Indicator species of soil nutrients and poplar plantation productivity in southeastern Quebec

Jeremy Labrecque
Department of Natural Resource Science
McGill University, Montreal
ID: 119952207

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Abstract

Two sites, situated approximately 60 kilometers apart in southern Quebec, were studied to determine what nutrients were most limiting and to compare growth variation on microsite (3-9m) and landscape scales (100-1000m). One site was found to be 20% more productive than the other growing at 6.9 m^3 ha^{-1} in its fifth year of growth. Principal component analysis found no nutrients to be limiting at the more productive site while the other site appeared to be N and K limited. Microsite scale variation was found to be at least as important as landscape scale variation in explaining measures of productivity in most cases. Potential problems posed by microsite scale variation could be addressed using an indicator species analysis. Empirical distribution function analysis revealed that some species present in hybrid poplar plantations (e.g. *Fragaria spp.* and *Polytrichum spp.*) may be good indicators of low and high productivity sites respectively.

Resumé

Deux sites de plantations situés approximativement 60 kilomètres l'un de l'autre ont été étudiés afin de déterminer quels nutriments était les plus limitants et de comparer la variance à l'échelle de 3-9m (microsite) à la variance à l'échelle de 100-1000m. Un site était 20% plus productif que l'autre avec un taux de croissane de 6.9 m^3 ha^{-1} dans ça cinquième année. L'analyse de la composante principale a dévoilé que aucun des nutriments n'était limitant tandis qu'à l'autre site le N et la K parassait être limitants. La variance à l'échelle 3-9m semble être au moins aussi importante que la variance à l'échelle 100-1000m dans son explication des mesures de productivité, dans la majorité des cas. Le potentiel de problèmes rencontrés dans l'échelle de variation des microsites peut être expliqué en se servant d'une analyse d'espèces indicatrices. L'analyse de la fonction de distribution empirique a révélé que certaines espèces présentes dans les plantations de peupliers hybrides (e.g. *Fragaria spp.* et *Polytrichum spp.*) pourraient être de bons indicateurs de sites à productivité élevé ou basse.

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Chapter 1:

Introduction and literature review

1.1 Introduction

As short rotation forestry gains a foothold on the international stage, Canadian forestry companies have been implementing their own short rotation forestry strategies. These strategies have met with mixed success based largely on geography with British Columbia being quite successful while colder climates such as a Quebec and Ontario have had limited success. Other than climate, there are many other factors that may contribute to this limited success such as site selection, distance to the water table and pests.

This thesis will examine site selection as a possible limiting factor to short rotation forestry productivity. Upon casual visual inspection, much variation exists on small scales in hybrid poplar plantations which may indicate that a better understanding of site selection may lead to gains in productivity. Four hybrid poplar plantations established in 2002, 2003 and 2004 were examined at two sites. Growth parameters, soil and foliar nutrient concentrations were measured and analyzed to determine if soil nutrients are limiting. Variation in growth parameters on two scales, microsite (3-9m) and landscape (100-1000m), were compared in order to determine which was more important. Knowledge of the scale of variation has the potential to influence management decisions. For instance, if the variation is largely on the landscape scale, site improvement through fertilizer or other intervention would be relatively easy. If variation on the microsite scale is more important, quick and easy approaches that could distinguish productive from non-productive sites would be useful rather than large scale site improvement.

Weed species composition can often be related to soil conditions offering information on site characteristics without costly and time-consuming soil sampling. The relative weed species abundance at the base of hybrid poplars was recorded and compared to the growth parameters of the tree. If certain plant species tend to be found on productive or unproductive sites, they can be used as a quick and easy indicator species for site selection.

The objective of the second chapter is to characterize the relationship between soil nutrient concentrations and growth parameters of the hybrid poplars and to determine whether variation in those parameters is more important at microsite or landscape scales. The third chapter will investigate relationships between growth parameters, soil nutrient concentrations and weed species abundances in order to determine if certain species associate with site with specific characteristics.

1.2 Literature review

The Canadian forest industry is the world's largest exporter of forest products at almost $40 billion or 15.9% of world trade. It also provides over 300,000 Canadian jobs (Natural Resources Canada 2007). Non-timber interests (e.g. conservation, oil and gas production) and increased international competition are now posing important threats to the forest industry (Anderson and Luckert 2007) forcing the Canadian forest industry to increase productivity while reducing its land base. Forest management strategies such as TRIAD (Rowe 1992) and QUAD (Messier et al. 2003) are designed with this goal in mind. Such systems are based on the idea that current levels of productivity can be maintained or increased while simultaneously decreasing the area harvested. QUAD accomplishes this, in part, by using short rotation forestry (SRF) on a small portion of the forest landbase.

SRF is practiced using fast-growing tree species with rotation periods of 10-30 years (Weih 2004). It achieves higher peaks of mean annual biomass increment earlier by using genetically improved species, and site selection, preparation and improvement. The main advantages of SRF are land use efficiency, flexibility in land use planning, better control over the flow and quality of the fibre and accessibility of plantations (Morley and Balatinecz 1993; Richardson et al. 2007) allowing countries like Brazil and Argentina to achieve 60% of the total production of their forestry industry within 2% of their total forest area. Other countries such as Chile and New Zealand are achieving nearly 100% of their production using only 20% of their total forest area (Sedjo 1999).

The species used for SRF in tropical and subtropical countries (e.g. *Pinus radiata* and *Eucalyptus spp.*) cannot achieve the same levels of productivity in colder Canadian climates (Weih 2004). Members of the Salicaceae family, most notably hybrid poplar clones, represent some of the promising tree species for use in short rotation forestry in Southern Quebec. Among characteristics that predispose hybrid poplars for SRF are a high initial growth rate, cold hardiness (Weih 2004), the wide natural distribution of the genus *Populus*, a well-studied genome and ease of hybridization and vegetative propagation (Dickmann 2001).

According to Tuskan (1998), site selection for short-rotation woody crop supply systems should be "agricultural quality land of moderate to high fertility with moderate to well-drained soils and complete ground cover control 6-9 months prior to planting." For this reason, plantations have been established primarily on former agricultural land that tend to be more fertile and have better drainage conditions than plantations established on former forest sites.

1.2.1 *Hybrid poplar and response to nutrients and soil pH*

The goal of short rotation forestry is to select trees with accelerated growth rate compared to native species, with the ultimate goal of harvesting within a shorter timeframe to reduce rotation times. For the genus *Populus*, which requires nutrients in high concentrations, nutrient management becomes particularly important both because of high nutrient demands and high nutrient export upon harvesting (Berthelot et al. 2000).

The influence of soil nutrients on hybrid poplar productivity has been examined through manipulative experiments. The factors most often investigated are nitrogen application and irrigation (Hansen et al. 1988; Heilman and Xie 1993; Heilman et al. 1994; Marino and Gross 1998; Hofmann-Schielle et al. 1999; Baum and Makeschin 2000; van den Driessche 2000; van den Driessche et al. 2003; Karacic and Weih 2006). Other soil nutrients such as phosphorus, potassium, copper, zinc and magnesium input have also been investigated (Czapowskyj and Safford 1993; Chen et al. 1998; van den Driessche 1999; van den Driessche 2000; Brown and van den Driessche 2005; DesRochers et al. 2006). Most of these studies are performed either in a greenhouse setting, in pots or as plantations established on former agricultural land. The fact that few studies have been carried out on previously forested sites (van den Driessche 1999; Brown and van den Driessche 2002, 2005) indicates a gap in our knowledge that merits further research.

Nitrogen is generally thought to be the most limiting nutrient for plantations established on both former agricultural and forest sites due to the fact that poplars have high N content due to high N uptake (Heilman et al. 1996). Many fertilizer trials have applied N or other nutrients at different rates and in different forms. Most studies on former agricultural land show an increase in productivity of hybrid poplars following N fertilizer addition (Safford and Czapowskyj 1986; Hansen et al. 1988; Pregitzer et al. 1990; Liu and Dickmann 1992, 1996; Heilman and Xie 1993; Marler et al. 2001; Coleman et al. 2004; Cooke et al. 2005; Coyle and Coleman 2005; Christersson 2006; Coleman et al. 2006; Karacic and Weih 2006). Coleman et al. (2006) found that biomass increased 82% in two *P. deltoides X nigra* clones after three annual applications of 50 kg N ha^{-1}. Coleman et al. (2004) found that adding 50 kg N ha^{-1} $year^{-1}$ increased biomass by

40% after two growing season but rates above 50 kg N ha^{-1} $year^{-1}$ had no additional benefit for biomass gain.

In addition to biomass gain, the application of N fertilizer can affect tree architecture and morphology. In one study, poplars grown in a greenhouse with luxuriant levels of N had more leaves, sylleptic branches and sylleptic leaves (Cooke et al. 2005). Individual leaf area and leaf litterfall can also increase with N additions (Heilman and Xie 1994; Cooke et al. 2005; Coleman et al. 2006). In the absence of water stress, increased soil N has a positive impact on stomatal conductance (Liu and Dickmann 1996; DesRochers et al. 2006).

Application of fertilizer may also increase susceptibility to drought stress. Van den Driessche et al. (2003) found that NPK fertilization without irrigation decreased survival 17% and volume adjusted for survival 22% when compared to control plots. The same fertilizer treatment in conjunction with irrigation increased volume adjusted for survival by 78%. Similar reactions to fertilizer addition were found by Desrochers et al. (2006) where first year response to N fertilization was negative and van den Driessche et al. (2005) where two sites demonstrated a negative effect of N fertilization while a third showed no effect. These three studies were all located in northern Alberta which tends to be more P limited (Strong and La Roi 1985) suggesting any N addition could have raised N levels to levels where increased xylem cavitation could have occurred making the poplars more susceptible to drought (Harvey and van den Driessche 1997). At two sites in northern Wisconsin, greater mortality occurred on a site with higher N, particularly when that site was fertilized (Hansen et al. 1988). Brown and van den Driessche (2002, 2005) and van den Driessche (1999) found no such negative effects of fertilization on previously forested sites. Van Cleve and Oliver (1982) also found no adverse effects of fertilizers on a post-fire *P. tremuloides* stand. On a previously forested site in eastern Maine, Czapowskyj and Safford (1993) did find increased mortality among trees treated with nitrogen in the form of urea.

