

**Long-term effects of base cation fertilization on nutrient cycling and species composition of
a sugar maple stand in southern Quebec: application of the Rb/K reverse tracer**

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Short title:

Long-term effects of base cation fertilization on sugar maple

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Abstract

To improve the understanding of the long-term effect of forest potassium (K)-fertilization, I revived a 23-year-old base cation fertilization experiment in a sugar maple stand in southern Quebec (45°59.6'N 73°59.9'W). My main objectives were to determine (i) the long-term percent of K derived from fertilizer in the soil-plant system using the rubidium (Rb)/K reverse tracer method, (ii) if fertilization had altered the diversity of the understory plant community, and (iii) if there was still an effect on the growth and nutrient status of the sugar maple trees.

In 1988, six 40 m × 40 m plots were delineated in a sugar maple stand. In June 1989, three of these plots received 500, 250, and 250 kg·ha⁻¹ of K₂SO₄, CaMg(CO₃)₂, and CaCO₃, respectively as fine particulate matter, and the other three were left as control. Mid-canopy leaves of sugar maple trees were sampled annually in August from 1988 to 1991 and 2011 to 2012. In 2012, understory species were surveyed using the Braun-Blanquet method and ten of the most abundant and ubiquitous species were sampled for leaf chemistry. Leaves of both understory and canopy sugar maple trees were digested for nutrient concentrations using trace metal grade HNO₃. In 2012, two soil pits were dug in each plot and individual horizons were sampled. Soil was extracted with 1 M NH₄Cl. K, Ca, Mg, and Rb concentrations were determined by inductively coupled plasma mass spectrometry (ICP-MS) for both digested and extracted samples. Growth of sugar maple trees was assessed using tree cores taken in 2012.

Fertilization increased sugar maple leaf K two years following fertilization, but the effect was no longer detectable in 2011/2012. Only Ca and Mg showed increased concentrations in the leaves

the fall of the year of fertilization. The percent of leaf K derived from fertilizer in 2011/12 is nearly what it was in the fall of 1989, two months after fertilization. There was no significant difference between control and fertilized plots in the concentration of K in the sapwood of the sugar maple trees, but there was 27 ± 2 % of K derived from fertilizer in the wood in 2012. There was no difference in relative growth of sugar maple, or understory vegetation diversity or species richness in fertilized plots. Nutrient analysis of understory vegetation showed no differences in concentrations of leaf K between treatments, but percent K from fertilizers amounted to over 25 % in several species. There was no effect of treatment on soil chemistry but there was a large proportion of the original fertilizer recovered in the soil profile. The total amount of K from fertilizer held in the soil-plant system was $54 \text{ kg} \cdot \text{ha}^{-1}$ or 24 % of the original $225 \text{ kg} \cdot \text{ha}^{-1}$ of fertilizer K applied. Overall, these results suggest: (i) a short-term improvement of K status following fertilization, (ii) efficient recycling of K fertilizer in the soil-plant system of maple forests, and (iii) no obvious long-term change in understory species composition following forest fertilization.

Résumé

Pour améliorer notre compréhension de l'effet de la fertilisation en potassium (K) des forêts à long terme, nous avons remis en fonction une expérience de 23 ans de fertilisation en cations basiques dans un peuplement d'érable à sucre dans le sud du Québec (45°59.6'N 73°59.9'W). Nos objectifs étaient de déterminer (i) le pourcentage de potassium (K) provenant d'engrais dans le système sol-plante 23 ans après la fertilisation en utilisant méthode de traçage inverse du rubidium (Rb) / K, (ii) si la fertilisation a modifié la biodiversité de la communauté végétale des strates arbustives et herbacées, et (iii) s'il y avait encore un effet sur la croissance et l'état nutritionnel des érables à sucre.

En 1988, six 40 x 40 m parcelles ont été délimitées dans un peuplement d'érable à sucre. En juin 1989, trois de ces parcelles ont reçu 500, 250 et 250 kg·ha⁻¹ de K₂SO₄, CaMg(CO₃)₂ et CaCO₃, respectivement, sous forme de particules fines, et les trois autres parcelles n'ont pas été fertilisées (contrôle). Les feuilles en périphérie de la couronne d'érables à sucre ont été échantillonnées annuellement en août de 1988 à 1991 et 2011 à 2012. En 2012, les espèces du sous-étage ont été échantillonnées selon la méthode de Braun-Blanquet et dix espèces les plus communes ont été analysées pour la chimie des feuilles (digestion humide au HNO₃). En 2012, deux pédons ont été creusés dans chaque parcelle et les horizons ont été échantillonnés jusqu'à une profondeur de 70 cm. Les sols ont été extraits au NH₄Cl (1 M). Les concentrations de Rb, K, Ca, et Mg dans les feuilles et les sols ont été déterminées par spectrométrie de masse à plasma inductif (ICP-MS). La croissance des érables à sucre a été évaluée en utilisant des carottes d'arbres récoltées en 2012.

La fertilisation a augmenté le K des feuilles d'érable à sucre deux ans après la fertilisation, mais l'effet n'était plus détectable en 2011/ 2012. Les concentrations en Ca et Mg ont augmenté à l'automne de l'année de la fertilisation. Le pourcentage du K foliaire provenant des engrais en 2011/12 est à peu près ce qu'il était à l'automne 1989. La fertilisation n'a pas augmenté la concentration de K de l'aubier des arbres d'érable à sucre, mais $27 \pm 2\%$ du K provenait des engrais en 2012. La croissance relative de l'érable à sucre, et la diversité et la richesse en espèces de la végétation du sous-étage dans les parcelles fertilisées n'ont pas été affectées par la fertilisation. L'analyse des éléments nutritifs de la végétation du sous-étage n'a montré aucune différence dans les concentrations en K des feuilles entre les traitements, mais le pourcentage en K dérivé des engrais s'élevaient à plus de 25% chez plusieurs espèces. Il n'y avait aucun effet du traitement sur la chimie du sol, mais il y avait une grande proportion de l'engrais récupéré dans le profil du sol. La masse totale de K dérivé des engrais dans le système sol-plante était de $54 \text{ kg}\cdot\text{ha}^{-1}$ ou 24 % des $225 \text{ kg}\cdot\text{ha}^{-1}$ d'engrais K appliqué. Ces résultats suggèrent: (i) une amélioration à court terme de la nutrition en K suivant la fertilisation, (ii) un recyclage efficace des engrais en K dans le système sol-plante de cette érablière, et (iii) aucun changement évident à long terme de la composition en espèces du sous-étage suivant la fertilisation du peuplement.

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1.0 Introduction

Sugar maple (*Acer saccharum* Marsh.) is one of the most important North American hardwood species. It is widely distributed in its range and provides significant recreational and economic value through the production of timber and maple syrup (Hendershot and Jones 1989; Houle et al. 2007). During the 1980s, sugar maple experienced an extensive, well-documented decline in Eastern Canada and the North-Eastern United States (Houle et al. 2007). Suggested causes for the maple decline, either exclusively or in combination, include: natural and anthropogenic stress factors such as severe climate events (droughts and freeze-thaw), insect defoliators and root pathogens, poor forest management, soil acidification, and nutrient imbalances (Bernier et al. 1989; Hendershot and Jones 1989; Houston 1999; Côté and Ouimet 1996; Payette et al. 1996; Duchesne et al. 2002). Symptoms of decline, which frequently ended in tree death, included: dieback of fine twigs, loss of crown vigour, and reduced radial increment growth (Huggett et al. 2007). Other hardwood species also experienced decline during this period, but sugar maple and red maple were the hardest hit species (Hendershot and Jones 1989). As a response to the decline, an International North American Sugar Maple Decline Project (NAMP) and the Forest Ecosystem Research and Monitoring Network (RESEF) in Quebec were created during the late 1980s to monitor tree-health (Houston et al. 1999; Périé and Ouimet 2003).

Multiple sites across southern Quebec showed severe nutrient imbalances, with particularly low leaf potassium (K), phosphorus (P) and to a lesser extent calcium (Ca) and magnesium (Mg) concentrations (Bernier et al. 1989; Juice et al. 2006). These nutrient imbalances corresponded to areas of sugar maple decline that were unexplained by natural stress factors (Bernier et al. 1989).

Furthermore, imbalances and deficiencies of base cations were reported to weaken the ability of sugar maple trees to sense and react to secondary biotic and abiotic stresses (Huggett et al. 2007). Subsequently, in addition to the NAMP and RESEF, in 1988, the Quebec government created a 5-year management programme called the Fight Against Maple Dieback Program whose objectives included a large-scale operational fertilization program, targeting the most affected regions (Anonymous 1994; Hendershot and Courchesne 1994). As a result, multiple fertilization experiments were conducted in the late 1980s continuing through to the late 1990s to explore the relationships between soil fertility and sugar maple health (Hendershot et al. 1994; Côté et al. 1995; Moore et al. 2000). The majority of these research experiments were aimed at studying short-term responses, usually lasting no more than 5 years post fertilization, although some suggested that their duration of responses to K application would likely be long lasting (Côté and Ouimet 1996; Bernier et al. 1989). The present study is a continuation of one of those base cation fertilization experiments, with a greater focus on the influence of K traced using the rubidium (Rb)/K reverse tracer method (Hafez and Stout 1973), and an expansion of the original study to include the effects of fertilizer on understory vegetation. My main goal was to assess the long-term effects and recovery of the K-fertilizer in the soil-plant system 23 years after fertilization.

2.0 Literature Review

2.1 Forest fertilization

Forest fertilization is a management practice backed up by some of the most detailed experiments in forestry (Miller 1981). The majority of forest fertilization occurs in plantation forest systems and although there were 109 million hectares (2.8 % of the global forested area) of productive plantations in 2005, forest fertilization is still considered a minor use of global fertilizers compared to agriculture (FAO 2005; Smethurst 2010). Generally forest fertilization is effective for a longer time frame than in agriculture, as trees have greater recycling of the nutrients that fall in the leaves, and are not harvested annually (Smethurst 2010). Forest fertilizers are applied according to fertilizer prescriptions based on nutritional diagnoses and site quality assessments developed to optimize production without jeopardizing wood quality (Timmer et al. 2003; Farrelly et al. 2009).

Forest fertilizers can be applied either as a foliar application or on the ground. The two most popular ground application techniques are broadcast and banding. Broadcast fertilization consists of applying the fertilizer evenly across the soil surface of a designated area, whereas banding is the application of fertilizer within a defined radius of selected study trees. As such, broadcast will have a greater effect on the soil chemistry and understory species. Often, the size of the root zone determines which type of application to use; the larger the root zone, the more widespread the fertilizer (Attiwill and Adams 1996). The effectiveness of the fertilizer application will be influenced by the time of application, both in terms of seasonality and the life stage of the trees (Miller 1981). The effectiveness of the fertilizer treatment is predominantly assessed by

comparing the absolute concentration of nutrients in tissues, while taking into consideration the relative growth rate of control vs. fertilized trees (Tripler et al. 2006; Vadeboncoeur 2010).

In the past, nitrogen was found to be the most globally limited nutrient, as demonstrated by its ability to increase net primary production upon addition, and as such has been a very common nutrient in forest fertilization experiments (LeBauer and Treseder 2008). However, although nitrogen addition can be beneficial to forests, excess nitrogen via either acid deposition (Watmough and Dillon 2003) or fertilization (Clark et al. 2007) can cause deficiencies and imbalances in base cations by displacing them from soil exchange sites. This relationship may, in part, explain some of the base cation deficiencies and imbalances occurring in Quebec forests.

2.2 Sugar maple

Sugar maple is a species best suited to fertile, moist, and well-drained soils. It is mostly found on soils with pH between 5.5 and 7.3, has very acidic leaf litter, and consequently poor soil ameliorating potential, which contributes to the acidity of the soils under sugar maple dominance (Fowells 1965; Côté and Fyles 1994). It reproduces with seeds annually, the best crops occurring in intervals of 2 to 5 years depending on environmental and climatic conditions, and vegetatively with stump sprouts (Fowells 1965). Sugar maple is an integral member of six different forest cover types and associated with 17 other types in Eastern North America alone (Fowells 1965). Sugar maple has extensive root branching and commonly has intraspecific root grafting (Godman 1990). This could be of concern for possible edge effects associated with fertilization if the roots reach outside a designated treatment area. More specifically, a tree in one plot may be taking up nutrients from a plot of a different treatment, clouding the effect of fertilization.

