16.22:1	1.80:1	7.79:1