Nitrogen fertilization is costly making it preferable to evaluate whether or not it is required. Often less than 20% of the N applied is absorbed by the target trees (Baker et al. 1974) although this can be affected by the presence of weeds. Hansen et al. (1988) found that N fertilizer recovery was dominated by herbaceous competition early in a plantation but as the canopy closes up, trees achieved up to 27% recovery. Fortunately, N within the plantation trees themselves is very tightly conserved often with negligible losses (Nelson et al. 1987; Meiresonne et al. 2007) so once taken up into the system it stays there. When the trees are harvested, up to 84% of the N of the system may be exported (Berthelot et al. 2000).

Stem growth has been found to correlate with first year foliar N (Brown and van den Driessche 2002) and stem volumes up to four years in the future have been observed to have strong correlations with first year foliar N (Brown and van den Driessche 2002, 2005), first year foliar P (Bowersox and Ward 1977; Brown and van den Driessche 2005; van den Driessche et al. 2005) and first year leaf area (Harrington et al. 1997; van den Driessche 1999; Brown and van den Driessche 2005).

Although N is more often found to be limiting for hybrid poplars, P deficiencies have also been documented under field conditions (Bowersox and Ward 1977; van den Driessche 2000; van den

Driessche et al. 2003). This may especially be true for plantations established on forested sites as they may not have received pre-establishment P additions, in contrast to plantations established on former agricultural sites (Brown and van den Driessche 2005). Three studies conducted on forested land on Vancouver Island found hybrid poplars to be P deficient (van den Driessche 1999; Brown and van den Driessche 2002, 2005). P fertilization effects have been known to last one rotation in various *Pinus* plantations (Ballard 1978; Pritchett and Comerford 1982; Comerford et al. 2002; Turner et al. 2002). Four years after fertilizer application, Bowersox and Ward (1977) found that, though nearly half the extractable P was removed from the plantation, foliar P was not affected. This suggests that if a site has low soil P concentration, one fertilizer application before planting may suffice for an entire rotation.

Fertilizer addition also affects mycorrhizal colonization of hybrid poplar roots. Baum and Makeschin (2000) found that both N and P fertilization decreased mycorrhizal colonization in a *P. tremula x tremuloides* plantation while only P decreased colonization in a *P. trichocarpa* clone. A decrease in mycorrhizal colonization can lead to a decrease in nutrient and water absorption (Bjorkman 1970). Trees with higher foliar P responded better to water stress because they reduce xylem cavitation (Harvey and van den Driessche 1997) and foliar P has been found to increase with water availability (van den Driessche et al. 2003).

Potassium is very mobile in the soil and, in plants, is involved in charge balance, osmotic regulation and the functioning of many enzymes (Dickmann et al. 2001). Studies that have examined K show some potential for positive effects on growth. Czapowskyj and Safford (1993) found that a combination treatment of lime (L) and NPK fertilizer yielded more biomass than all other treatments including LNP, LN and LP. In an NPK factorial experiment, however, Desrochers et al. (2006) failed to find an effect of K addition. Potassium may become important in subsequent rotations because whole tree harvesting can remove up to 52% of K from the system (Berthelot et al. 2000).

In a hydroponic study, Lu and Sucoff (2001) found that aspen had a high Ca requirement compared to other temperate forest species. This is supported by a field study that found that aspen site index correlated positively with soil Ca (Chen et al. 1998). In poplars, Ca helps cell membrane integrity and hormone signaling (Dickmann et al. 2001).

Very little research has been done on the effects on Mg on hybrid poplar growth though one study found no effect of Mg on growth (Hofmann-Schielle et al. 1999).

Soil pH can have an important influence on hybrid poplar plantations. Increasing soil pH can increase survival or growth of hybrid poplars (Czapowskyj and Safford 1993; van den Driessche et al. 2005) and can influence N mineralization rates (Curtin et al. 1998). Desrochers et al (2003) found that increasing pH from 5 to 6 increased foliar P content but further increase to 7 caused a reduction in foliar P content.

1.2.2 *Indicator species*

Landres et al. (1988) define an indicator species as, "an organism whose characteristics (e.g., presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest.” Site selection is an important decision when establishing plantations and different sites can be limited by different nutrients. Soil sampling is one way of determining pH and nutrient levels but can be costly and can be difficult to quantify on small scales. The relative abundance or presence/absence of an indicator species can provide a less costly way of gathering information pertinent to management. Using individual species or groups of species as indicators has been a common practice in ecology (Dufrene and Legendre 1997; Caro and O'Doherty 1999;) and has been used to make conservation or management decisions (Brooks et al. 1998; Lindenmayer 1999; Lindenmayer et al. 2000). In this context, those decisions could include which species or clone to plant, whether the site requires preparation or whether the site should be planted at all.

There exists no literature on using indicator species to inform site selection decisions such as species allocation or whether a site requires preparation. Some studies have found relationships between understory species and site index (Strong et al. 1991; Szwaluk and Strong 2003; Chen et al. 2004). However, plant communities can differ between different stages of succession (Matlack 1994; D'Amato et al. 2009), therefore indicator species present within the first five years after the clearcut or other disturbance will be best suited for site or species selection because this is the same stage of succession in which plantations are established.

In a plantation, the planted trees can be used as a bioassay to provide information on site quality. Species that tend to be found in more productive plots can be considered indicator species insofar as they respond to the same environmental stimuli as the planted tree. This caveat is important because a positive or negative association between planted tree productivity and the relative abundance or presence/absence of a species may be the result of facilitation or competition interaction between the two rather than a response to the same stimulus.

Weeds can compete with poplars for water (Netzer and Noste 1978) and for nutrients (Hansen et al. 1988). Therefore any species that successfully competed with hybrid poplars would appear in less productive plots. This, however, would only indicate that hybrid poplar does poorly in the presence of such species but not necessarily that the plot itself is poor. Weeds can also facilitate hybrid poplar growth by preventing N leaching or by increasing N mineralization when fertilizers are added (McLaughlin et al. 1985). Alternatively, hybrid poplar growth can facilitate weed growth for shade tolerant species particularly when trees are planted at heights of one meter or taller. A greater abundance of a shade tolerant species would be found on more productive plots because more productive trees create more shade. When selecting indicator species, the potential for competition or facilitation should be kept in mind.

1.3 Thesis structure and objectives

This thesis is structured in four chapters. The first chapter is this introduction and literature review of the soil and foliar characteristics that are important for hybrid poplars and an introduction to indicator species. The second chapter will investigate the growth of hybrid poplar at two unfertilized sites and examine the relationship between soil pH, nutrient content and particle size on foliar nutrient levels and hybrid poplar productivity. The relative proportion of within-plot variation to between-plot variation will also be compared in order to determine at which scales variation in growth parameters is most important. The third chapter will use the results of the second chapter with a weed species survey in order to attempt to indentify species that could be indicators of productive sites. The fourth chapter will provide a conclusion regarding the results of the previous two chapters.

Chapter 2:

The relationship between site productivity, soil and foliar nutrient levels at two sites in southeastern Quebec

2.1 Introduction

The Canadian forestry industry is the world's largest exporter of forest products (Natural Resources Canada 2007) yet faces important challenges from non-timber interests such as conservation and oil production as well as increased international competition (Anderson and Luckert 2007). Short rotation forestry provides an opportunity to increase the productivity of plantations without increasing the land base.

In temperate climates, hybrid poplar is preferred because the genus *Populus* has a wide natural distribution, can be propagated easily by cuttings, has a well-studied genome (Dickmann et al. 2001), a high initial growth rate and is cold hardy (Weih 2004). In Canada, the productivity of hybrid poplars can reach up to 37 m^3 ha^{-1} yr^{-1} in the mild climate of the coast of British Columbia but in southern Quebec the colder temperatures limit hybrid poplar plantations to an average of 9 m^3 ha^{-1} yr^{-1} (Van Oosten 2000; Messier et al. 2003).

Traditionally, hybrid poplar plantations have been established on former agricultural land but as these sites become more expensive and less available, foresters are establishing hybrid poplar plantations on forested land. Forest soils are often lower in pH which can limit the availability of soil nutrients (Curtin et al. 1998; Schaffers 2002) and there can be heavy competition for nutrients with weed species (Hansen et al. 1988).

Most studies of hybrid poplar on forest soils have been manipulative experiments involving the addition of fertilizers or irrigation (Czapowskyj and Safford 1993; van den Driessche 1999;

Brown and van den Driessche 2002, 2005). These types of studies can quantify potential gains from various fertilizer applications but are unable to address potential nutrient deficiencies beyond the nutrients used in the study. Mensurative studies, such as this one, can provide information on how soil nutrient levels affect productivity as well as information on scales of variation in productivity.

Manipulative experiments have, however, provided a lot of information on nutrient requirements of poplar plantations. The addition of N on forested sites has generally shown positive effects (Czapowskyj and Safford 1993; Brown and van den Driessche 2002, 2005) increasing volume growth up to 4.3-fold after one growing season (van den Driessche 1999). Adding N to plantations on former agricultural land most often has positive effects as well (Hansen 1988; Coleman 2004,2006) though some studies have shown no effect (DesRochers et al. 2006) or negative effects such as increased mortality (van den Driessche et al. 2003, 2005). This may suggest that N is more often deficient on forested land.