Leaf and soil nutritional analyses are often used as an indicator for available nutrients. The optimum leaf nutrient concentrations for sugar maple in Quebec are 20-22, 1.0-1.3, 6.0-7.7, 8.7-11, and 1.2-1.4 mg·g⁻¹ for N, P, K, Ca, and Mg respectively (Côté et al. 1993). For soils, the optimal ratios suggested for sugar maple for the H-Ah and upper mineral horizons are 6 and 4 for Ca/Mg, and 0.5 and 1 for K/Mg (Ouimet et al. 2013). The suggested norms for saturation in the H-Ah and Upper B horizons for sugar maple in Quebec are 60 and 50 for Ca and <10 and <10 for Mg (Ouimet et al. 2013).

2.3 Potassium in forests

Potassium (K) is an essential macronutrient and is the only univalent cation that is essential for all living organisms (Evans and Sorger 1966). However, K is greatly understudied in forest ecosystems in comparison to other nutrients such as N and P (Tripler et al. 2006). K has been known to be an important nutrient for plants since the mid 1800s (Lucanus 1865). It is essential for the growth, development and normal metabolic processes (Evans and Sorger 1966) and can help mitigate the severity of tree disease (van den Driessche and Ponsford 1995; Shaw et al. 1998). It is a very mobile ion, and as such is often tightly cycled in forest ecosystems, or in other words, is retained well in the soil-vegetation system (Côté et al. 1995; Hendershot and Courchesne 1994). This tight cycling of K by plants results in upper soil horizons often having higher concentrations of K compared to lower horizons (Jobbágy and Jackson 2001). Specifically, roots pull up mineral K that has been weathered from the parent material of the soil profile. This is later deposited in the organic matter when the leaves fall to the ground and decompose, later recycled again by the trees and results in very little K moving down the soil

profile. Therefore it is uptake and recycling of K that causes an accumulation in the upper horizons.

Fertilization with K has been shown to increase K cycling in organic and eventually the deeper mineral soil horizons (Hendershot and Courchesne 1994). However, since the concentration of K can have significant annual variation in both the organic and mineral soils, it can be very difficult to accurately detect treatment responses (Côté et al. 1995). Moreover, K from fertilizer has been known to travel laterally up to 16 m along the soil surface several decades after fertilization, contaminating closely placed control plots (Buxbaum et al. 2001) making treatment assessments difficult. Lateral travel of fertilizer may be via the soil solution, root grafts and lateral root extension, or leaf displacement (Buxbaum et al. 2001).

A meta-analysis and review completed by Tripler et al. (2006), found that 76 % of studies show a positive and significant increase in K concentrations in plant tissues after soil K fertilization or manipulations. While K fertilization tends to increase tree basal area growth and/or foliar K concentrations in these studies, there is no obvious connection to the amount of K applied and basal area growth. Instead, the success of forest fertilization in general, as with the majority of forest ecosystem experiments, depends more on site and species specific responses to the fertilizer treatments (Babst et al. 2012). Fertilization with K either alone, or in combination with lime or other nutrients has been shown to increase the content of K in leaves of sugar maple experiencing decline (Hendershot and Jones 1989; Fyles et al. 1994; Stone and Christenson 1975; Moore et al. 2000; Ouimet and Fortin 1992; Wilmot et al. 1996). These increases in leaf K were often correlated to increases in tree growth, however some found no response (Lea et al.

1980; Stone 1980; Moore and Ouimet 2006) or negative responses in growth (Côté et al. 1995). It is not possible to generalize an overall positive or negative effect of K fertilization on sugar maple trees at this time as there is still a lot to be gained in terms of how important K is for tree growth and how it affects forest community dynamics (Tripler et al. 2006).

2.4 Calcium, Magnesium, and liming in forests

Calcium is important in regulating physiological processes involved in plant growth, responses to environmental stress, and repair of damaged tissues (Huggett et al. 2007). Magnesium is a key nutrient for protein synthesis, root production, and photosynthesis (Cakmak and Yazici 2010). Unfortunately, monitoring of North American hardwood forests continues to show a decrease in base cations, notably Ca and Mg, in upper soil horizons and surface waters (Watmough et al. 2005). These decreases have been attributed to acid deposition, decreases in base cations in atmospheric deposition, and soil leaching and sequestration of these elements in the forest biomass caused by the accumulation of acidic compounds (Courchesne et al. 2005; Juice et al. 2006; Watmough et al. 2005). The decrease of these elements has been linked to deficiencies and imbalances associated with sugar maple decline (Ouimet and Camiré 1995).

The effects of soil acidification and nutrient depletion associated with acid deposition are not restricted to nutrient content of tree tissues as it affects both growth and health of all forest vegetation (Pabian et al. 2012). Liming continues to be a common mitigation technique used to counteract these negative effects of soil acidification including preventing dieback, and to increase the content of Ca and Mg thus correcting nutrient imbalances and deficiencies (Pabian et al. 2012; Long et al. 2011; Demchik and Sharpe 2000; Moore and Ouimet 2006). The majority

of forest liming occurs in Central and Northern Europe to counteract high levels of soil acidification and atmospheric deposition of N and S, otherwise known as the ‘acid rain’ effect in the 1970s and 1980s (Smethurst 2010). In base-poor and declining northern hardwood stands, liming has the potential to limit damage caused by acid deposition and increase growth and vigour of sugar maple (Moore and Ouimet 2006). Long-term effects of liming on sugar maple are limited, but do exist (Long et al. 2011; Moore et al. 2012).

Although useful for replacing depleted Ca and Mg, correcting acidity, and increasing growth, liming can have negative effects on forest ecosystems including mobilization of heavy metals, higher rates of nitrate leaching, and shallower root systems (Kreutzer 1995, Löfgren et al. 2009). Depending on the method of application, liming has also been known to produce mixed results on the foliar concentrations of elements in sugar maple, including inducing nutrient imbalances (Burke and Raynal 1998; Moore and Ouimet 2006). To counteract this possibility, other nutrients such as K are often added at the same time to ensure a positive effect on the growth of the target trees (Burke and Raynal 1998). However, the addition of K is not a fail safe measure to ensure a response, as demonstrated by a study done in Entrelacs, Quebec that found no significant change in mineral soil chemistry during the first five years after application of K_2SO_4 and $CaCO_3$ or K_2SO_4 and $CaMg(CO_3)_2$ (Côté et al. 1995). Moreover, the addition of K may cause a K-Mg antagonism resulting in undesirable growth responses (Moore and Ouimet 2010).

Additionally, the response of a forest to liming varies by species and length of study. It has been suggested that the liming of acidic forest soils may show more desirable effects in the long-term compared to that revealed by short-term studies (Burke and Raynal 1998; Long et al. 2011). This

may be due to the slow dissolution rates of some types of lime when applied in a forest, causing a delay in the release of the nutrient and subsequently the effect of the fertilizer (Burke and Raynal 1998). Before recommendations or conclusions for widespread use of lime in forests can be made, long-term studies of both tree and understory vegetation responses are required to evaluate the possible negative effects of forest liming (Long et al. 2011). As it stands, there is an inadequate understanding surrounding the interactive effects of forest liming over both spatial and temporal scales (Smethurst 2010).

2.5 Forest understory vegetation and fertilization

The majority of forest fertilization experiments, with the growing exception of more recent studies, focused on the effects of fertilization on overstory trees without much consideration to the effects of fertilization on understory communities (Ostertag and Verville 2002). However, understory vegetation diversity is a helpful measure to quantify possible changes in plant community structure (VanderSchaaf et al. 2000) and forest health post fertilization. Greater knowledge of the effects of fertilization on understory vegetation is needed to understand whether side effects of fertilization are compatible with the goals of sustainable forestry, specifically, the preservation of biodiversity (Demchik and Sharpe 2000; VanderSchaaf et al. 2000; Strengbom and Nordin 2008). So far, the results of studies looking at the effects of fertilizer on the understory have been extremely mixed and highly dependent on the type of fertilizer applied.

Fertilization has been shown to impact abundance, diversity, species richness, and cover of understory plants (Ostertag and Verville 2002; Strengbom and Nordin 2008; He and Barclay

2000; Thomas et al. 1999;). Although the effects of fertilization on these variables are often positive, such as an increase in diversity (VanderSchaaf et al. 2000), opposite responses are common. For example, an increase in abundance in one species is commonly associated with a decrease in species richness or diversity (Sullivan et al. 2012; Demchik and Sharpe 2000).

One-way that fertilizer affects the plant community is by altering the interactions among species, by increasing the competitiveness or production of some species (Ostertag and Verville 2002; He and Barclay 2000). This can either be due to species taking advantage of the fertilizer and outcompeting other species or species experiencing nutrient toxicity (Chapin et al. 1986). Another is through changes in shading and light resources from an increased productivity in the canopy and thus a favouring of the shade tolerant understory species (Thomas et al. 1999; Fox et al. 2007).

In addition to light resources, the composition and structure of the overstory can have a significant influence on the understory vegetation through the alteration of water, and soil nutrient availability, throughfall quantity and chemistry, and physical litter characteristics (Barbier et al. 2008). So if the overstory has been greatly altered through either an increase or decrease in canopy growth, litter production, or nutrient retention associated with fertilization, it can have a compound effect on the understory in addition to the change in nutrient supply available to the understory via the soil. Plants also react differently to soil pHs (Barbier et al. 2008). It is therefore possible that the application of lime and subsequent increases in soil pH can cause certain species to decrease or increase in abundance. On the other hand, sugar maple

leaves tend to acidify the soil overtime (Côté and Fyles 1994); possibly cancelling out any possible decreases in acidity associated with the fertilization.

More research is needed to confirm that fertilization is continuing to have a positive effect on the growth of trees, while having little or not long-lasting negative effects on other aspects of the ecosystem such as understory vegetation growth (Strengbom and Nordin 2008). For this study, understory vegetation refers to herbaceous, ferns, allies, and woody species generally less than 2 m in height.

2.6 Rubidium/Potassium Reverse Tracer Method

Quantifying the amount of K directly sourced from the fertilizer as a way of assessing the uptake of K fertilizer is rarely done. In most cases, the uptake tends to be measured by comparing the concentration of nutrients in the tissue of control trees to concentrations in fertilized trees (Tripler et al. 2006). Less often is the uptake assessed by tracing the nutrients back to the fertilizer. Yet I believe, in order to accurately describe the response of a stand to fertilization, the uptake of the fertilizer should be proven. Tracing nutrients can be done by comparing either isotopes (e.g. $^{15}\text{N}/^{14}\text{N}$), or using sister elements as proxies (e.g. Ca/Sr) (Binkley et al. 1985; Bailey et al. 1996).

Potassium has three isotopes. ^{39}K is the most abundant form of K while ^{41}K and ^{40}K are stable and radioactive isotopes of K, respectively (Smythe and Hemmendinger 1937; Fujiyoshi et al. 2009). Tracing K with isotopes is not a common method in plant ecology (Sulzman 2007, Table 1.1) and I have struggled to find a study that made use of a K isotope to trace K in a forest

ecosystem. This may, in part, be due to the high variability in the ratio of $^{40}\text{K}/^{39}\text{K}$ in forest soils (Fujiyoshi et al. 2009). Instead, K is traced using rubidium (Rb) in what is called the Rb/K reverse tracer method.

The Rb/K reverse tracer method compares the naturally (control) occurring ratio of the two elements to those in fertilized tissues to determine how much K utilized by the tree came from the fertilizer (Hafez and Stout 1973). It is a method analogous to isotopic tracing, and works because Rb and K have comparable structure – almost identical atomic radius - and are considered to behave similarly with regard to plant absorption as plant roots do not distinguish between Rb and K (Evans and Sorger 1966; Drobner and Tyler 1998; Buxbaum et al. 2001). Commercial fertilizers are usually very low in Rb and are therefore assumed to have no Rb present in their mixtures. Thus any differences in the ratio of the two elements between fertilized and control tissues are assumed to reflect the changes in leaf K resulting from the fertilization (Hafez and Stout 1973). If a plant absorbs fertilizer, the ratio of Rb to K is proportionally lower in treated tissues than in control (Buxbaum et al. 2001). However, a strong increase in soil K concentrations may impede the uptake of Rb in plant tissues (Drobner and Tyler 1998) and consequently decrease the Rb/K ratio and provide an overestimate of percent K derived from fertilizer (Drobner and Tyler 1998). Factors other than fertilization and the natural concentration of each element that can influence the ratio of Rb/K also include soil pH, and age of plants (Drobner and Tyler 1998; Kosla et al. 2002).

Although base cations can increase the soil pH (Lawrence et al. 2012), the alteration of the uptake of Rb through an increase in soil pH does not occur until the soil pH increases to near

neutrality (Drobner and Tyler 1998). Given that the pH of hardwood forest soils in eastern North America often remains acidic following liming, despite significant increases in pH (Moore et al. 2008; Long et al. 1997; Timmer et al. 2003), the decrease in the content of Rb in plant tissues and subsequent effect on the estimates of K derived from fertilizer should not be of great concern in forest studies.

3.0 Objectives/ Hypothesis

The health of sugar maple forests remains a major concern in some areas of Canada (Ontario and Quebec) and the United States (Pennsylvania and Vermont), despite the recovery of most northern hardwood forests from the forest decline and dieback of the 1980s (Moore and Ouimet 2006). As suggested by Côté et al. (1995), long-term studies on the effect of fertilization on nutrient cycling are needed to design integrated forest management that can help optimize forest nutrition and aid in minimizing forest decline. It is therefore my goal to expand on the knowledge of the long-term effects of base cation fertilization by reopening a 23-year-old K-Ca-Mg fertilization experiment in a sugar maple stand in southern Quebec. As K has been argued to be the more frequently limiting nutrient (Bernier et al. 1989), the present study will focus on that element.

Specifically, my objectives were to determine (i) the long-term changes of K, Ca, and Mg concentrations in the soil-plant system, (ii) the percent of K derived from fertilizer in the soil-plant system, (iii) the long-term effect of fertilization on tree growth, (iv) effects of fertilization

on understory vegetation species diversity, and finally (v) to assess the amount of original K fertilizer still held in the soil-plant system 23 years after fertilization.

Four main hypotheses/predictions were formulated for my thesis. 1. As K is tightly cycled, I expected a long-term retention of fertilizer-K in the soil-plant system with a persistent positive effect on leaf K and growth of sugar maple and soil K concentration. 2. Since Ca and Mg were also applied, I hypothesized that fertilization would increase foliar Ca and Mg as seen in a previous 10-year forest liming experiment (Moore and Ouimet 2006), paired with long-term increases of these nutrients in the soil. 3. As I had a very dense understory cover, especially in fertilized plots, and since forbs (understory plants) can have high levels of K compared to other vegetation groups (Pabian et al. 2012), I predicted that a large proportion of the fertilizer K would be in the understory. 4. Because fertilization is aimed at increasing overstory growth and thus canopy cover, I expected, as was suggested by VanderSchaaf et al. (2000), a long-term indirect negative effect of fertilization on understory vegetation diversity coupled with a positive effect on the abundance of shade tolerant understory plants.

4.0 Materials and Methods

4.1 Study Site

The study site (Table 1) is located at the Station de biologie des Laurentides of the University of Montreal near Saint-Hippolyte, Quebec approximately 80 km north of Montreal in the Laurentians (Hendershot and Courchesne 1994). The surrounding area received an average of 1195 mm of total precipitation per year between 1981 and 2010, 297 cm of which fell as snow,

with an average annual temperature of 4 °C (Développement durable, Environment et Parcs 2013). In 1988, at the start of the experiment, the forest was a 50-year-old stand, of fire origin, with sugar maple accounting for 90 % of the canopy and 71 % of the basal area. Other species included yellow birch, red maple, American beech, and large-toothed aspen (Hendershot and Courchesne 1994; Fyles et al. 1994).

The dominant soil type is classified as Orthic Ferro-Humic Podzols (Agriculture Canada Expert Committee on Soil Survey 1987), derived from igneous and metamorphic rocks, and poor in Mg and K (Côté et al. 1995). A detailed description of the soil profile at the onset of the experiment can be found in Hendershot and Courchesne (1991). Table 2 shows the average thickness and measured bulk density of each soil horizon found in and near the study site. Soil thickness and organic bulk density were measured in 2012. The mineral bulk densities were estimated based on values provided in Courchesne et al. (2005). Soil pH and CEC are adapted from Hendershot and Courchesne (1991).

Table 1 Study site characteristics.

Characteristic	Saint-Hippolyte
Latitude	45° 59' 37.93" N
Longitude	73° 59' 55.92" W
Elevation	400 m
Soil type	Orthic Ferro-Humic Podzols
Mean annual precipitation	1195 mm
Mean annual temperature	4 °C
Stand age in 1988	50 years
Stand type	sugar maple-yellow birch

Table 2 Soil characteristics at the study site

Horizon	pH	CEC ($\text{cmol}\cdot\text{kg}^{-1}$)	Bulk density ($\text{kg}\cdot\text{m}^{-3}$)	Avg. thickness	
				Control (cm)	Fertilized (cm)
L	4.89	77.0	320	2.8 ± 0.2	1.9 ± 0.1
F	4.36	42.9	320	3.3 ± 0.2	2.3 ± 0.2
H	4.10	16.7	320	2.2 ± 0.1	2.6 ± 0.2
Ae	4.15	4.79	1000	2.5 ± 0.1	2.0 ± 0.1
B1	4.51	11.0	876	5.2 ± 0.3	14 ± 0.8
B2	4.71	4.05	1055	34 ± 0.4	40 ± 0.7
B3	5.02	2.69	1098	14 ± 0.4	7.0 ± 0.3

Note: Soil pH and CEC are adapted from Hendershot and Courchesne (1991). The mineral bulk densities were estimated based on values provided in Courchesne et al. (2005). Soil thickness and organic bulk density were measured in 2012.

4.2 Experimental design

In 1988, six 40 m x 40 m plots were delineated with a 5 m buffer between plots. Three plots were randomly selected to receive a mixture of $500 \text{ kg}\cdot\text{ha}^{-1} \text{ K}_2\text{SO}_4$, $250 \text{ kg}\cdot\text{ha}^{-1} \text{ CaMg}(\text{CO}_3)_2$, and $250 \text{ kg}\cdot\text{ha}^{-1} \text{ CaCO}_3$; the equivalent of 225, 155, and $33 \text{ kg}\cdot\text{ha}^{-1}$ of K, Ca, and Mg, respectively. The remaining three plots were left as control. Broadcast fertilizer was applied by hand as fine particulate matter in June 1989 (Hendershot and Courchesne 1994; Fyles et al. 1994). Figure 1

shows the experimental design and plot orientations. Plots 1 and 4 are downslope of the other four plots as there is a low southeast-facing slope running through the experimental stand.

For each year of sampling (1988-1991 and 2011-2012) mid-canopy leaves were sampled, and diameter at breast height (DBH) of the co-dominant and dominant sugar maple trees was recorded, with the exception of 2011, in which no growth measurements were taken. In 2012 sugar maple trees were cored for growth assessment, understory vegetation was surveyed to assess the plant community structure, and understory leaves and soils were sampled (Table 3). The following sections outline how each type of sample was obtained and processed.

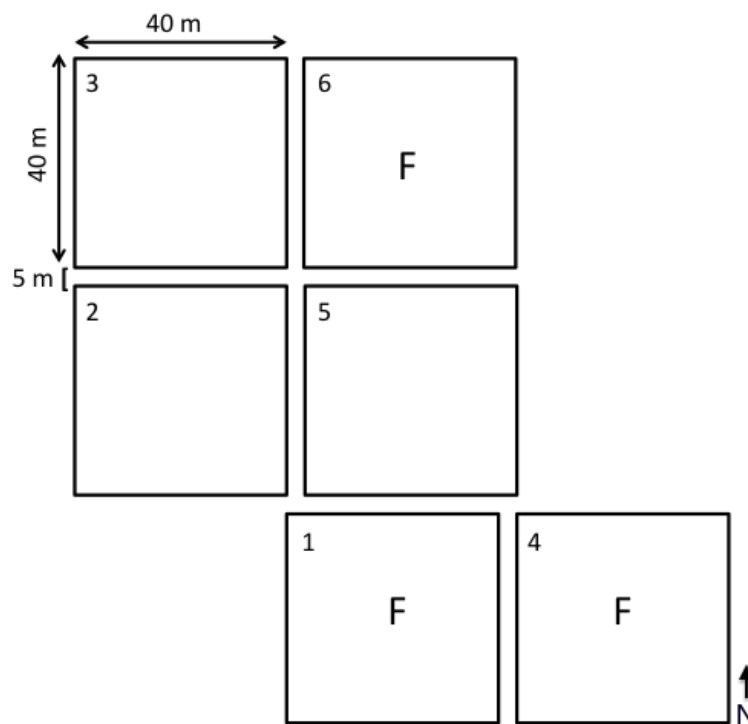


Figure 1 Experimental design: fertilized plots (F) were assigned randomly and treated once with a mixture of 500, 250, and 250 kg·ha⁻¹ of K₂SO₄, CaMg(CO₃)₂, and CaCO₃ respectively.

Table 3 List of ecosystem components sampled in each year of sampling

Component	1988	1989	1990	1991		2011	2012
Sugar maple leaves	✓	✓	✓	✓		✓	✓
Sugar maple DBH	✓	✓	✓	✓			✓
Sugar maple cores							✓
Vegetation survey							✓
Understory leaves							✓
Soil							✓

4.3 Sugar maple trees

4.3a Leaves

Mid-canopy leaves of 60 dominant and co-dominant sugar maple trees - 10 in each plot - were sampled each year in mid-August from 1988-1991 and again in 2011 and 2012. In 2011, not all trees were found as the tags had broken or fallen off the tree and were therefore difficult to find. The missing study trees were found by going back in the spring of 2012 when the forest was more open and the tags more visible. Those missing trees were then given new tags and sampled in the late summer of 2012. To assess the change in leaf chemistry using a complete dataset, the long-term results of this experiment are based on the pooling of the samples taken in 2011 and 2012.

Leaves were sampled by the same researcher each year using an aluminum telescopic tree pruner. Leaf samples were made of at least 20 leaves. They were brought back to the lab in a paper bag, dried at 65 °C to a constant weight, and ground with petioles intact. Samples were ground using a Cyclotec™ 1093 Sample Mill that ground the samples into a fine powder. The machine was cleaned between samples and then flushed with some of the next sample's leaves before the powder was collected to minimize contamination between samples. Control leaves were all ground before fertilized leaves for the same reason. For the digestion, 0.15 g of leaf samples were weighed and placed in an open glass test tube (Pyrex 9860 rated for 500 °C) only used for plant material and previously acid washed. Two ml of trace metal grade HNO₃ was added to each test tube and samples were left to sit overnight (~15 hrs) covered with a sheet of Parafilm® to avoid any contamination from the air. The following day, the test tubes were placed into a heated block and the temperature was gradually increased to 120 °C with occasional stirring. After five hours, the temperature was brought back down to room temperature and the samples were diluted to 50 ml with nano-pure water. K, Ca, Mg, and Rb concentrations were then determined by inductively coupled plasma mass spectrometry (ICP-MS) after an additional 5 times dilution with the nano-pure water. Each digestion batch was evaluated with a certified standard (Peach leaves no. 1547, National Institute of Standards and Technology). Average recovery for quality controls based off the peach leaf standard was 108, 108, and 90 % for K, Mg, and Ca, respectively. A sub-sample of digests was also tested using flame atomic absorption spectroscopy (AAS) to ascertain the Ca concentrations determined with the ICP-MS.

4.3b Diameter growth

Growth measurements of sugar maple trees were taken in the field using dendrometer bands from 1988-1991. Bands were placed at 1.3 m above ground and measurements were taken at the end of each growing season. During the 2012 field season, diameter at breast height (DBH) was measured using a DBH tape and cores were taken from each sugar maple tree at 1.3 m above ground. Cores were placed in plastic straws in the field and stored in a freezer immediately upon returning to the laboratory to minimize fungal growth. Immediately preceding processing, cores were taken out of the freezer and an Exacto knife was used to slice lengthwise across the core and expose the growth rings. Cores were placed on a scanner and WinDENDRO was used to determine tree ring width. Increment cores were cross-dated before growth analysis was performed.

Relative basal area growth, which is a growth measurement independent of tree size (Carlson et al. 2008), was calculated using two different approaches. The DBHs were used to calculate the relative basal area growth of each tree in control and fertilized plots in 2012, by taking the ratio of the tree basal area in 2012 to the tree basal area in 1988 (pre-fertilization). Basal area was calculated using the following formula.

$$Basal\ area = \pi \times \frac{DBH^2}{4}$$

Relative basal area growth was also calculated using the increment cores. The radial increment of all the trees in each treatment was converted to a basal area increment, then averaged for the period of 1979 to 1988 to obtain a 10-year pre-fertilization average growth for each treatment.

Annual relative basal area growths were then obtained by dividing each post-fertilization year by the average of 1979-1988. Using the average rate of growth before fertilization as a covariate allows me to evaluate the direct effect of fertilization on tree growth as doing so reduces the plot effects and any natural variation in growth.