Although hybrid poplar plantations have often been found to be limited by soil N concentration, P addition has also been shown to have a positive affect in greenhouse experiments and on former agricultural land (Bowersox and Ward 1977; van den Driessche 2000; van den Driessche et al. 2003) as well as on forested sites (van den Driessche 1999; Brown and van den Driessche 2002, 2005). Calcium is another soil nutrient that has been found to be important in poplar growth. Calcium requirements of *Populus tremuloides* can be quite high and can reduce the negative effects of low pH (Lu and Sucoff 2001). In *Populus tremuloides* stands, site index of aspen was found to correlate with soil Ca levels (Chen et al. 1998).

Potassium has been found to improve hybrid poplar growth (Czapowskyj and Safford 1993) but not all studies have found an effect of K (Desrochers et al. 2006). Magnesium has been studied very little in hybrid poplar plantations though one study found no effect on growth (Hofmann-Schielle et al. 1999).

The scale of variation is another important consideration for hybrid poplar plantations on forest soils. Many studies have found considerable amounts of microsite variation (tree to tree) on apparently homogeneous landscapes (Ceulemans et al. 1992; Heilman et al. 1994; Laureysens et al. 2004), though this variation has never been quantified or compared to larger scale variation (plot to plot). This information can be important to foresters because large scale variation can be more easily addressed with fertilization than microsite variation.

The goals of this study are threefold:

1) Quantify growth of hybrid poplar at two sites. At one of these two sites, two plantations of different ages will be examined.
2) Examine the relationship of soil variables to tree growth parameters using principle component regression and the relationship of foliar nutrients to tree growth as well as foliar nutrients to soil variables using correlation analysis.
3) Quantify the relative contribution of variation on two scales: between-plot (100-1000m) and within-plot (microsite variation; 3-9m).

Nitrogen and/or phosphorus are expected to be a limiting nutrient given that both have been found to be limiting in the literature in hybrid poplar plantations. Having observed the variation in hybrid poplar growth at different scales at sites adjacent to the ones in this study, it is expected that within-plot variation be more important than between plot variation.

2.2 Methods

2.2.1 *Sites*

Three plantations were sampled at two different sites in Southeastern Quebec. The McGill5 (MCG5) plantation was at the Lake McGill site near Gould, Quebec (45°35'00"N, 71°20'47"W) and the Dorset 4 and Dorset 5 (DOR4 and DOR5) were at the Dorset site near St-Hilaire-de-Dorset, Quebec (45°52'53"N, 70°41'14"W). MCG5 was planted in 2002 and DOR4 and DOR5 were planted in May 2003 and 2002 respectively as 1-2m bare-root stock. Both sites were relatively homogeneous with the biggest difference visual difference from plot to plot being soil moisture . Dorset is a predominately flat site whereas the terrain at McGill was gently rolling.

The McGill sites had an average July temperature of 15.7°C whereas Dorset was slightly warmer with an average July temperature of 17.7°C (see reference, Table 1). McGill received, on average, 17% more precipitation (Table 1).

The plantations were established with a variety of different clones in rectangular swaths, around 50-100m in width and 200-500m in length, which were logged approximately ten years earlier. The swaths are regularly spaced along roadsides and were separated by approximately 200m. For the purposes of this chapter only plots with *Populus maximowiczii x P. balsamifera* clones were used. Before planting, the regrowth was coarsely chopped and harrowed to a depth of approximately 30cm. The hybrid poplars were planted at an average height of 150cm and at 3 × 3 m spacing (1111 stems ha^{-1}).

2.2.2 *Sampling plots*

Sample plots were established by Domtar after the first growth season with between one and five plots per rectangular swath. Each plot consisted of nine trees arranged in a square 3 trees by 3 trees. Because the trees were planted 3m apart the distance between the closest trees in the plot was 3m and the furthest ones approximately 9m apart. To be able to identify the same trees when remeasuring, a stake was placed next to the first tree in the plot, a GPS point was recorded and each of the nine trees in the plot was marked with spray paint. One composite soil sample per plot was collected in the autumn each site was established and analyzed according to the references in Table 2.

2.2.3 *Measurements*

The trees in every plot in MCG5, DOR4 and DOR5 were measured when the plots were established at the end of the first growing season (2002 for MCG5 and DOR5, 2003 for DOR4) and remeasured at the end of the summer of 2006. The number in the plantation abbreviation indicates the age of the plantation when it was resampled. The diameter at breast height and basal diameter (15cm above the ground) was measured for each tree. The total height of the tree and the height at the previous year's terminal bud were measured using a telescoping pole. Stem volume was estimated as a cone using the following equation: π * (basal diameter/2)^2 * height/3 (van den Driessche et al 2003). Yield per hectare was calculated by multiplying the average volume in the plot by the number of trees per hectare (1111 trees ha^{-1}) and by the proportion of live trees in the plot. Yield per hectare is equivalent to volume growth corrected for survival.

The fourth leaf on the first lateral branch was collected from each tree in the plot in August of the first growing season at DOR5, DOR4 and MCG5 and in August 2006 at DOR5 and MCG5. All leaves in each plot were analyzed together. They were digested according to Parkinson and Allen (1975) and analyzed for N on a flow-injection analyzer (Quikchem 4000, Lachat instruments). P, K, Ca and Mg were analyzed on an ICP (Optima 4300-DV, Perkin-Elmer).

2.2.4 *Statistical analysis*

T-tests were used to detect differences in the mean soil pH, nutrient levels, particle size and hybrid poplar growth parameters and survival between the three plantations (α=0.05)

Soil data have a strong disposition toward collinearity (Lechowicz 1988) therefore the variance inflation factor (VIF) of each independent variable at each site was calculated. VIF is calculated by taking the inverse of $1 - R_i^2$ where R_i is the multiple correlation coefficient of variable *i* when regressed on all other independent variables in the model (Belsley et al. 1980). The VIFs were calculated in order to verify the level collinearity in the soil data.

Principal component regression (PCR) is an alternative to multiple linear regression when data sets demonstrate high multicollinearity (Legendre and Legendre 1998). Though possible to eliminate variables based on VIFs, the multicollinearity was such in this study that many of the variables would have been removed. It was preferred, instead, to proceed with the PCR analysis so as to not have to eliminate variables from the model. The independent variables used were pH, C:N, K, Ca, Mg, P:Al, sand content and clay content and the dependent variables were height growth, basal area growth, volume growth, survival, and yield per hectare. Each variable was tested for normality and subsequently transformed with either a log or square root arcsine transform if required. Soil C:N, K and clay were log transformed while all foliar nutrient variables except for K required log transformation. To achieve a normal distribution, survival was required to be arcsine square root transformed. The independent variables were standardized to have a mean of zero and a standard deviation of one and were decomposed into orthogonal principal components (PC) to remove the multicollinearity. The dependent variables were then regressed individually against the PCA scores using backwards stepwise regression until all PCs were significant at the $\alpha = 0.15$ level (Graham 2003). A *p x k* matrix composed of the *p* independent variables and of *k* PCs retained in the backwards stepwise regression was multiplied by a *k x 1* vector of the regression coefficients from the principal component regression (Legendre and Legendre 1998). The resulting *p x 1* vector is a vector of principal component regression coefficients. The coefficients do not have a statistical distribution and must therefore be interpreted without significance tests.

A correlation analysis was carried out on three sets of variables. Foliar nutrient levels after the first growing season and after the 2006 growing season (except for DOR4 for which 2006 data was unavailable) were correlated with growth variables (first year and 2006 leader growth, height growth, basal area growth, and volume growth, survival and yield) in one analysis and with soil variables in a second one.

The source of variation of different response variables was analyzed using a variance component analysis with site as the only random variable. Variance component analysis can be used to determine the relative importance of variation at different scales for nested models (Fletcher and Underwood 2002). Different levels of mortality in different plots made the data set naturally unbalanced; therefore, the analysis was carried out using restricted maximum likelihood (REML) which does not require a balanced data set. Dividing the variance component for between-plot variability by total variability, which in this case was the sum of both variance components, gives the proportion of variability explained by between-plot variation. The proportion of within-plot variation is calculated as one minus the proportion of between-plot variation. The analysis was carried out in SAS using PROC VARCOMP.

2.3 Results

2.3.1 *Soil characteristics*

Soil nutrient levels were similar at DOR4, DOR5 and MCG5 (Table 3) although P:Al was higher at DOR5 than at MCG5.

2.3.2 *Survival and growth*

First year survival was lowest at DOR5 and highest at DOR4 (Table 4). When the sites were remeasured in 2006, the average annual survival at DOR4 was closer to that at DOR5. Average annual survival at MCG5 was significantly higher than at DOR5.

Hybrid poplar growth at MCG5 was significantly higher than at both DOR4 and DOR5 (Table 5). When comparing DOR4 and DOR5, there was only a significant difference in basal area growth despite the plantation at DOR4 being one year younger. The most productive plot at MCG5 grew 6.9 m^3 ha^{-1} after five growing seasons or 1.4 m^3 ha^{-1} yr^{-1}. At DOR5, the most productive plot grew 5.0 m^3 ha^{-1} or an annual average of 1.0 m^3 ha^{-1} yr^{-1}.

2.3.3 *Principal component regression*

Many of the soil variables were highly multicollinear as demonstrated by high VIFs (Table 6). Belsley et al (1980) suggest that VIFs greater than 10 are considered high. Due to this multicollinearity, multiple regression was not appropriate and principle component regression was used instead.

The first PC at each site was dominated by K, Ca and Mg (Table 7) except MCG5 where pH dominated instead of K. The first PC explained over half of the variation in soils variables at DOR5 and over one third of the variation at DOR4 and MCG5. Other variables figured prominently in PC1 such as clay at DOR5 and pH at MCG5. The second PC was dominated largely by soil texture and P:Al, which was positively associated with sand. The remaining PCs explain from as little as 29% of the soil variability at DOR5 to as much as 39% at DOR4. Many of these PCs are clearly dominated by one or two soil variables although there was not as much similarity between them as there was in the first two PCs.

At DOR5, C:N had a strong negative relationship with basal area, volume and yield per hectare (Table 8). Survival was explained predominately by a positive relationship with K. At DOR4, C:N was an important explanatory variable of basal area and survival although the relationship was negative with the former and positive with the latter. K also had an important positive effect on basal area growth and survival at DOR4. The most important variable at DOR4 was clay content which was positively related to basal area growth, survival and volume yield. Soil Ca was also important in explaining the latter two but less so. At MCG5, the only significant regression was for survival where P:Al and sand content both displayed a negative relationship.

2.3.4 *Foliar analysis*

Foliar data for the first growing season were available for DOR4, DOR5, and MCG5, while data for the fifth growing season were available only for DOR5 and MCG5.

Foliar N, P and K levels were suboptimal during the first growing season (Figure 1). Increases in foliar N, P and K levels relative to 2002 were greater at MCG5. At DOR5, only foliar P approached the bottom edge of optimal levels for that nutrient while at MCG5, foliar N and K overlapped with the bottom of the optimal range in nutrient levels.

Foliar Ca and Mg demonstrated similar dynamics though different from that of foliar N, P, and K. First year levels were all within optimal levels even slightly above for foliar Mg at both Dorset sites. Statistically significant decreases in foliar Ca and Mg from concentrations after the first growing season in 2002 to 2006 were seen at both DOR5 and MCG5 but in both cases levels stayed within the optimal range.

All three sites showed strong correlations between first year foliar Mg and Ca and survival (Table 9). This was the only pattern all three sites shared in common. Volume growth and yield per hectare correlated negatively with first year foliar N at DOR4 and positively at DOR5. DOR5 was the only site to show significant correlations of growth variables with first year foliar K. At MCG5 first year foliar K showed a strong positive correlation with first year leader growth but the result was not significant. First year foliar Mg showed positive correlations with many measures of growth at DOR5. At DOR4, foliar Mg correlated positively with all measures of growth but only survival was significant.

Foliar N, P and K had uniquely negative correlations with growth variables and survival at DOR5 in the first year, but by the fifth year those correlations were nearly uniquely positive with volume growth being significant for all three foliar nutrients. The fifth year foliar nutrients correlated a lot more with growth and survival variables at DOR5 than at MCG5 although this may be due in part to the smaller sample size at MCG5 because *r* values for foliar P and K at MCG5 were high. Leaf weight was strongly correlated with most growth and survival variables at both sites and fifth year foliar K was strongly correlated with fifth year leader growth at MCG5.

There were relatively few strong relationships between the foliar data and soil data (Table 10). The strongest relationship was the correlation between first year foliar Ca and Mg with soil pH, soil Ca and soil Mg at DOR5 and MCG5. At DOR 4, this relationship was weaker. Despite being adjacent, DOR4 and DOR5 did not show similar correlations between soil and foliar nutrients. At DOR5, foliar Ca and Mg correlated positively with soil N and soil K.

In fifth year foliar data, the strong relationship between foliar Ca and soil pH, soil Ca and soil Mg is still present but foliar Mg does not maintain this pattern at DOR5 where Mg correlated best with P:Al. Leaf weight did not correlate with any foliar nutrients at either site.

2.3.5 *Variance components*

The proportion of total variability explained by between-plot variability was highest at DOR5 where it explained more than half of the total variation for all measures of growth except for first year leader growth (Table 11). MCG5 had the second highest proportion of total variability explained by between-plot variability ranging from 32% for basal area growth to 57% for 2006 leader growth. Between-plot variability was even lower at DOR4 and a 3 year old plantation adjacent to DOR4 (data not shown). At DOR4, between-plot variability never explained more than 25% of the total variability and explained as little as 14% of the total variability of 2006 leader growth at DOR4.

2.4 Discussion

2.4.1 *Survival and growth*

Studies conducted in more favourable climates had much higher volume growth than the sites in this study (Bowersox and Ward 1977; Yu et al. 2001; Brown and van den Driessche 2002, 2005; Coyle et al. 2006). Some sites with similar climates had comparable growth. The three sites in this study had higher average annual basal diameter growth, approximately equal height growth and higher mortality than a ten year old plantation of *Populus maximowiczii x trichocarpa* clones planted on a clearcut forest site in eastern Maine (Czapowskyj and Safford 1993). Another clearcut forest plantation of a *Populus maximowiczii x balsamifera* clone in western Quebec performed just as well as MCG5 in terms of basal diameter and height growth per growing season though mortality was higher and more similar to that at DOR4 and DOR5 (Guillemette and DesRochers 2008).

2.4.2 *Principle component regression*

Principle component analysis revealed that the first two PCs at all three sites, which accounted for between 61% and 71% of the total soil variability, were similar. Despite this similarity and the fact that DOR4 and DOR5 were adjacent sites, each site demonstrated markedly different responses to soil nutrients as demonstrated by the PCR analysis.

PCR revealed a positive effect of soil K on survival at both DOR4 and DOR5 and on basal area growth at DOR4. One study in western Quebec found that adding K to N fertilizer increased growth in a *P. maximowiczii x balsamifera* clone (Guillemette and DesRochers 2008). Another study found that K added with N and P reduced mortality (Leroy 1969; Guillemette and DesRochers 2008). Most studies that have tested the efficacy of K fertilization found that it did not have an effect on growth or survival (Nakos 1979; Czapowskyj and Safford 1993; DesRochers et al. 2006) though one found a negative effect on growth (Van Cleve and Oliver 1982).

Nitrogen fertilization has been tested in many trials and has shown positive results (Brown and van den Driessche 2002, 2005; Coleman et al. 2006; Hansen et al. 1988; Nakos 1979; van den Driessche 1999) although not uniquely (van den Driessche et al. 2003) which suggests a beneficial role of higher soil N or lower C:N ratio. C:N was found to be inversely related to the productivity of a *Pinus radiata* plantation in New Zealand (Watt et al. 2008). DOR5 appeared to be N limited as basal area, volume growth and yield per hectare were all strongly negatively related to C:N ratio. DOR4 may have also experienced some level of N limitation as basal area was negatively related to C:N and first year foliar N was positively related to volume growth. The N limitation of these plantations is consistent with Updegraff et al. (1990) who found that N limitation may be more important in places with long periods of cold, such as the sites in this study, which can limit soil microbial activity.

Smaller soil particle size increased survival at both DOR4 and MCG5. MCG5 showed a negative effect of sand content on survival and DOR4 showed a positive relationship between clay content and survival, volume yield and basal area growth. Generally, sites with higher clay content experience higher mortality and poorer growth because they have poorer drainage and aeration (Hansen et al. 1988; Stanturf et al. 2001) though Tullus et al (2007) had a similar result to the one observed here having observed a strong negative relationship between sand content and height. Higher levels of clay could positively affect growth if water was limiting and poor drainage retained water in the soil. Though soil moisture was not measured, DOR4 had abundant standing water suggesting that a lack of water did not exist.

Only the PCR on survival was significant at MCG5 indicating a weak relationship between soil and growth variables. The trees at MCG5 were much larger than at DOR5 and DOR4 and may have been large enough to begin closing the canopy which would reduce competition with weeds and make soil nutrients more available (Hansen et al. 1988). There was, however, no evidence of that in weed data (see Chapter 3 – Table 13) which indicated there was a similar amount of bare soil at MCG5 than at DOR5.

2.4.3 *Foliar nutrients*

Many studies have observed a positive relationship between height growth and foliar N concentration (Chen et al. 1998; Hansen et al. 1988; Bungart and Huttl 2004; Coleman et al. 2006). DOR4 was the only site where a positive relationship was seen between first year leader growth and first year foliar N though this relationship was not significant. Leader growth in 2006 was positively correlated with foliar N in 2006 at DOR5 and MCG5 although it was only significant at the former. The suboptimal foliar N concentrations at all sites strengthen the possibility that it is one of the nutrients limiting growth. This pattern was apparent at DOR4 and DOR5 but not at MCG5. This can be explained by the N:P ratios at these sites. N:P ratios were higher at MCG5 than at the Dorset sites indicating that it may have been more limited by P than by N. This is consistent with the pattern of correlations between foliar N and P and volume growth at these sites.

Foliar Ca was found to correlate positively with survival at all three sites and for both the first year and 2006 growing seasons although the correlations were not significant at MCG5. The Ca component of lime application has been shown to increase survival of *Populus* species at a Ca deficient site (van den Driessche et al. 2005). It has also been found to be positively related to root elongation, which is important in young *Populus* cuttings, and to mitigate some of the negative effects of low pH in *Populus tremuloides* (Lu and Sucoff 2001). The low soil pH levels (<5.0) could have made foliar Ca levels important in mitigating the negative affects of low pH at these three sites. Wilmot et al (1995) also found foliar Ca to be inversely related to dieback in *Acer saccharum*. Dieback was an important source of height loss at the DOR4 and DOR5 with 22% and 17% of trees showing signs of dieback respectively (data no shown) and may have indicated vulnerability to mortality.

2.4.4 Variance components

For this study, the variance component analysis allowed the total variability at a site to be partitioned into components that represent the magnitude of variability between plots (100m-1000m scale) and the variability within plots (3-9m scale). The larger the between-plot variance relative to within-plot variance for a given growth variable, the more that measure of growth is affected by processes that operate on large scales relative to the effect of the microsite variation within plots. The variance component analysis indicates that about half the variation observed in height, basal area and volume growth at DOR5 was on a between-plot scale. The other half of the variation was due to microsite variation within plots and error. This can be contrasted with DOR4 where less variation is explained on a between-plot scale making microsite variability and error more important at that site. Other studies have found considerable microsite variability in poplar plantations (Ceulemans et al. 1992; Heilman et al. 1994; Laureysens et al. 2004).