Having two methods for assessing the growth response to fertilization in this stand provides me with a more robust assessment of the short and long-term growth response. The DBH method was used so I could expand the method deployed by the original researchers, using their starting diameters as my baseline. The increment cores were used to assess growth during each of the 22 years following fertilization.

Once each core was measured for growth, the sapwood - essentially the sections of the core post fertilization - was chopped up into small pieces using a ceramic knife. Samples were air dried, weighed and digested following the same procedure as for the sugar maple leaves using 0.15 g samples. They were then analyzed for K, Ca, Mg, and Rb by inductively coupled plasma mass spectrometry (ICP-MS).

4.3c Edge effects

In 2012, the position of individual study trees relative to the centre of the plot was obtained using a compass and a Haglof ultrasound vertex as a distance tracker. One observer stood in the centre of the plot, while the other (runner) went around to each tagged tree. The runner took the angle from each tree to the centre, while the observer took the distance from the center to the tree by pointing the hand-held ultrasound device to the receiver being held by the runner. The location of

trees was used to assess the effect of tree location within plots on the percent of K derived from fertilizer to determine if edge trees take up as much fertilizer as trees with roots completely confined in the plot. This was done by plotting the percent of K derived from fertilizer of each treated tree by the distance of the tree from the nearest edge of its plot and assessing if the slope of the relationship was significant. If the slope of the relationship changes as distance from edge increases, an edge effect is occurring.

4.4 Soil

4.4a Pit selection and sampling

Two soil pits 50 cm deep and at least 10 m apart were dug in each plot. Soil pits were at a minimal distance of 5 m from the edge of a plot, and 2 m from a sugar maple tree to avoid roots. For each pit, individual soil horizons were identified, their depth was measured, then sampled. Samples were stored in a Zip-loc bag in the field, and air-dried to a constant weight once back in the laboratory. Horizons were identified by the visual break between layers of soil, not necessarily according to depth. Horizons were labeled with increasing depth, as L, F, Ahe, B1, B2, and B3. B horizons correspond to mineral soil, and the other three labels were organic.

4.4b Extraction

When dried, soil samples were gently ground using a wooden rolling pin to break-up large soil aggregates, then passed through a 2 mm sieve, and extracted with 1 M trace metal grade NH_4Cl . More specifically, organic (1.0 g) and mineral (2.5 g) samples were extracted with 25 ml of NH_4Cl on an end-over-end shaker for 1 hour. Samples were then centrifuged at 5000 rpm for 10 minutes and filtered through a 0.45 μm GE Magna nylon membrane filter hooked up to vacuum

suction. Extractions were refrigerated until analysis (for no more than one week). Concentrations of K, Mg, Ca, and Rb were determined with ICP-MS. Two internal standards previously collected and verified from a neighbouring experiment were used as quality controls.

As it is not just the absolute, but relative abundance of nutrients to each other that may influence plant community composition and growth (Tripler et al. 2006), an expansion of these analyses to include the nutrient ratios in the soil profile and sugar maple leaves was done. Saturation in this case refers to the relative proportion of one base cation to the total of all bases measured (K, Ca, Mg, and Mn).

4.5 Understory vegetation

4.5a Diversity

In 2012, understory vegetation species were surveyed along two 40 m transects using a 1 m² fixed area circle at 1 m intervals along the transect. This represented an area of 115 m² and 110 m² for control and fertilized plots, respectively; falling within the recommended minimum area of 50-200 m² needed to capture the true description of undergrowth in temperate forests (Mueller-Dombois and Ellenberg 1974). At each point along the survey, the species and percent coverage were noted using the Braun-Blanquet method (Braun-Blanquet 1932, 1964).

The list of species from these surveys was then used to calculate the species diversity of each treatment. Diversity was measured two ways: as species richness, and using the Sorensen index. Species richness is the simplest way to describe community diversity, and is purely the number of species present in a specific area. The Sorensen Index is a measure of beta (β) diversity, and is computed by comparing the similarity of two groups. When the following formula produces a

β that is equal to 0, there is no species overlap and when β is equal to 1 there is complete species overlap (Sørensen 1948).

$$\text{Sorensen Index } (\beta) = \frac{2C}{S_1 + S_2}$$

Where...

C = the number of species common to both samples

S_1 = the number of species present in sample 1

S_2 = the number of species present in sample 2

The percent coverage and list of species were also used to determine ten of the most abundant and ubiquitous species from three groups of vegetation (herbaceous, ferns and allies, and woody) that would be chosen for sampling, and chemical analyses for leaf K concentrations and percent of K derived from fertilizer using the Rb/K reverse tracer method.

4.5b Digestion

Sampling of understory plants for chemical analysis involved collecting five healthy individuals or leaves of larger individuals of each species located within a 15 m radius of the centre of each plot. Samples were collected within these small areas to avoid any possible edge effects of treatment. Individuals with damaged or discoloured foliage were avoided where possible. Samples were immediately stored in paper bags and air-dried to a constant weight once in the laboratory. Because of the small size of most samples, they were ground using a three-tier system: the first stage was to crush leaves inside the paper bag used to collect and dry them, then

samples were cut using a knife with a ceramic blade (to minimize metal contamination). Samples that were too coarse to process were then ground using a coffee grinder. Once samples were deemed an appropriate size for digestion, 0.15 g were weighed and digested using the same methods as with the sugar maple leaves. Although using a coffee grinder may introduce metal contamination in our samples, replicates and quality controls showed no sign of this. If there had been a contamination, we would have seen large spikes in the concentrations of metals, which we did not.

4.6 Rubidium/Potassium Reverse Tracer Method

In order to validate the use of the Rb/K reverse tracer, I tested samples of the original fertilizers used in this experiment for the concentration of Rb using an ICP-MS. The fertilizers should contain, if any, only small amounts of Rb and therefore have a very small Rb/K ratio to maximize the efficiency of the reverse tracer method. The average ratio of Rb/K in the fertilizer mixture was found to be 0.0001, which is 105 times lower than the Rb/K ratio in the native (control) soil. As the amount of Rb is extremely low, and significantly lower than that of the soil, I can confirm that this technique is a valid approach to differentiate the source of K and compare the differences between fertilized and control samples. Therefore, the percent of K found in a tissue that came from a fertilized plot was calculated using the following formula from Hafez and Stout (1973):

$$\% K \text{ from fertilizer} = \frac{[Rb]/[K]_{\text{control}} - [Rb]/[K]_{\text{fertilized}}}{[Rb]/[K]_{\text{control}}} \times 100$$

4.7 Long-term retention of potassium derived from fertilizer in the soil/plant system

The average concentration of potassium in treated trees (leaf and wood), soils, and understory as well as the percent of K derived from fertilizer in each part of the system was used to calculate the amount of K stored in the soil-plant system in 2012 that came from the fertilizer. In other words, how much of the original fertilizer is held in the plant tissues of sugar maple, understory species, and soils 23 years after fertilization. The amounts of K from fertilizer in the soil plant compartments were calculated by averaging the product of the concentration of K in the respective tissues by the % K derived from fertilizer and then by the estimated mass of that tissue per hectare.

$$\text{Amount of K} = [K] \times \% K \text{ from fertilizer} \times \text{mass}$$

For the leaves of sugar maple, the mass was estimated using the amount of litter fall at this site (3500 kg·ha⁻¹) provided by Fyles et al. (1994). I am assuming litter fall to be approximately equal to live leaf mass although this is a slight underestimate. Some of the nutrients and sugars, and consequently a significant proportion of the weight of leaves, are taken back by the tree before falling to the ground, so the weight of the leaves measured as litter fall will be less than the weight of the leaves on the tree.

For the sapwood, the volume of fertilized trees was calculated using the diameters obtained in 2012 according to the following allometric equation (Richard et al. 2001, pp.9).

$$Volume (dm^3) = 7.5092 - 2.3793097H + 0.0336075D^2H$$

Where...

H = height in m

D = DBH in cm

The mass was estimated by multiplying the volume by a factor of 41% (the proportion of basal area I sampled) then by the density ($0.68 \text{ g}\cdot\text{cm}^3$) of dry sugar maple wood (U.S.D.A. 2007) and converted to a per hectare basis.

The soil mass per hectare was estimated by multiplying the bulk density of each horizon by the volume of each horizon. Volume was obtained by multiplying the depth of a horizon by the area of one hectare. The amount of extractable K derived from fertilizer is the product of the soil mass, average concentration of K, and percent K derived from fertilizer for each horizon. The amount of K derived from fertilizer for each horizon was then summed to obtain a value for the full soil profile. The final estimate for soil extractable fertilizer K was multiplied by a factor of 75 % to account for my estimate of 25 % in coarse fragments (rocks, roots, etc. > 2 mm) in the soil.

Understory K ($\text{kg}\cdot\text{ha}^{-1}$) from fertilizer was estimated using the biomass of $232 \text{ kg}\cdot\text{ha}^{-1}$ reported by Whittaker in Cole and Rapp (1980). This estimate is based from the increment biomass ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) of understory vegetation growing under a 60-year-old maple-birch-beech mixed forest growing on a soil classified as podzolic-haplortod at Hubbard Brook Experimental Forest, New Hampshire (Whittaker 1980). The biomass was multiplied by the average percent K derived

from fertilizer and average leaf K of all understory species to get the amount of K derived from fertilizer located in the understory vegetation. No discrimination for group of vegetation (herbaceous, ferns and allies, woody) was possible.

4.8 Statistical Analyses

Ideally, tree nutrition would have been analyzed with a repeated mixed measures protocol, but as the data was not complete due to compromised labeling of the dominant and co-dominant trees, nutrition data was analyzed with a random mixed model ANOVA focusing on treatments at each year (instead of over time). The analysis was conducted for each year separately, with the exception of 2011 and 2012, which were combined. The percent of K derived from fertilizer was assessed using an unpaired t-test, testing whether the mean of each year was different than zero and then whether each year was different than the others.

Tree core growth was analyzed using a repeated mixed measures, looking at the effect of treatment over time. Tree basal area growth from diameter readings between 2012 and 1988 was assessed with an unpaired t-test. Basal area growth should have also been assessed using repeated mixed measures but as with the leaves, labeling was compromised.

For the understory vegetation, I used (i) a random mixed model ANOVA for the chemistry, (ii) a distribution statistic for the percent K from fertilizer, and (iii) a discrimination analysis for the understory vegetation diversity. The discrimination analysis was based on the percent coverage (used as a proxy for abundance) of individual understory vegetation species measured during the vegetation survey.

For soils, I used a repeated mixed measures analysis as each horizon cannot be considered independent of the one above. The result of this analysis therefore focuses on the effect of the treatment at each horizon. The difference in the nutrient ratios and soil Ca and Mg saturation between control and fertilized plots was assessed using a random mixed model ANOVA.

All analyses were done in JMP 10 with the exception of the unpaired t-tests, which were performed in GraphPad Prism 6.

5.0 Results

5.1 Nutrient cycling

Fertilization increased leaf K concentration in sugar maple trees in the second and third year following fertilization, and the fall of the year of fertilization, but there was no difference in the leaf K concentration between treatments 23 years after fertilization (Fig. 2). Leaf Ca and Mg concentrations were only higher in fertilized plots in the year of fertilization (Fig. 2) with Ca concentration becoming higher in control plots by 1991 while leaf Mg showed no other significant effects of fertilization. There was no significant difference in K concentration of sapwood between control ($0.64 \pm 0.03 \text{ mg} \cdot \text{g}^{-1}$) and fertilized ($0.63 \pm 0.03 \text{ mg} \cdot \text{g}^{-1}$) trees sampled in 2012 ($p > 0.5$). As for understory plants sampled in 2012, striped maple was the only species that showed a significant difference in leaf chemistry with leaf K being higher in fertilized plots (Table 6).

Soil extractable K, Mg, and Ca decreased with increasing depth in both control and fertilized plots (Fig. 3). According to the repeated measures, there was no overall significant difference between treatments for either the whole soil profile or individual horizons for any of the three nutrients, although all three nutrients tended to be higher in fertilized plots. P-values for K, Mg, and Ca were 0.1 - 0.9, 0.2 - 0.6, and 0.1 - 0.8, respectively.

The K/Ca ratio of leaves in fertilized plots increased following fertilization, and continued to be higher in treated than in control plots 23 years after fertilization (Fig. 4). The ratio of K/Mg in leaves of fertilized plots was higher than in control plots in 1990 and 2011/2012 whereas Mg/Ca was only higher in fertilized plots in 1991 (Fig. 4). For soils, the only two nutrient ratios that were different in control and fertilized plots in 2012 were K/Ca in the B1 horizon and Ca/Mg in the L (Table 4). There was no difference between percent saturation in control and fertilized plots for either Ca or Mg (Table 5).

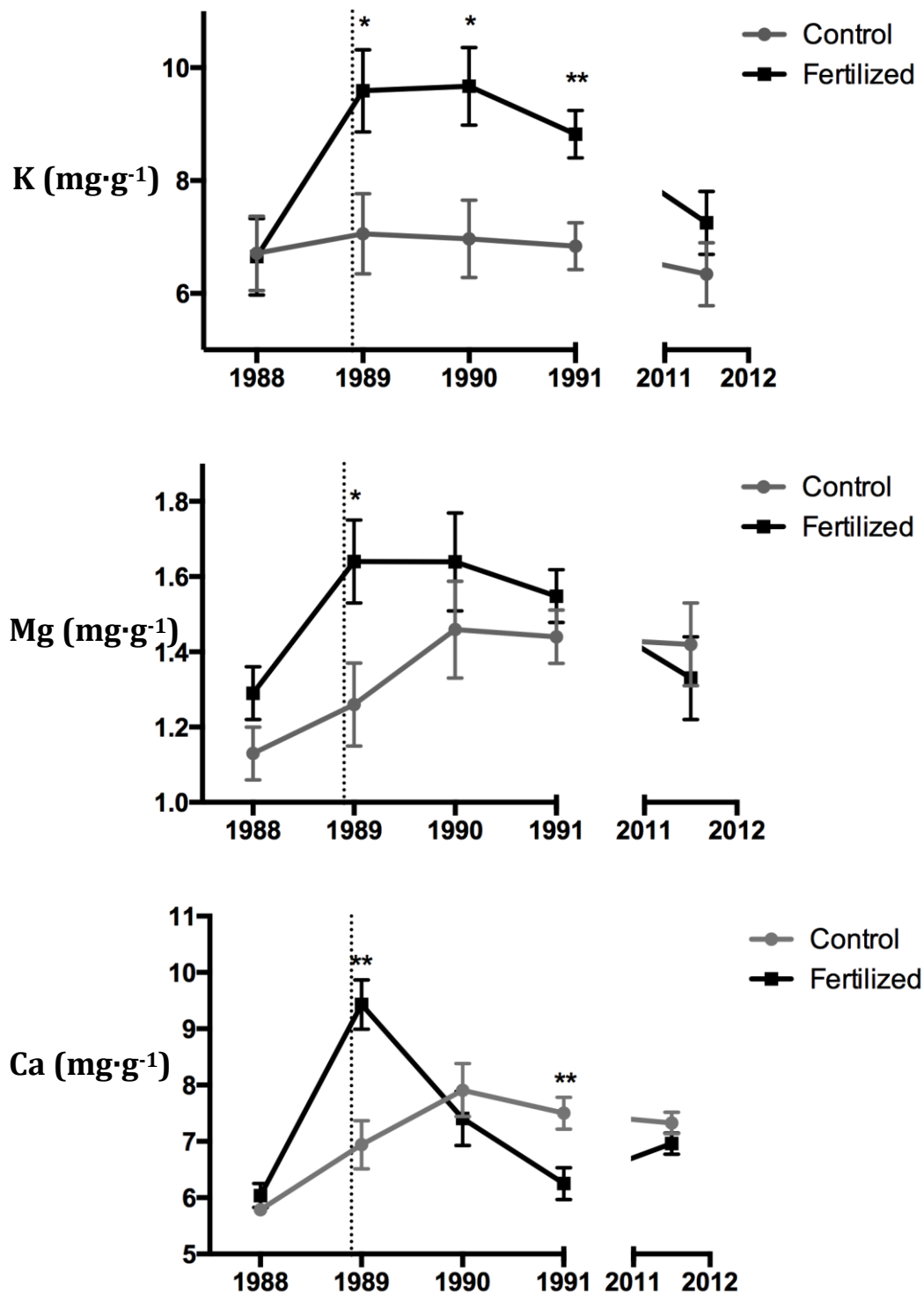


Figure 2 Leaf K, Mg, and Ca concentration of sugar maple in control and fertilized trees. Error bars represent the standard error of means. The dashed line is when fertilization occurred relative to leaf sampling. * $p < 0.1$, ** $p < 0.05$.

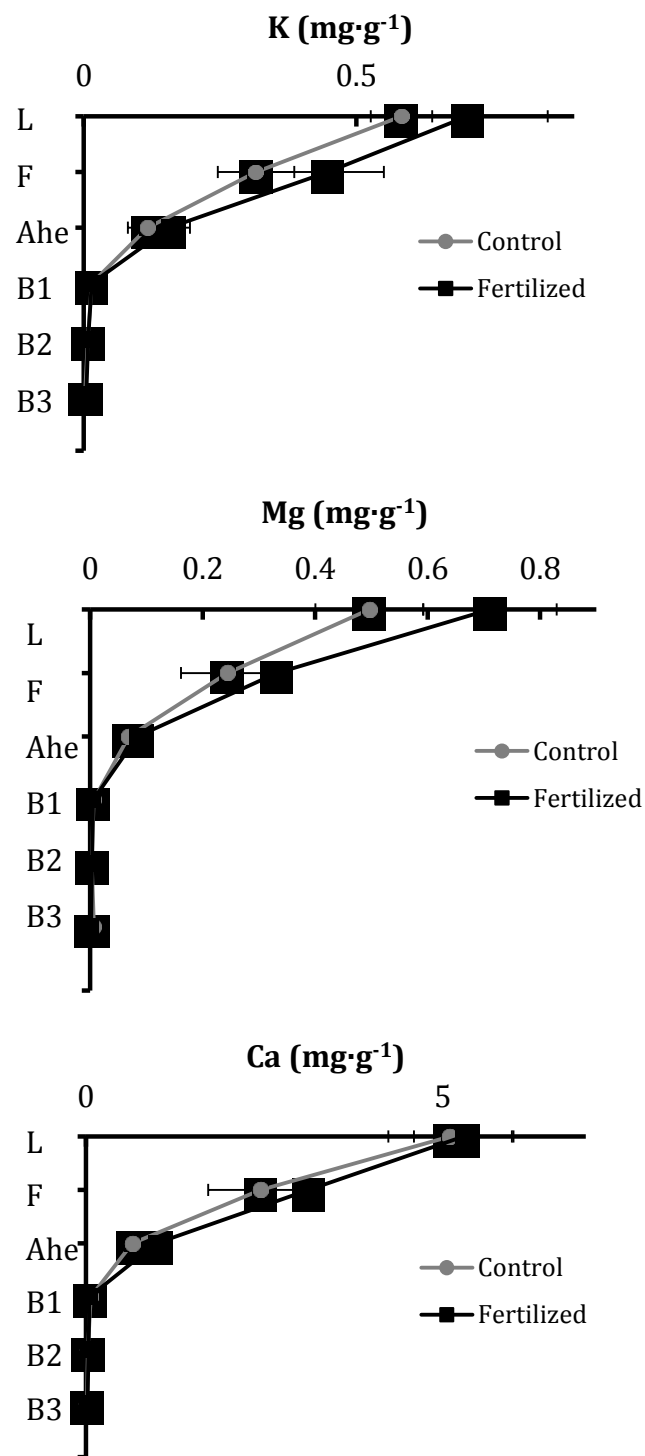


Figure 3 Extractable soil K, Mg, and Ca of each horizon in control and fertilized plots in 2012. Note: Ahe= 0-2 cm, B1= 3-10 cm, B2=11-40 cm and B3 = 41-50 cm

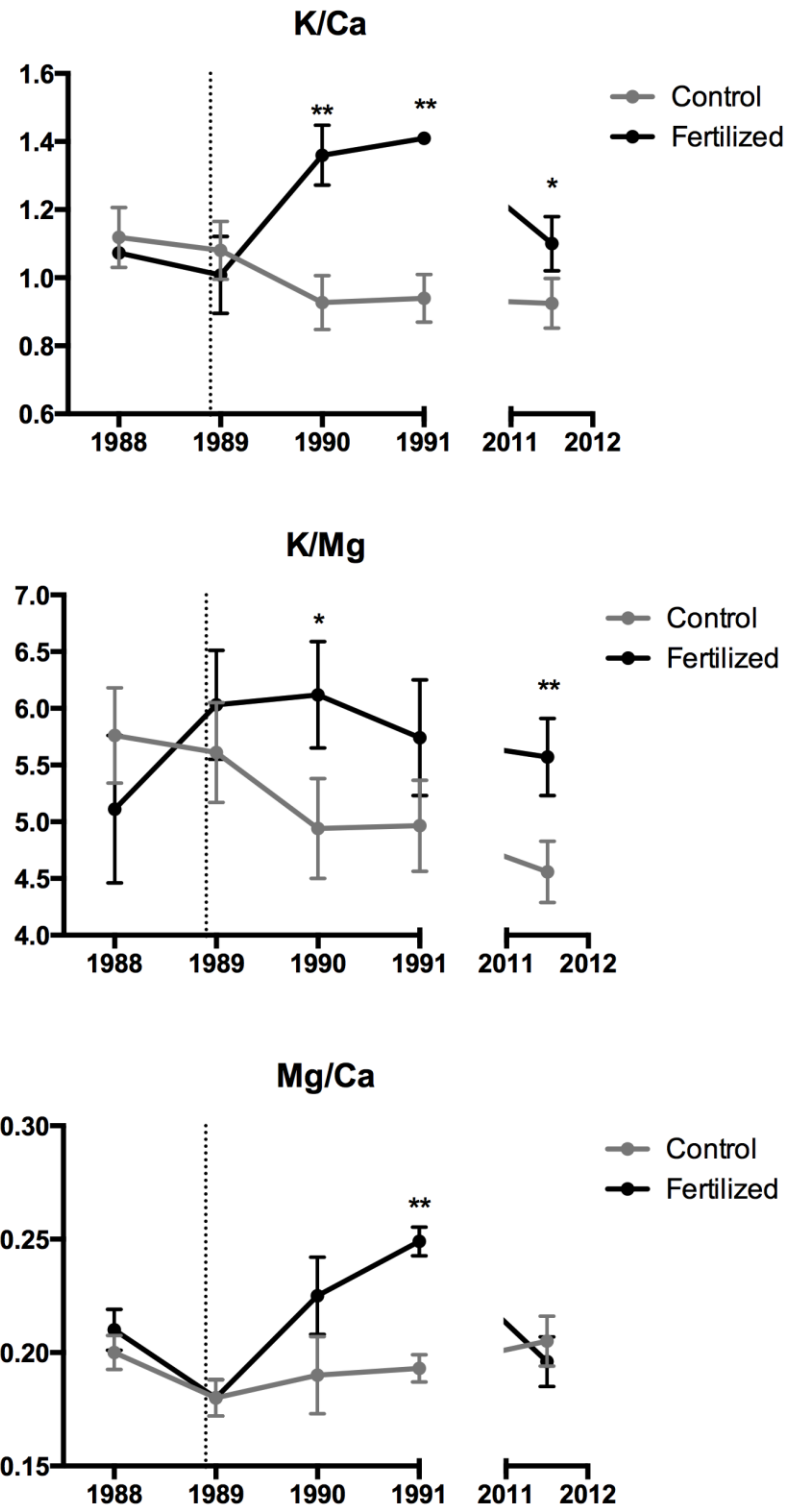


Figure 4 Leaf nutrient ratios of sugar maple trees for each year of sampling.

* $p < 0.1$, ** $p < 0.05$.

Table 4 Soil nutrient ratios (W/W) in control and fertilized plots in 2012.