Knowledge of the ratio of between-plot variation to within-plot variation helps to put the PCR analysis in perspective because the variance explained by the regression models only explains between-site variance. For example, if considering basal area at DOR5, the PCR only explained 54% of the total variance, that explained by between plot variance, with the other 46% of the variance found within plot having being eliminated in the averaging of the plots. This means that though the PCR model was significant, it only explained slightly over half of the total variance. At DOR4, between-plot variation only accounted for 23% of the total variance so the PCR model omits the other 77% of the variance occurs within plot.

Variance components can also show which scale of the variation is more important. Within plot variance is large in first year leader growth which may indicate that microsite differences are more important than differences on larger scales. Between plot variance in leader growth in 2006 at DOR5 and MCG5 was much higher than first year leader growth indicating that for these two plantations, larger scale effects became more important with time.

2.5 Conclusion

Growth at Dorset and McGill differed greatly. The latter site showed greater volume growth, better survival and greater volume yield per hectare yet the principal component regression analysis or the foliar nutrient correlation analysis did not elucidate why MCG5 was more productive. It is possible that DOR4 and DOR5 were limited by soil nutrients, as seen in the PCR analysis, and MCG5 was limited by a factor that was not measured in this study (e.g. soil moisture). This would explain the variance component analysis which demonstrated that the variation at MCG5, DOR4 and DOR5 all occur at different scales suggesting the possibility that these sites have different limiting factors. DOR5 would appear to be limited by a process working at a larger scale as the between-plot variance is more important than the other sites, particularly in 2006 leader growth.

The results also suggest that it may be more difficult than previously thought to generalize results from one site to another. If sites that are in the same general region have such different requirements, determining the intervention required to make different plantations productive will require more information before the establishment of the plantation. This is compounded by the fact that within-plot variation accounts for a large part of the variance suggesting that selecting microsites more effectively could also help improve productivity. Flexible, “on the fly” methods of characterizing both large and small scale variation are required in order to perform adequate site management.

Figures and Tables: Chapter 3

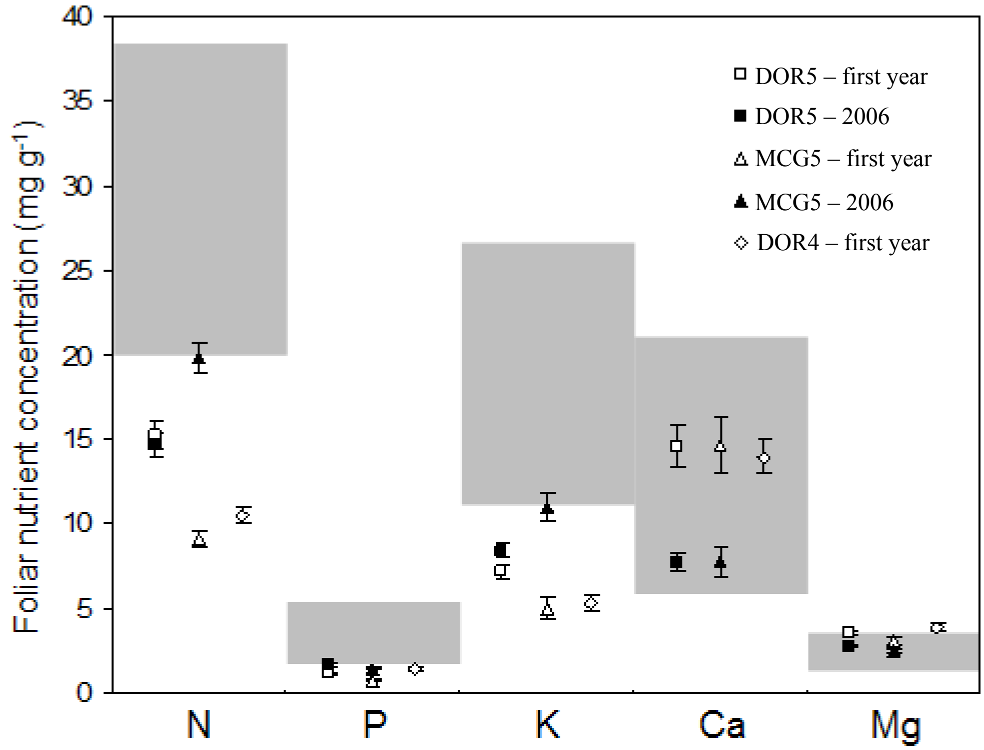

Figure 1 – Foliar nutrient concentrations for all three sites. The shaded areas represent a range within which nutrient levels are considered optimal for that nutrient for hybrid poplar (Camire and Brazeau 1998). Error bars represent the standard error.

Table 1. Precipitation at McGill and Dorset (mm)

Year	McGill	Dorset
2002	1092	968
2003	1166	925
2004	1382	1127
2005	1069	1023
2006	1515	1277
Total	6224	5320

Source: Environment Canada (2002-2006) data for St-Hilaire de Dorset and Lingwick weather stations. http://www.climate.weatheroffice.ec.gc.ca/climate_normals/

Table 2 - References for soil analysis

Soil variable	Reference
Organic C	Yeomans and Bremner 1988
Total N	Zellweger Analytics Inc. 1996
Extractable Ca, Mg, K, P, Al	Mehlich 1984
pH	Shoemaker et al 1961
Sand and clay content	Bouyoucos 1962

Table 3. Soil pH, nutrient levels and particle size at MCG5, DOR5 and DOR4

Variable	n	Mean	SE
MCG5			
pH	14	4.38	0.11
C:N	14	19.6	1.2
K (mg kg^{-1})	14	47	6
Ca (mg kg-1)	14	338	106
Mg (mg kg-1)	14	49	15
P:Al	14	6×10^{-3}	2×10^{-3}
Sand (%)	14	36	3
Clay (%)	14	24	2
DOR5			
pH	23	4.68	0.08
C:N	23	19.0	1.5
K (mg kg^{-1})	23	52	7
Ca (mg kg^{-1})	23	515	100
Mg (mg kg^{-1})	23	95	16
P:Al	23	14×10^{-3}	3×10^{-3}
Sand (%)	23	36	1
Clay (%)	23	29	1
DOR4			
pH	13	4.83	0.05
C:N	13	20.7	1.1
K (mg kg^{-1})	13	39	5
Ca (mg kg^{-1})	13	438	52
Mg (mg kg^{-1})	13	77	7
P:Al	13	12×10^{-3}	2×10^{-3}
Sand (%)	13	35	1
Clay (%)	13	26	1

Table 4. Percent survival after the first growing season and in 2006.

Site	n	Year planted	First year mean	First year SE	2006 mean	2006 SE	Mortality per year mean	Mortality per year SE
MCG5	14	2002	93^{a}	3	72^{a}	7	5.6^{a}	1.4
DOR5	23	2002	89^{a}	3	55^{a}	5	9^{b}	1
DOR4	13	2003	96^{a}	1	67^{a}	7	8.3^{b}	1.8

Note: Sites not sharing a letter in common indicates a significant difference ($\alpha = 0.05$)

Table 5. Measures of growth by site.

Site	n	First year leader (cm)		2006 leader (cm)		Height (cm)		Basal area (cm^2)		Volume (dm^3 $tree^{-1}$)		Yield per ha (m^3/ha)	
		mean	SE	Mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
MCG5	14	9.3a	1.7	119a	13.3	223a	27	13.3a	2.1	2.27a	0.47	1.87a	0.49
DOR5	23	6.3b	0.6	54b	6.4	102b	17	8.2b	1.5	1.09b	0.27	0.74b	0.22
DOR4	13	5.3b	0.5	56b	4.9	71b	12	3.2c	0.6	0.33b	0.08	0.27b	0.07

Note: Sites not sharing a letter in common indicates a significant difference ($\alpha = 0.05$)

Table 6. Variance inflation factors for soil variables demonstrating the amount of multicollinearity between soil variables. Belsley et al. (1980) suggest that VIFs greater than 10 are considered high and should not be used in regression analysis.

Variable	VIF
MCG5	
pH	7.0
C:N	1.2
K	3.4
Ca	50.4
Mg	55.6
P:Al	8.4
sand	5.9
clay	24.6
DOR5	
pH	2.2
C:N	1.4
K	20.0
Ca	83.0
Mg	104.0
P:Al	1.8
sand	2.8
clay	18.0
DOR4	
pH	7.1
C:N	2.8
K	47.0
Ca	26.0
Mg	75.0
P:Al	2.2
sand	13.0
clay	5.3

Table 7. Principal components (PC) of soil variables at DOR4, DOR5 and MCG5. The percent variance show how much of the total variation is explained by that PC and the eigenvector loadings represent how much the variation in a given soil variable contributes to a PC

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**
MCG5								
Eigen value	2.95	2.36	1.06	0.72	0.53	0.30	0.06	0.02
Percent variance	0.37	0.30	0.13	0.09	0.07	0.04	0.01	0.00
Cumulative variance	0.37	0.67	0.80	0.89	0.95	0.99	1.00	1.00
Eigen vectors								
pH	**0.46**	0.12	-0.04	0.53	-0.03	**0.67**	-0.03	-0[illegible]
C:N	0.01	0.33	**-0.74**	0.10	**0.55**	-0.15	-0.10	0.[illegible]
K	0.35	-0.34	0.00	**-0.62**	0.33	0.27	**-0.44**	-0[illegible]
Ca	**0.54**	0.10	0.28	0.06	0.12	-0.21	0.04	**0.75**
Mg	**0.55**	0.06	0.06	0.02	0.01	**-0.55**	0.18	**-0.60**
P:Al	0.23	0.36	**-0.40**	**-0.47**	**-0.62**	0.13	0.16	0.10
sand	-0.11	**0.51**	0.36	-0.32	**0.42**	0.27	**0.48**	-0.12
clay	0.09	**-0.60**	-0.28	-0.03	0.12	0.12	**0.72**	0.10
DOR5								
Eigen value	4.28	1.43	0.88	0.66	0.47	0.21	0.06	0.00
Percent variance	0.54	0.18	0.11	0.08	0.06	0.03	0.01	0.00
Cumulative variance	0.54	0.71	0.82	0.91	0.97	0.99	1.00	1.00
Eigen vectors								
pH	0.34	0.28	0.11	-0.35	**-0.81**	-0.12	0.08	-0.04
C:N	-0.23	-0.08	**-0.88**	0.18	-0.34	0.12	0.00	-0.06
K	**0.43**	-0.12	-0.21	0.22	0.16	**-0.58**	**0.59**	0.03
Ca	**0.44**	0.23	-0.07	0.32	0.01	**0.40**	-0.07	**0.70**
Mg	**0.44**	0.24	-0.02	0.32	0.10	0.37	-0.02	**-0.71**
P:Al	0.00	**0.72**	-0.32	-0.36	0.38	-0.25	-0.19	0.02
sand	-0.30	0.36	0.22	**0.68**	-0.23	**-0.41**	-0.21	0.00
clay	**0.41**	-0.38	-0.12	-0.01	0.00	-0.33	**-0.75**	-0.03
DOR4								
Eigen value	3.09	1.81	1.15	0.85	0.67	0.38	0.05	0.01
Percent variance	0.39	0.23	0.14	0.11	0.08	0.05	0.01	0.00
Cumulative variance	0.39	0.61	0.76	0.86	0.95	0.99	1.00	1.00
Eigen vectors								
pH	-0.05	-0.20	**-0.84**	-0.30	0.17	-0.22	0.23	-0.18
C:N	-0.34	-0.16	-0.30	0.39	**-0.70**	0.32	0.11	0.09
K	**0.51**	0.23	0.09	0.18	-0.28	-0.14	**0.53**	**-0.52**
Ca	**0.45**	-0.31	-0.21	0.32	0.10	0.27	**-0.59**	-0.35
Mg	**0.53**	-0.19	-0.12	0.20	0.16	0.14	0.34	**0.69**
P:Al	0.25	**0.43**	-0.15	**-0.58**	-0.22	**0.57**	-0.11	0.06
sand	0.11	**0.61**	-0.31	0.28	-0.15	**-0.47**	-0.36	0.25
clay	0.27	**-0.44**	0.15	**-0.41**	**-0.54**	**-0.44**	-0.22	0.14

Note: Vector loadings in bold are considered high (≥ 0.4)

Table 8. Principal component regression coefficients of different measures of productivity regressed on soil variables. 'NS' results indicate that no principal component was found to be a significant explanatory variable of a given variable.

	Height	**Basal Area**	**Volume**	**Survival**	**Yield per hectare**
MCG5					
pH	NS	NS	NS	0.24	NS
C:N	NS	NS	NS	-0.09	NS
K	NS	NS	NS	-0.18	NS
Ca	NS	NS	NS	-0.01	NS
Mg	NS	NS	NS	-0.01	NS
P:Al	NS	NS	NS	**-0.42**	NS
Sand	NS	NS	NS	**-0.41**	NS
Clay	NS	NS	NS	0.25	NS
Components	-	-	-	2,4	-
R^2	-	-	-	0.52	-
DOR5					
pH	0.12	0.05	0.05	0.20	0.05
C:N	-0.09	**-0.42**	**-0.39**	-0.13	**-0.43**
K	0.16	-0.10	-0.09	**0.62**	0.11
Ca	0.16	-0.03	-0.03	0.01	0.21
Mg	0.16	-0.01	-0.01	0.04	0.23
P:Al	0.00	-0.15	-0.14	-0.01	-0.26
Sand	-0.11	0.11	0.10	-0.09	0.21
Clay	0.15	-0.06	-0.05	-0.10	0.08
Components	1	3	3	1,6,7	1,3,4
R^2	0.14	0.23	0.20	0.46	0.43
DOR4					
pH	-0.02	0.07	NS	-0.14	0.04
C:N	-0.16	**-0.30**	NS	**0.39**	-0.07
K	0.23	**0.30**	NS	**0.38**	0.22
Ca	0.21	0.10	NS	**0.34**	**0.33**
Mg	0.24	0.19	NS	0.28	0.15
P:Al	0.11	-0.12	NS	0.29	0.18
Sand	0.05	0.25	NS	-0.11	0.05
Clay	0.12	**0.31**	NS	**0.53**	**0.82**
Components	1	1,6	-	1,2,5,6	1,2,4,5,6,7
R^2	0.21	0.41	-	0.87	0.91

Note: Coefficients in bold are considered high (≥ 0.3)

Table 9. Correlation coefficients between foliar nutrient variables and measures of growth and productivity. 'NA' indicates that data were not available for that site.

	First growing season					**2006**					
	N	**P**	**K**	**Ca**	**Mg**	**N**	**P**	**K**	**Ca**	**Mg**	**Leaf weight**
MCG5											
first year leader	-0.05	-0.21	0.52	-0.44	-0.43	0.11	-0.41	0.43	-0.31	**-0.58**	0.38
fifth year leader	0.03	0.22	0.01	-0.25	-0.37	0.42	0.50	**0.61**	-0.32	-0.33	**0.60**
height	0.21	-0.05	0.07	0.01	-0.09	0.18	0.50	0.53	0.06	-0.17	**0.82**
basal area	0.26	0.07	-0.06	0.13	-0.02	0.17	0.48	0.49	0.00	-0.24	**0.75**
volume	0.03	-0.12	0.01	0.16	-0.01	0.13	0.46	0.52	0.09	-0.14	**0.66**
survival	0.13	-0.06	-0.13	0.41	**0.56**	-0.08	0.18	-0.14	0.49	0.33	0.36
volume yield	0.18	0.01	0.09	0.27	0.12	0.18	0.40	0.45	0.20	-0.12	**0.77**
DOR5											
first year leader	-0.34	-0.40	-0.14	0.13	0.18	**0.47**	0.16	-0.01	0.27	0.07	0.26
fifth year leader	-0.19	-0.17	-0.31	0.14	**0.54**	**0.49**	**0.53**	0.29	**0.59**	0.03	**0.75**
height	-0.28	-0.24	**-0.54**	0.41	**0.69**	0.41	**0.53**	**0.56**	**0.55**	-0.25	**0.66**
basal area	**-0.51**	-0.37	**-0.56**	0.34	0.43	0.43	**0.48**	**0.56**	0.31	**-0.57**	**0.60**
volume	**-0.52**	-0.37	**-0.59**	0.32	**0.46**	**0.46**	**0.50**	**0.56**	0.38	**-0.50**	**0.65**
survival	-0.21	-0.13	-0.03	**0.42**	**0.50**	**0.44**	0.25	-0.17	**0.57**	0.12	**0.44**
volume yield	**-0.48**	-0.32	**-0.54**	0.27	**0.53**	**0.58**	**0.46**	0.40	**0.58**	-0.29	**0.65**
DOR4											
first year leader	0.38	-0.45	0.17	0.49	0.22	NA	NA	NA	NA	NA	NA
fifth year leader	0.40	0.26	0.38	**0.58**	0.46	NA	NA	NA	NA	NA	NA
height	0.29	0.45	0.15	0.54	0.44	NA	NA	NA	NA	NA	NA
basal area	0.46	0.35	0.12	**0.78**	0.48	NA	NA	NA	NA	NA	NA
volume	**0.56**	0.19	0.15	**0.68**	0.33	NA	NA	NA	NA	NA	NA
survival	0.52	-0.13	0.38	**0.62**	**0.59**	NA	NA	NA	NA	NA	NA
volume yield	**0.64**	0.03	0.23	**0.74**	0.31	NA	NA	NA	NA	NA	NA

Note: correlation coefficients in bold indicate they are significant ($\alpha = 0.05$)

Table 10. Correlation coefficients between foliar nutrient levels and soil nutrients levels. 'NA' indicates that data were not available for that site.