Horizon	K/Ca		K/Mg		Ca/Mg	
	Control	Fertilized	Control	Fertilized	Control	Fertilized
L	0.11 (0.02)	0.12 (0.01)	1.2 (0.21)	1.0 (0.1)	10.3 (0.5)	7.7 (0.4)**
F	0.14 (0.03)	0.14 (0.03)	1.4 (0.2)	1.3 (0.2)	10.2 (0.9)	9.5 (0.9)
Ahe	0.18 (0.02)	0.15 (0.02)	1.8 (0.5)	2.0 (0.5)	9.7 (1.8)	12.1 (1.8)
B1	0.22 (0.02)	0.29 (0.01)**	2.4 (0.3)	3.1 (0.3)	10.9 (0.5)	10.7 (0.4)
B2	0.27 (0.05)	0.21 (0.05)	3.4 (0.6)	2.3 (0.6)	13.3 (2.1)	10.5 (2.1)
B3	0.17 (0.03)	0.22 (0.04)	3.5 (1.0)	4.3 (1.3)	19.6 (2.2)	18.5 (2.7)

*Note: The values are the mean of three replicates for each horizon, with SE given in parentheses. ** $p < 0.05$. B3 is the deepest soil horizon.*

Table 5 Soil percent saturation in control and fertilized plots in 2012

Horizon	K saturation		Ca saturation		Mg saturation		Mn saturation	
	Control	Fertilized	Control	Fertilized	Control	Fertilized	Control	Fertilized
Ahe	9.3 (1.2)	7.0 (1.2)	74.3 (1.2)	77.7 (1.2)	13.0 (0.6)	13.0 (0.6)	3.3 (0.7)	2.4 (0.7)
B1	9.2 (1.2)	10.2 (1.2)	76.7 (2.6)	78.2 (2.3)	12.4 (1.4)	10.8 (1.2)	1.8 (0.3)	0.8 (0.3)

Note: The values are the mean of three replicates for each horizon, with SE given in parentheses.

Percent saturation was calculated with the omission of Al.

Table 6 Leaf K concentration of understory plant species in 2012.

Species	Control (mg·g ⁻¹)	Fertilized (mg·g ⁻¹)
<i>Acer pensylvanicum</i> (striped maple)	9.8 (0.6)	12.6 (0.5)**
<i>Acer saccharum</i> (sugar maple)	7.4 (0.7)	9.1 (0.7)
<i>Aralia nudicaulis</i> (wild sarsaparilla)	15 (2.2)	17 (2.3)
<i>Corylus cornuta</i> (beaked hazel)	8.3 (0.2)	8.1 (0.3)
<i>Dennstaedtia punctilobula</i> (hayscented fern)	24 (1.0)	26 (1.2)
<i>Dryopteris disjuncta</i> (oakfern)	29 (2.3)	29 (2.3)
<i>Lycopodium obscurum</i> (rare clubmoss)	9.1 (0.2)	9.7 (0.2)
<i>Maianthemum canadense</i> (Canada mayflower)	29 (2.5)	31 (2.5)
<i>Trientalis borealis</i> (starflower)	16.7 (0.8)	16.6 (0.7)

*Note: The values are the mean of 15 replicates for each treatment, with SE given in parentheses. ** $p < 0.05$.*

5.2 Percent of potassium derived from fertilizer

Significant amounts of K derived from fertilizer were measured in the leaves of fertilized sugar maple trees for every year after fertilization. The percent K from fertilizer increased from 1989 to 1991 to reach a maximum of 36 %. By 2012, the percent K from fertilizer was 15 ± 2 % in the leaves and 27 ± 2 % in the sapwood of sugar maple. As a group, fertilized trees had different

percentages of K derived from fertilizer between study years with the exception of the comparison of 1989 and 1990 ($p > 0.1$) and 1989 and 2011/12 ($p > 0.2$).

The percent of K derived from fertilizer in understory plants ranged from 8 % in *Dryopteris* to 29 % for *Maianthemum* with sugar maple saplings/seedlings having similar values to the ones observed for mature trees (Table 7).

The percent of K from fertilizer increased non-linearly with the distance from the edge of the plot, with the highest percent of K derived from fertilizer located in the middle of the plots. No trend in percent of K from fertilizer was detected within the first 8 m from the edge with trees averaging 11 % K from fertilizer. Further in the plots, percent K increased linearly to reach a maximum of 47 % K from fertilizer close to the centre (Fig. 6).

There were significant amounts of K derived from fertilizer for three (Ahe, B2 and B3) of the six horizons sampled (Fig. 7). The percent of K from fertilizer was between 10-20 % down to the first mineral horizon (B1) before increasing with depth in the B2 and B3 horizons. The highest percent K derived from fertilizer (48 %) was observed in the deepest horizon sampled (B3).

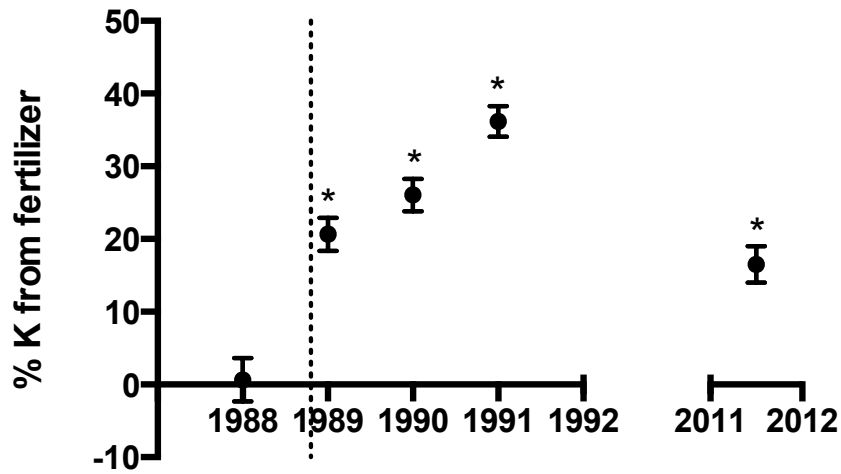


Figure 5 The percent of leaf K derived from fertilizer in sugar maple trees. The dotted line denotes the time of fertilization. $*p < 0.0001$ signifies if the average in each year was different from zero.

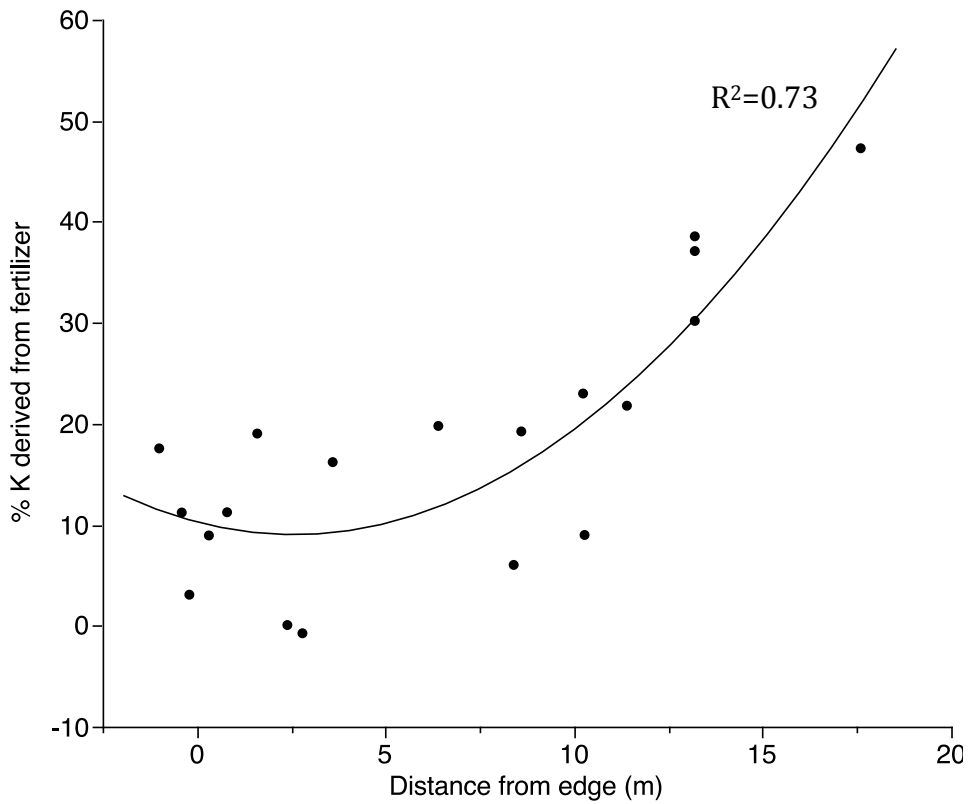


Figure 6 The percent of leaf K derived from fertilizer as a function of the distance from the nearest edge of the fertilized plots for the years 2011 and 2012 (N = 19 trees).

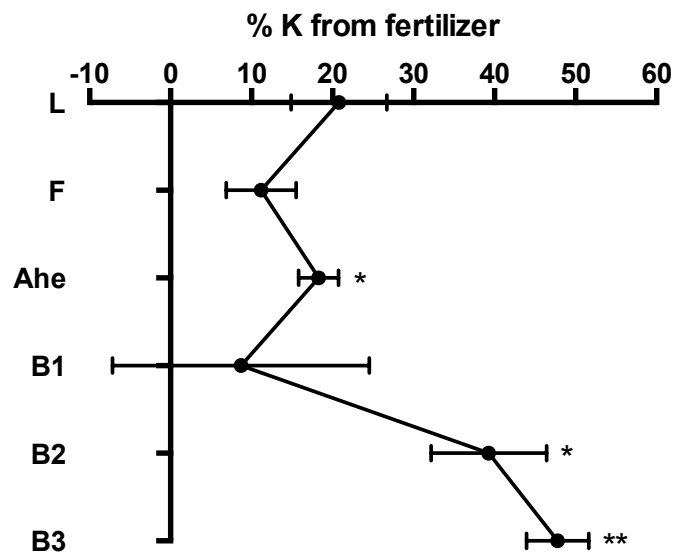


Figure 7 The percentage of extractable soil K derived from the fertilizer in 2012. * $p < 0.05$, ** $p < 0.01$. Note: B3 is the deepest soil horizon

Table 7 Percent of leaf K derived from fertilizer in understory plants in 2012.

Species	% K from fertilizer
<i>Acer pensylvanicum</i> (striped maple)	26 (3)*
<i>Acer saccharum</i> (sugar maple)	15 (3)*
<i>Aralia nudicaulis</i> (wild sarsaparilla)	13 (4)*
<i>Corylus cornuta</i> (beaked hazel)	22 (4)*
<i>Dennstaedtia punctilobula</i> (hayscented fern)	25 (3)*
<i>Dryopteris disjuncta</i> (oakfern)	8 (3)*
<i>Lycopodium obscurum</i> (rare clubmoss)	27 (4)*
<i>Maianthemum canadense</i> (Canada mayflower)	29 (2)*
<i>Trientalis borealis</i> (starflower)	25 (4)*

*Note: The values are the mean of 15 replicates, with SE in parenthesis. * $p < 0.05$, Testing for mean > 0 .*

5.3 Long-term retention of potassium derived from fertilizer

In total, $54 \pm 5.2 \text{ kg} \cdot \text{ha}^{-1}$ or 24 % of the original fertilizer applied was accounted for in the soil-plant pools sampled in 2012 (Table 8). The majority (57 %) of the recovered fertilizer-K was found in the soil, with comparable amounts from the organic (53 %) and mineral horizons (47 %). Sugar maple leaves and sapwood, and understory leaves accounted for 9, 18, and 16 %, respectively.

Table 8 Recovery of K fertilizer in the soil-plant system in 2012.

Section of soil-plant system	K from fertilizer ($\text{kg} \cdot \text{ha}^{-1}$)
Sugar maple tree leaves	4.7 ± 0.1
Sugar maple tree sapwood	9.6 ± 0.8
Soil (extractable fraction)	31 ± 2.3
Understory	8.6 ± 2.0
Total	54 ± 5.2

Note: the initial amount of K applied with fertilization was $225 \text{ kg} \cdot \text{ha}^{-1}$

5.4 Sugar maple growth

Using tree diameters taken in 1988 and in 2012, I found no difference in the relative basal area growth of control (1.4 ± 0.1) and fertilized (1.2 ± 0.2) plots. Furthermore, when the data from the cores was used, the repeated measures showed no effect of treatment on growth (Fig. 8).

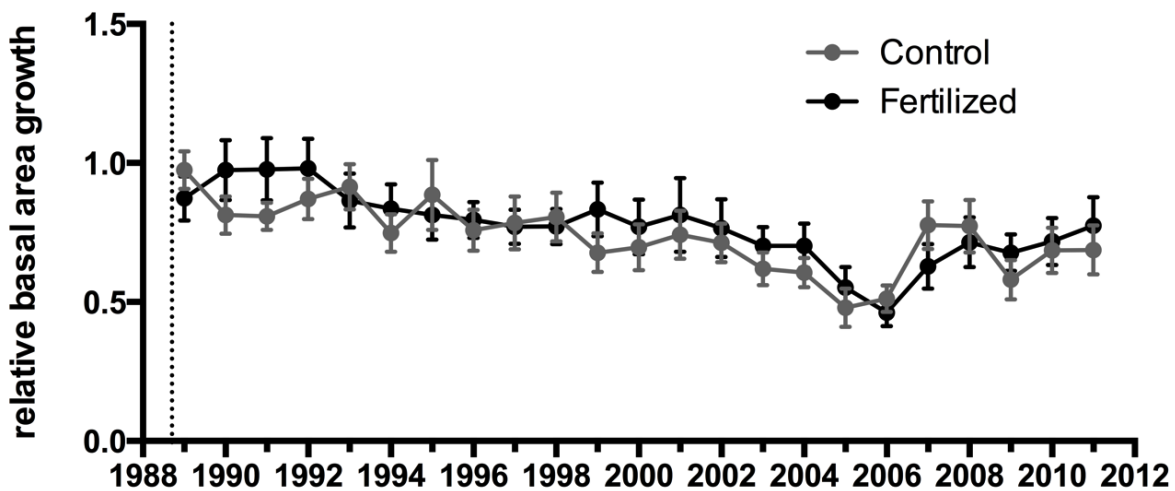


Figure 8 Relative growth of basal area in sugar maple trees using data from core samples taken in 2012. Values are relative to pre-fertilization (the average of 1979 to 1988). Error bars are the standard error of the means. The dashed line is when fertilization occurred.

5.5 Understory vegetation species diversity

There was no difference in the understory vegetation species richness between control (25 ± 1) and fertilized (23 ± 1) plots (Fig 9). The Sorensen index revealed that fertilized plots were no more dissimilar to control than they were to other fertilized plots and vice versa (Table 9). The range of similarity was between 67 % and 88 % (Table 10). As there was no difference in the species richness and Sorensen index between control and fertilized plots, I can conclude that there was no long-term effect of fertilization on understory plant diversity in my stand.

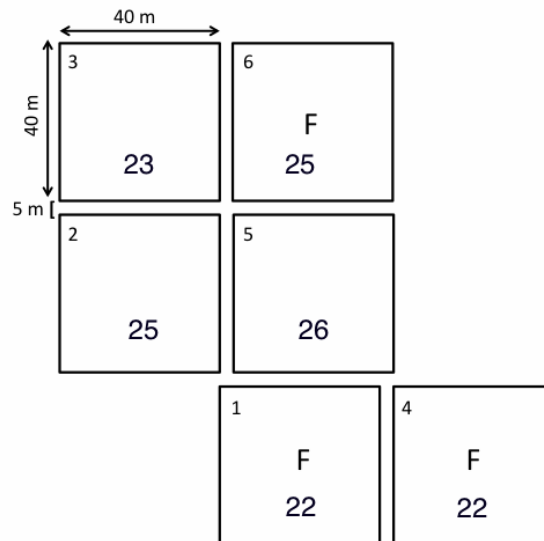


Figure 9 The species richness (number of species) in each plot.

Table 9 The Sorensen index for the average similarity between understory species in control and fertilized plots.

Sorensen Index	Control (%)	Fertilized (%)
Control	77 ± 5	79 ± 3
Fertilized	79 ± 3	75 ± 1

Table 10 The Sorensen index matrix for the similarity between individual plots. The closer the values are to 1, the more similar the two plots are.

	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6
Plot 1	1	0.81	0.76	0.73	0.67	0.77
Plot 2		1	0.88	0.72	0.71	0.88
Plot 3			1	0.80	0.73	0.88
Plot 4				1	0.88	0.77
Plot 5					1	0.71
Plot 6						1

Using a discriminant analysis, four species were found to discriminate between treatments. These species were striped maple, wild sarsaparilla, American beech, and rare clubmoss (Table 11). American beech, and striped maple occur with higher percent coverage in control plots while rare clubmoss and wild sarsaparilla are higher in the fertilized plots (Fig. 10). All four species occurred at more points along the vegetation survey transects of control plots than fertilized plots (Table 12). So although there was no long-term effect of fertilizer on the understory diversity, there was an effect on the percent coverage and count of some species.

Table 11 The ability of each understory species to discriminate between treatments in relation to percent coverage.

Species	F Ratio	Prob>F
<i>Abies balsamea</i> (balsam fir)	1.0	0.3
<i>Acer pensylvanicum</i> (striped maple)	8.0	0.005*
<i>Acer rubrum</i> (red maple)	3.0	0.09
<i>Acer saccharum</i> (sugar maple)	1.0	0.3
<i>Aralia nudicaulis</i> (wild sarsaparilla)	19.3	<0.001*
<i>Canadanthus spp.</i> (mountain aster)	3.6	0.06
<i>Corylus cornuta</i> (beaked hazel)	3.8	0.05
<i>Dryopteris disjuncta</i> (oakfern)	2.0	0.2
<i>Fagus grandifolia</i> (American beech)	4.8	0.03*
<i>Lonicera involucrata</i> (bearberry honeysuckle)	1.2	0.3
<i>Lycopodium annotinum</i> (stiff mossclub)	2.1	0.1
<i>Lycopodium complanatum</i> (groundcedar)	1.3	0.3
<i>Lycopodium obscurum</i> (rare clubmoss)	6.9	0.009*
<i>Rhamnus alnifolia</i> (alderleaf buckthorn)	1.2	0.3
<i>Trillium spp.</i> (trillium)	1.5	0.2
<i>Vaccinium spp.</i> (huckleberry)	1.3	0.3

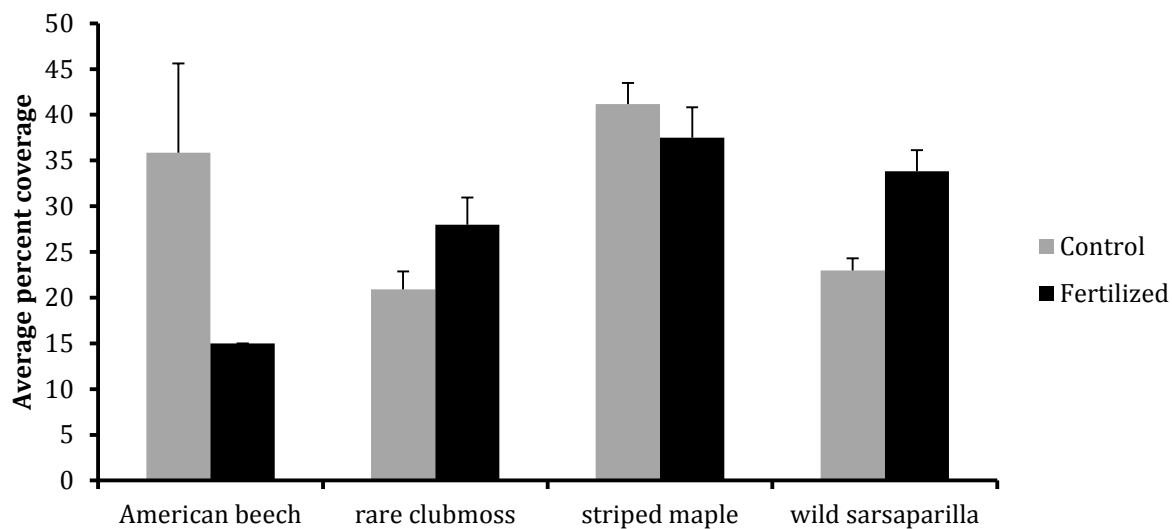


Figure 10 The percent coverage of each discriminating understory plant species in control and treated plots.

Table 12 The number of times each discriminating species occurred along all transects of each treatment.

Species	Control	Fertilized
<i>Acer pensylvanicum</i> (striped maple)	97	55
<i>Aralia nudicaulis</i> (wild sarsaparilla)	90	78
<i>Fagus grandifolia</i> (American beech)	10	1
<i>Lycopodium obscurum</i> (rare clubmoss)	49	25

Note: There were a total of 115 1-m² survey points along control vegetation transects and 110 along fertilized.

6.0 Discussion

6.1 Nutrient cycling

Prior to fertilization, the concentrations of K in sugar maple leaves were slightly above critical values but Ca, and Mg were both below (Côté et al. 1993). Following fertilization, K and Mg increased to above and/or near optimal concentration and remained so in the long-term (Fig 2). Ca rose to optimal concentration the second year following fertilization, but dropped back down in all measurement points thereafter. These results would suggest that the fertilizer improved K and Mg status of the trees, but was unable to correct Ca deficiencies over the long term.

It could be that the larger amounts of the more soluble K fertilizer displaced the Ca from exchange sites in fertilized plots as they added nearly twice the amount of K compared to Ca. This is supported by the nutrient ratio of K/Ca increasing in fertilized plots after fertilization (Fig. 4) and by the high loss of Ca in the soil solution compared to K in the first four years after fertilization (Hendershot and Courchesne 1994). The increase in the ratio means that there were greater amounts of K found in the leaves of sugar maple compared to Ca in the fertilized plots. This could be why there was comparably more Ca in control plots, as there was no K added to those plots to displace the Ca.

Côté et al. (1995) found that K_2SO_4 tended to increase foliar K in sugar maple, but when $CaMg(CO_3)_2$ was added to the mixture, foliar K decreased. It is therefore possible, that the addition of dolomitic lime to my plots limited the effect of the potassium fertilizer in terms of the uptake of K and furthermore the percent of K from fertilizer found in leaves of sugar maple trees.

Had lime not been applied I may have seen an even greater effect of treatment on K concentrations and percent of K derived from fertilizer in the leaves of sugar maple trees.

The lack of long-term effects of fertilization on the soil could be explained in part because there was only one single application of fertilizer and only one point of measurement 23 years after fertilization (Wilmot et al. 1996). Considering the mobility/solubility of K-fertilizer and to a lesser degree of Ca and Mg lime, it is likely that a large proportion of the added nutrients had been lost and that the system is back to its original nutrient status. It could also be that they did not apply enough fertilizer, as suggested by the lack of significant increase in soil solution pH in the first four years after fertilization (Hendershot and Courchesne 1994). The one-time fertilization corresponded to 9.7, 6.7 and 1.4 kg ha⁻¹ yr⁻¹ of K, Ca and Mg, respectively. These amounts may not have been enough to compensate for the accelerated loss of Ca and Mg associated with acid deposition in the late 1980s. Finally, soils are known for their spatial heterogeneity and the soils at my site were no exception (Hendershot 1991). If more soil samples had been taken to minimize spatial variation, I would likely not have measured higher fertilizer-K, Ca and Mg retained in the soil, but I may have been able to detect a small but significant effect of fertilization on base cation availability. It is suggested that future studies place greater effort on the extent of their soil sampling.

6.2 Percent potassium derived from fertilizer

As the pH of the soil solutions in my stand did not increase dramatically following the initial application of fertilizer and lime (Hendershot and Courchesne 1994), it is unlikely that the soil pH would have an influence on the content of K, and as such my estimates for the percent of K

derived from fertilizer should be sound. The Rb/K tracer therefore allowed me to see a long term effect of fertilizer on sugar maple trees, showing that although there was not a significant difference between the concentration of foliar K in control and fertilized plots in 2012, there was still a significant amount of K present that had originated from the fertilizer. Moreover, the percent of K derived from fertilizer increased simultaneously to increases in concentrations of K in leaves of sugar maple trees from 1989-1991, a good demonstration that the method works. The immediate response in 1989 is likely attributable to the high solubility of the K_2SO_4 used in the fertilizer (Hendershot and Courchesne 1994). The large jump from 1989 to 1991 ($p < 0.001$) in the percent of K derived from fertilizer may mirror the time it took for the fertilizer to move down the soil profile into the rooting zone of sugar maple trees and/or represent an increased K cycling due to treatment (Hendershot and Courchesne 1994). It would have been ideal to sample more years continuously to determine how long or if the increase would have continued.

Sugar maple sapwood, soil, and understory leaves also showed a significant amount of K originating from fertilizer in present day samples. This high proportion of fertilizer-K without a similar increase in leaf K concentration suggests that the fertilizer has displaced the native K from the soil exchange sites. K, Ca, and Mg can all be displaced following fertilization when the cations in fertilizers enter soil solution and displace native cations from the surface of the soil particles, which is likely as the total amount of fertilizer applied was relatively high for forest fertilization (Vadeboncoeur 2010; Tripler et al. 2006). This is supported by the higher amounts of K, Ca, and Mg found in the soil solution of fertilized plots during the first four years after fertilization (Hendershot and Courchesne 1994).