	First year					2006					
	N	**P**	**K**	**Ca**	**Mg**	**N**	**P**	**K**	**Ca**	**Mg**	**Leaf weight**
MCG5											
pH	0.21	-0.15	-0.12	**0.67**	**0.60**	-0.26	0.24	**-0.54**	**0.82**	0.52	-0.15
OC	-0.08	-0.34	-0.20	0.47	0.33	0.10	0.18	-0.08	0.27	0.19	-0.08
N	-0.04	-0.38	-0.24	0.47	0.38	-0.23	0.06	-0.18	0.38	0.29	-0.16
C:N	-0.06	0.08	0.10	-0.01	-0.09	**0.62**	0.23	0.19	-0.21	-0.20	0.15
K	0.42	0.30	0.03	0.13	-0.04	0.13	0.51	0.16	0.13	0.19	0.13
Ca	0.00	-0.31	-0.38	**0.73**	**0.54**	-0.32	0.26	-0.53	**0.83**	**0.64**	-0.17
Mg	-0.11	-0.32	-0.52	**0.61**	**0.59**	-0.18	0.43	-0.45	**0.67**	**0.67**	-0.18
P:Al	0.04	0.10	-0.22	0.13	0.05	0.16	0.48	0.14	0.01	-0.09	0.09
Sand	-0.11	-0.23	0.31	0.14	-0.34	-0.19	**-0.62**	-0.02	0.03	-0.51	-0.17
Clay	0.39	0.31	-0.01	-0.31	0.00	0.18	0.50	0.15	-0.15	0.30	0.14
DOR5											
pH	-0.02	-0.14	-0.28	**0.52**	**0.55**	-0.01	0.15	-0.36	**0.64**	-0.03	0.14
OC	0.18	0.09	0.19	0.31	0.20	-0.16	0.05	-0.33	0.31	0.27	0.06
N	0.10	-0.06	-0.07	**0.51**	**0.47**	-0.06	0.14	-0.32	**0.47**	0.15	0.22
C:N	0.10	0.23	**0.43**	**-0.49**	**-0.57**	-0.25	-0.18	-0.05	-0.34	0.24	-0.31
K	0.09	-0.06	-0.06	**0.64**	**0.61**	0.07	0.25	-0.19	**0.51**	0.14	0.26
Ca	0.06	-0.03	-0.22	**0.61**	**0.66**	-0.06	0.17	-0.29	**0.72**	0.18	0.23
Mg	0.03	-0.14	-0.20	**0.56**	**0.61**	0.04	0.18	-0.34	**0.71**	0.15	0.30
P:Al	-0.04	-0.08	-0.08	0.20	0.15	-0.32	0.11	-0.19	0.35	**0.46**	0.15
Sand	-0.14	-0.14	0.01	**-0.53**	-0.28	-0.04	0.05	0.01	-0.10	0.21	-0.15
Clay	0.11	-0.03	-0.01	**0.57**	**0.50**	0.01	0.17	-0.04	0.25	-0.17	0.16
DOR4											
pH	0.01	-0.20	-0.31	0.24	**0.62**	NA	NA	NA	NA	NA	NA
OC	0.32	0.29	0.22	**0.56**	0.00	NA	NA	NA	NA	NA	NA
N	0.23	0.38	0.25	0.51	0.00	NA	NA	NA	NA	NA	NA
C:N	0.12	-0.38	-0.17	-0.05	0.07	NA	NA	NA	NA	NA	NA
K	0.14	0.42	0.29	0.53	0.22	NA	NA	NA	NA	NA	NA
Ca	0.17	0.06	0.02	0.31	0.27	NA	NA	NA	NA	NA	NA
Mg	0.21	0.17	0.11	0.42	0.30	NA	NA	NA	NA	NA	NA
P:Al	0.21	0.03	0.57	0.29	0.19	NA	NA	NA	NA	NA	NA
Sand	-0.27	0.43	-0.07	0.20	0.32	NA	NA	NA	NA	NA	NA
Clay	0.41	-0.25	0.04	**0.61**	0.21	NA	NA	NA	NA	NA	NA

Note: correlation coefficients in bold indicate they are significant ($\alpha = 0.05$)

Table 11. Variance components of growth measurements at different scales. Values represent the proportion of variance explained at that scale.

Site	Between plot	Within plot
Height		
MCG5	0.53	0.47
DOR5	0.51	0.49
DOR4	0.25	0.75
Basal area		
MCG5	0.31	0.69
DOR5	0.54	0.46
DOR4	0.23	0.77
Volume		
MCG5	0.34	0.66
DOR5	0.53	0.47
DOR4	0.18	0.82
First year leader		
MCG5	0.44	0.56
DOR5	0.24	0.76
DOR4	0.19	0.81
2006 leader		
MCG5	0.64	0.36
DOR5	0.83	0.17
DOR4	0.14	0.86

Connecting text between chapters 2 and 3

Chapter 2 examined how growth parameters were related to soil nutrient concentrations. It was determined that the McGill and Dorset sites differed importantly both in terms of growth parameters and in terms of nutrient relations suggesting the two sites behave very differently. This result was corroborated by the variance component analysis which indicated that the scale of variation was different at the two sites. With these levels of variation both within a site and between a site, site selection is required in order to improve yields. Chapter 3 explores the possibility of using weed species as possible indicator of productive and unproductive sites.

Chapter 3:

Indicator species of productive hybrid poplar sites and soil nutrients at two sites in southeastern Quebec

3.1 Introduction

Hybrid poplar plantations, such as those analyzed in the previous chapter, have shown large differences in growth parameters between sites separated by 60 kilometers as well as high within-plot variation when compared to between-plot variation. Particularly when within-plot variation is greater than between-plot, site selection becomes complicated because microsite selection becomes an equally or more important decision than choosing which sites to plant even when sites may by separated by hundreds of meters or tens of kilometers.

In order to establish successful plantations at sites such as these, foresters have one of three options. The soil characteristics of the plantation can be characterized on the scale where variation is most important. In cases where the scale of variation is small this is not a cost-efficient measure. A second option would be to perform site improvement on the entire site. While more feasible than characterizing the soil variation on small scales, this can potentially be a wasteful practice because some resources are wasted on microsites that do not require them.

The third option is to use easy to acquire, on-site information that could distinguish productive microsites from less productive ones. Examples of easy to gather data are physical characteristics of the site (slope, aspect, rockiness) and plant species composition. For hybrid poplar, this information can influence where planting blocks are located, which sites should be site prepared, which clone to plant at a particular site and which sites require more focused site improvement.

Plants have different requirements in terms of soil nutrients, pH and moisture. Therefore, the presence or absence of plant species can reflect the conditions at that site. Understory plant species have been shown to have relationships to soil nutrients levels (Pregitzer and Barnes 1982; Small and McCarthy 2005; Bona et al. 2008), site-index (Strong et al. 1991; Szwaluk and Strong 2003; Chen et al. 2004) and disturbance (Kashian et al. 2003). For example, Chen et al (2004) found that canonical correspondence analysis of understory species in monodominant *Populus* stands in British Columbia were related to site index.

Pregitzer and Barnes (1982) used an empirical distribution function (EDF) analysis to compare the distribution of species groups along different edaphic gradients that allowed them to conclude that species groups were distributed higher or lower than other species groups along a given gradient. The technique has the advantage of being non-parametric, therefore not requiring any assumptions about the distribution of the data. It is simple enough that it can be performed quickly and easily in the field. Though Pregitzer and Barnes (1982) used the technique solely on edaphic data, the technique can feasibly be applied to growth parameter data as well. Using growth parameter data along with the of plant species abundances within a certain radius of each tree, an EDF analysis can be performed where the productivity of a planted tree (e.g. volume growth, survival, yield per hectare) is used as an ecological assay of how productive the site is. Plant species on the high and low end of the productivity gradient are potential indicators of productive and unproductive sites respectively.

For the EDF to work as a measure of productivity, the assumption that both the plant species and the planted tree are responding to the same environmental stimulus is required. Depending on the species, this is not always an accurate assumption. The planted tree and understory plant species abundance can also covary positively if there is facilitation between the two. For example, a shade tolerant species may benefit from the additional shade provided by a more productive tree and will therefore be more abundant in areas where trees are more productive without necessarily responding to the same environmental stimuli. Alternatively, they can covary negatively if there is competition between the two species in question which can occur if a resource gets depleted (Goldberg 1990). Due to the relatively poor soils and the fact that the trees are planted when they are already 130cm tall (i.e. taller than the surrounding weeds), competition from weeds is expected to be mainly for nutrients and water and not for light.

The goal of this chapter is to examine the relationship between plant species distributions, soil data and hybrid poplar productivity in an attempt to suggest potential indicator species of productive and unproductive sites. The relationship of potential indicator species to each other will be investigated across different sites.

3.2 Methods

3.2.1 *Sites*

Four sites in southeastern Quebec were sampled. Lake McGill near Gould, Quebec (45°35'00"N, 71°20'47"W) was the site of one plantation (MCG5) and three other plantations (DOR3, DOR4 and DOR5) were located near St-Hilaire-de-Dorset, Quebec (45°52'53"N, 70°41'14"W). MCG5 was planted in 2002 and DOR3, DOR4 and DOR5 were planted in 2004, 2003 and 2002 respectively. The McGill and Dorset sites experienced similar temperatures over the five years of the study but McGill received, on average, 17% more precipitation (see Table 1 - Chapter 2).

The plantations were established with a variety of different clones in rectangular swaths, around 50-100m in width and 200-500m in length, which were logged approximately ten years earlier. Before planting, the regrowth was coarsely chopped and harrowed to a depth of approximately 30cm. They were planted at an average height of approximately 150cm and at 3 × 3 m spacing (1111 stems ha^{-1}). For this study a mixture of clones was used including *Populus maximowiczii x balsamifera* (MXB), *P. deltoides x nigra* (DXN), *P. trichocarpa x deltoides* (TXD), *P. DXN x maximowiczii* (DNXM) and *P. nigra x maximowiczii* (NXM). NXM was the most common clone in these plots.

3.2.2 *Sampling plots*

At each site, Domtar established sample plots in the plantations after the first growth season with between one and five plots per rectangular swath. Each plot consisted of nine trees arranged in square 3 trees by 3 trees. Because the trees were planted 3m apart the distance between the closest trees in the plot was 3m and the furthest ones approximately 9m apart. This range of distance will be considered to be the microsite scale. Landscape scale was considered to be the distance between plots which ranged from 100m to 1000m. To be able to identify the same trees when remeasuring, a stake was placed next to the first tree in the plot, a GPS point was taken and each of the nine trees in the plot was marked with spray paint. A composite soil sample was collected at each plot (except at DOR3) and analyzed according to the references in Table 2 (see chapter 2).

3.2.3 *Measurements*

The trees in every plot in MCG5, DOR3, DOR4 and DOR5 were measured at the end of the first growing season (2002 for MCG5 and DOR5, 2003 for DOR4 and 2004 for DOR3) and remeasured at the end of the summer of 2006. The number at the end of the site name indicates the age of the plantation when it was remeasured. The diameter at breast height and basal diameter (15cm above the ground) was measured for each tree. The total height of the tree and the height at the previous year's terminal bud were measured using a telescoping pole. Stem volume was estimated as a cone using the following equation: π * (basal diameter/2)^2 * height/3 (van den Driessche et al 2003). Yield per hectare was calculated by multiplying the average volume per tree in the plot by the number of trees per hectare (1111 trees ha^{-1}) and by the proportion of live trees in the plot.