The average percent of K derived from fertilizer was 12 % higher in wood than in leaves of sugar maple in 2012. I hypothesize that the wood is higher in fertilizer-K than the leaves because of the longer residence time of K in the wood and thus the ability of the wood to hold on to the K it had previously taken up. In contrast, leaves have to replenish most of their K on a yearly basis. The fertilizer-K in understory leaves of sugar maple on the other hand, was similar to the fertilizer-K in mature sugar maple leaves, suggesting that the understory sugar maple are taking up K from a similar pool, possibly via sugar maple intraspecific root grafting (Godman 1990). Although the percent of K derived from fertilizer was highest in the deeper horizons (Fig. 7), the actual concentration of K in those horizons was extremely small (Fig. 2), so there is actually more fertilizer-K in upper horizons. This may be why there is a higher percentage of K derived from fertilizer in the shallower rooting understory plants compared to the mature sugar maple trees. This higher percent of K derived from fertilizer for the understory as a group compared to sugar maple trees further supports the presence of an edge effect. This is because the understory plants were only sampled within a 15 m radius of the centre of each plot, which is bordering the point where we see an edge effect occurring (5 m vs. 8 m from an edge, Fig. 6), whereas the sugar maples were sampled from all locations of the plots.

The edge effect observed for the percent of K derived from fertilizer, specifically an increase in trees that are farther from an edge, could be caused by multiple factors. One, the roots of fertilized trees may be reaching into unfertilized areas and are therefore out of reach of added nutrients, decreasing the percentage of K derived from fertilizer for those trees. Second, leaves of control trees may be carried by the wind and fall near the edge of fertilized plots or leaves of fertilized trees near an edge may fall outside fertilized plots, both reducing the cycling of

fertilizer-K from decomposition of leaf matter and thus the percent of K derived from fertilizer along the edges. This travelling of leaves would also have an influence on the effect of the fertilizer on the soil chemistry, namely by increasing or decreasing the concentration of K in the organic matter in control and fertilized plots, respectively; thus causing the lack of difference between the soil chemistry in control and fertilized plots. It is also possible that the slope of my plots is causing the fertilizer to move laterally out of south-western edges of the fertilized plots via the soil solution (Buxbaum et al. 2001). Finally, it is also possible that these edge effects are only a recent phenomenon, as the survey is based on the 2011-2012 trees. It would be interesting to repeat this aspect of the study on a more recently fertilized stand to see exactly when this edge effect occurs to help narrow down the controlling factors.

The presence of an edge effect suggests that my plots were likely too small and too close together. Future fertilization studies should use larger plots with greater distance between each other with trees that are more evenly spread out in the plots (many of my study trees were clustered together).

6.3 Long-term retention of potassium from fertilizer

Since there is still a significant amount of K derived from the fertilizer in my plots and not a significant difference in the foliar and soil K concentrations, it is likely that the fertilizer K has displaced the native K, as discussed in the previous sections. So, the question we must ask is: where did the rest of the fertilizer-K go? Is it gone from the system, deeper in the soil than I measured, held in the plants that I didn't look at or were not able to use in my estimate, or is the loss simply overestimated?

Including the edge-affected sugar maple trees in my analysis pulls down the overall recovery of fertilizer-K by $2.2 \text{ kg}\cdot\text{ha}^{-1}$, a 30 % difference in that section of my estimate. I also underestimated the amount of K from fertilizer held in the wood of the sugar maple trees. My estimate is only based on the sapwood of the trees – what I calculated to be 41 % of the tree. So there is over half of the wood unaccounted for, including the heartwood and bark. If I assume the remaining portion of the trees to have similar concentrations of K and percentage of K derived from fertilizer, it would increase my overall estimate for the system by $13.8 \text{ kg}\cdot\text{ha}^{-1}$, an over 1.4 times increase in the amount of fertilizer-K stored in the wood. Hendershot et al. (1993) illustrated that the effect of fertilizer was delayed in deeper horizons, highlighting the time required for the nutrients to get down to the bottom of the soil profile. It is likely that after 23 years, the fertilizer has travelled far into the soil, suggesting that I did not sample deep enough to recover all of the fertilizer that is still present in the soil system. This theory is supported by my highest percentages of K derived from fertilizer being located in the lower B2 and B3 soil horizons (Fig. 7). As the majority of the fertilizer-K that I did account for was located in the soil, this may be my greatest source of overestimation of the loss of fertilizer.

Losses of soil K by percolation at the site during the growing seasons of 1988-1992 were assessed at $1.44 \pm 0.85 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (Hendershot and Courchesne 1994). This corresponds to a loss of ca. $33 \text{ kg}\cdot\text{ha}^{-1}$ for the period of 1989 to 2012, which does not account for the full loss of fertilizer-K I have measured with the reverse tracer method (Table 8). However, most of the losses of soil K and other cations occur during the snowmelt in this kind of forest, which the previous estimate did not reflect (Hendershot et al. 1992). Using results from Hendershot et al. (1992) for the Hermine Watershed, a forest located less than 5 km away from my study site and

characterized by the same species composition and soil type, I can estimate the loss of soil K by surface drainage and percolation during the short but intense snowmelt period. By multiplying the discharge during the 12 days of intense snowmelt by the concentration of base cations in the stream during that period and adjusting for the proportion of K (30-50 %) relative to other base cations in soil solution (Courchesne et al. 2005), I assessed the loss of K during snowmelt to be between ca. 5.2 and 7.3 kg·ha⁻¹·yr⁻¹. This would translate into a loss of ca. 120-170 kg K ha⁻¹ during snowmelt for the period of 1989-2012 and a total loss of soil K for the 23-year period of approximately 150-200 kg·ha⁻¹. This output of K would be consistent with the loss of fertilizer-K I estimated using the Rb/K tracer.

Without accounting for my underestimate of soil K fertilizer, just considering the edge effects and unaccounted wood increases, my overall estimate of fertilizer K recovered in 2012 increases by 16 kg·ha⁻¹ giving me a loss of 171 kg·ha⁻¹ or 69 % of the original fertilizer compared to my previous estimate of 76 %. This estimated loss of fertilizer K derived from the reverse-tracer approach closely matches the amounts of soil K lost derived from lysimeter and stream data mentioned above. With the high likelihood of significantly more fertilizer-K still remaining in the system than initially measured, I estimate that more than 30 % of the fertilizer-K is still present on the site after 23 years of fertilization. I therefore conclude that sugar maple systems are able to efficiently retain fertilizer-K.

6.4 Sugar maple growth

A lack of growth response following fertilization with lime is not an uncommon occurrence (Moore and Ouimet 2006). A reason for the small growth response to fertilizer could be that the

forest decline in my stand reported before the start of the experiment was not entirely due to low nutrient availability. The assessment of decline was based on visual inspection and foliar samples in 1988. Comparing concentrations to critical nutrient values developed in later years (Côté et al. 1993) shows that although the levels of Ca, Mg, and N (Fyles et al. 1994) were below critical levels, K and P (data not shown) were not. It is therefore unlikely that the P limitation seen in Ontario sugar maple forests (Gradowski and Thomas 2006; Casson et al. 2012) were limiting growth in my stand.

It could be that these symptoms of decline attributed to nutrient limitations were instead the result of the other proposed natural factors such as water availability – either too much or too little, insect defoliators (the forest tent caterpillar and Bruce spanworm), or temperature extremes (freeze-thaw) (Houston 1999; Roy et al. 2002, Bernier et al. 1989; Payette et al. 1996; Côté and Ouimet 1996). Or it could be that Ca was the most limiting nutrient in my stand, as shown by the inability of the fertilizer to maintain increased levels of Ca (Fig. 2). Alternatively, since N was reported to be low in the 1990s (Fyles et al. 1994) it may be possible that what appeared to be a deficiency in base cations was actually a deficiency in N. But since most researchers were finding excess N, this was not likely considered a possibility at the time. It is unlikely that the poor growth response is attributable to K-Mg or K/Ca antagonism, as there is a lack of significant differences within either ratio between control and fertilized plots (Table 4).

Nutrient imbalances, more than deficiencies may be the greater issue of concern in my stand suggested by the very high soil nutrient ratios found on my site in comparison to the suggested soil norms for sugar maple in Quebec for both K/Mg and Ca/Mg (Ouimet et al. 2013). Moreover,

the percent saturation of Ca is higher than the suggested norms for organic and mineral soils by over 14 and 27 %, respectively (Ouimet et al. 2013). These ratios and Ca saturation have increased from original reporting, suggesting that the stand Ca status is still readjusting following fertilization (Ouimet et al. 2013 Table 2).

6.5 Understory vegetation species diversity

Associating Sorensen indexes to plot location reveals that plots that are closer to each other tend to be more similar (Table 10). This is also true for species richness (Fig. 9). As such, it is probable that understory diversity in my stand is more likely governed by the spatial variation of intrinsic factors, or in other words, some underlying physical or chemical characteristic of the stand, rather than by the fertilizer treatment. Additionally, of the species sampled for digestion, striped maple was the only species to have an increase in foliar K, further suggesting that fertilization was likely not as important for understory vegetation.

The lack of effect of fertilization and lime on understory diversity is not a rare outcome, even for long-term studies (Abrams and Dickmann 1983; Demchik and Sharpe 2000; He and Barclay 2000). It is possible I would have got significant results had I divided the understory plants into groups as suggested in a study done by VanderSchaaf et al. (2000) which found that diversity changes due to fertilization varied by plant growth form. Unfortunately, due to the small sample size of species, testing the effect of fertilization on groups of understory species was not possible.

My results however, differ from those reported by Moore et al. (2012) who found an increase in

sugar maple seedlings in fertilized plots 15 years after application of dolomitic lime. Although the soil type in Moore et al. (2012) is similar to mine, both Orthic Ferro-Humic Podzols, it is conceivable that I did not see a similar increase in sugar maple seedlings as the soil in my stand did not respond as strongly to fertilization as theirs (Moore et al. 2012).

Wild sarsaparilla and rare clubmoss – the two species that were found to have higher percent coverage in sample points in fertilized plots, are shade tolerant perennial species (USDA 2013; Dave's Garden 2013), which may have increased in coverage following an increase in canopy closure. The conflicting results of increased percent coverage (Fig. 10) and decreased frequency (Table 12) in fertilized plots of these two species may be caused by some unmeasured phenomenon such as placement of rocks, or fallen trees obstructing the ability of these species to respond to the fertilizer. Striped maple and American beech are also shade tolerant species but they both have low lime tolerance (USDA 2013). This low lime tolerance, more than their shade tolerance is likely the largest determinant for why they did not increase in fertilized plots.

The decrease in coverage of American beech in fertilized plots may have important implications for the current debate regarding the take over of sugar maple forests by beech (Duchesne et al. 2005; Duchesne and Ouimet 2009). As this change in American beech coverage is not unique to my study - Moore et al. (2012) also saw a decrease in beech coverage in fertilized plots 15 years after application with dolomitic lime - I suggest that other base cation fertilization studies should be reopened to incorporate a survey on the relative abundance of beech and sugar maple to see if the reduction of beech in fertilized plots is a consistent result. If it is a consistent result, this could have a major influence on controlling against this take over, allowing management to

favour the more desirable sugar maple. If nothing is done to limit base cation deficiency (Ca in particular) in northern hardwood stands, it is possible that we will continue to see an increase in beech trees at the expense of sugar maple trees (Moore and Ouimet 2006).

7.0 Conclusion

I have shown a short-term improvement of K and Mg status following fertilization as displayed with marked increases in the concentration of sugar maple leaf K and Mg in fertilized plots. I have demonstrated the efficient recycling of K fertilizer in the soil-plant system of a maple ecosystem through my assessment of high proportions of K being derived from fertilizer, and the recovery of over 24 % of the original fertilizer without including all pools of the ecosystem. I found no change in growth of sugar maple between treatments at any point during the 23-year study. And finally, I have found no obvious long-term change in understory species composition following forest fertilization suggesting that the understory vegetation of this forest stand is resistant to forest fertilization-induced changes, as the overall vegetation composition of control and fertilized plots did not differ. Although my results contrast in some responses to other long-term fertilization studies, it does not undermine the usefulness of fertilization in forest ecosystems. After all, Ostertag and Verville (2002) point out that discrepancies between fertilization studies may simply be due to differential responses to unique fertilizers.

These results do not support the majority of my hypotheses. Specifically, no long-term influence of fertilizer on the concentration of K, Ca, and Mg in the soil-plant system; no change in growth of sugar maple; no change in understory diversity; and although I found large amounts of

fertilizer K in the understory, the greatest amount of fertilizer K was found in the soil. I did however, confirm the efficient K recycling, demonstrated by significant recovery of fertilizer K in the soil-plant system.

In conclusion, base cation fertilization of the sugar maple stand in my study has influenced the cycling of K more than 23 years after fertilization with little effect on understory dynamics and tree growth. As such, I can suggest that the fertilization in my study does not endanger the preservation of the diversity of the system.

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