3.2.4 *Relative plant abundance*

For each tree measured, relative abundance of all plant species was recorded within a 45 cm radius from the base of the tree. A 90 cm diameter hoop was placed over the tree with the trunk in the centre and the plant species within the hoop were estimated for relative abundance in multiples of 5%. Species that were present but not sufficiently abundant to be recorded at 5% were given a token abundance of 1%. Species names used are those found in Gleason and Cronquist (1991).

3.2.5 *Empirical distribution function*

The empirical distribution function (EDF) is useful with noisy ecological data. It allows the comparison of distributions of a plant species along a gradient of soil characteristic or growth measure. For a given site gradient variable x, the EDF is the sum of the relative abundances of the plant in question that occurs at sites where the variable is either equal to or less than x. For instance, Figure 2 depicts the EDF's of *Impatiens capensis* and *Polytrichum spp.* at MCG5 and a theoretical species (no effect) that occurs at every site in equal abundance. A distribution where abundance was equal at all sites would be expected if a species had no relationship to the independent variable in question. Sixty percent of the relative abundance of *I. capensis* occurred at sites where the soil Ca content is less than or equal to 1000 ppm therefore, for soil Ca, the EDF(1000) for *I. capensis* is equal to 0.6. By contrast, all occurrences of *Polytrichum spp.* were at sites where soil Ca was less then 1000 ppm making the EDF for that species 1. If a species was unaffected by the soil Ca we would expect it to be equally abundant at all sites. In this case, such as species would have an EDF of 0.79.

For growth parameters the same principle was used. For instance, if 80% of a species occurred at sites where volume growth was less than or equal to one cubic decimeter then the EDF(1) of that species is equal to 0.8.

By comparing the empirical distribution function of each plant species to the expected empirical distribution function of a theoretical species that is identical in every way except that it shows no response to the variable in question, it is possible to determine whether a species is associated with higher or lower levels of a soil, productivity or foliar variable within the sites sampled. This comparison is done using the Kolmogorov-Smirnov (KS) two-sample test.

The KS test is a non-parametric method used to test whether two distributions are significantly different based on the empirical distribution function. The maximum difference between two EDF's is compared to the KS statistic which is calculated using the sample sizes of each species. When using the KS test to compare a species to the theoretically neutral one (e.g. the no effect species in fig. 1), the sample size for the neutral species was considered to be equal to the sample size of the species being compared. This was done so the number of sites sampled did not influence the outcome of the KS test and to make the neutral species as similar to the test species as possible.

Pregitzer and Barnes (1982) used this analysis to compare different species to each other but used only presence/absence data and not relative abundance. In this study, relative abundance was used because some species were present at nearly every site but showed important differences in abundance from site to site.

Species that demonstrated some potential as an indicator species when compared to a neutral species were then compared to each other using the KS test to get a better idea of the consistency of relationships between species at different sites.

3.3 Results

Of the 98 species or genera identified at the four different sites, 63 were found in 5% of the plots at one site at least (Table 13; those species not found in at least 5% of the plots at one site are listed in Table 12) and 41 were present at all four sites. Only two species found at the McGill sites were absent at Dorset and eight species found at Dorset were absent at McGill. This combined with the fact that two-thirds of all species encountered were present at all sites suggests that the plant communities at the different sites were similar.

Of the 41 species present on all sites, 12 showed no relationship to any of the measured variables (Table 14 and 15). Twenty-three species were not found at every site and of those, six showed no response. Only three species showed a relationship to different soil and growth variables at different sites. *Impatiens capensis* was found more often in soils higher in Ca and Mg at both DOR5 and MCG5 but its only association with growth parameter variables was found at DOR4 where it occurred in plots with better survival. It was also associated with higher soil K and clay content and lower soil P:Al ratio content at DOR5 as well as higher pH at MCG5.

Polytrichum spp. was associated with sites that had lower soil Ca, K and Mg at DOR5 and MCG5. It was found in plots with low volume growth at DOR4 and DOR5, low survival at MCG5 and low yield per hectare at DOR4 and MCG5.

Sphagnum spp. also demonstrated an affinity for plots with lower soil Ca and K as well as pH but only at DOR4 and DOR5. It was also associated with lower volume growth, survival and yield per hectare at those two sites. At both DOR5 and MCG5 it was associated with sites with lower foliar N content.

The other species in the analysis that showed responses to soil, growth or foliar variables only tended to show that response at a single site. For example, *Vaccinium* and *Viburnum cassinoides* were both found at plots with lower soil Ca, K and Mg as well as sites with lower foliar Ca but only at DOR5. *Vaccinium* species were also associated with lower volume growth and survival weighted volume growth at DOR4 and DOR5. At DOR5 *Clematis virginiana* was associated with higher soil pH, Ca, K, Mg, volume growth, survival and survival weight growth as well as lower sand content.

When species were compared to each other, rather than a neutral species, more consistent relationships between sites were seen (Table 16). Figure 3 in particular demonstrates the relationship between *Polytrichum spp.* and *Tiarella cordifolia* at the four different sites. *T. cordifolia* was found on more productive plots at MCG5, DOR4 and DOR5 but the species showed no difference in distribution along the volume gradient at DOR3.

G. aparine, *Fragaria*, *I. capensis* and *T. cordifolia* all demonstrated a much stronger affiliation with sites that had higher volume growth, survival and survival weighted volume growth when compared with *Polytrichum* at DOR4, DOR5 and MCG5. DOR3 showed no response in any of the comparisons. *Fraxinus* was also found to be associated with more productive sites at MCG5. *Vaccinium* was not present at MCG5 and *Sphagnum* was likely too infrequent at MCG5 for a significant result.

Comparison of *G. aparine*, *Fragaria*, *I. capensis* or *T. cordifolia* to *Vaccinium* and *Sphagnum* for volume growth, survival and yield per hectare gave significant results at both DOR4 and DOR5.

3.4 Discussion

3.4.1 *Indicator species*

Empirical distribution function analysis discovered positive and negative relationships between many plants and the soil conditions, growth parameter data and foliar nutrient contents. However, the responses were rarely uniform from site to site even when considering only the Dorset sites. This indicates that either none of the species stand out as good indicators of soil pH, nutrients or texture or that they are not abundant enough to be useful as an indicator. When considering the growth parameter and foliar data, inconsistent results may also indicate that each site had different nutrient limitations and therefore different species were indicators of productive sites.

Some species, despite being abundant did not demonstrate a relationship to any of the response variables. Species such as *Rubus idaeus* (Lawesson and Oksanen 2002) and *Acer rubrum* (Abrams 1998; Beckage and Clark 2003) have broad niches making them poor indicators of specific conditions. Other species were either not very abundant at any site (e.g. *Thalictrum*, *Rubus alleghiensis*) or were abundant and good indicators at one or some sites but not very abundant at others (e.g. *Sphagnum*, *Tussilago farfara*, *Fraxinus*).

Clematis virginiana demonstrated a relationship with all growth parameters and many soil variables at DOR5 but this is most likely due to the fact that it is a climbing vine which is more abundant when it has more substrate to climb on. Therefore, *C. virginiana* productivity is facilitated by the hybrid poplar's productivity and is not necessarily the product of responding to similar environmental conditions as the hybrid poplar. This may be the case with many shade tolerant plants as well because more productive sites produce more shade. For instance, *Cornus canadensis* is a small rhizomatous herb of cool woods and bogs that prefers partial shade to full light (Newcomb 1977; Rowe 1983; Johnston and Elliott 1996). It can lay dormant in the soil and grow when a disturbance increases the amount of light reaching the soil (Strong and Sidhu 2005) but its preference for partial shade means that, in this study, it may be more strongly affected by light levels which are governed mainly by the planted hybrid poplars and the productivity other plant species taller than the potential indicator species. This may explain why it was associated with less productive sites at DOR4 but more productive sites at MCG5. The trees at the latter site were more than 1.5m taller and had over six times the volume growth rate than the former site which led to more shade. The shade gradient may have swamped out the gradient that influenced *C. canadensis* distribution at DOR4.

Sphagnum appeared to be highly associated with plots low in soil pH, Ca, K, as well as low volume growth survival and yield per hectare at DOR4 and DOR5. *Sphagnum* is found in mainly nutrient-poor, wet habitats (Vanbreemen 1995) and has the ability to create acidic environments which slow decomposition rates and nutrient cycling (Turetsky 2003). Because *Sphagnum* only occurred at two of 33 plots at MCG5, it was not abundant enough to obtain a significant result. The presence of *Sphagnum* more than likely indicates poor drainage or a high water table, two conditions which hybrid poplar do not tolerate very well (Tullus et al. 2007). Another bryophyte, *Polytrichum*, was also indicative of poor soil conditions and poor growth particularly at MCG5. *Polytrichum commune*, a widely distributed species in the genus, is found on wet soil or rocks and strongly to weakly acidic soils (Bosley et al. 1998) which would make it a good potential indicator species of unproductive sites.

Vaccinium species were found to be highly indicative of poor plots at DOR5 in terms of soil variables (pH, Ca, K, Mg, P) and growth variables (2006 leader growth, volume growth and yield per hectare) which is consistent with what is known of the two *Vaccinium* species encountered at the site, *V. myrtilloides* and *V. angustifolium*. The former *Vaccinium* species was much more frequent than the latter. Both species are found on acidic, infertile soils and in a range of soil moisture levels (Flinn and Pringle 1983; Maillette 1988; Moola and Mallik 1998; Lafond 2009) but *V. myrtilloides* is much more shade tolerant and, unlike *V. angustifolium*, can survive in deep shade, though in a less productive form but producing abundant fruit in the higher light conditions after a fire or clearcut (Vanderkloet and Hall 1981; Moola and Mallik 1998). In Quebec, the large overlap between the two species means that *V. angustifolium* generally replaces *V. myrtilloides* in higher light conditions and *V. myrtilloides* replaces *V. angustifolium* in shadier conditions (Maillette 1988).

Hybrid poplar are less productive at lower soil pH (Bona et al. 2008) therefore the acidophilic nature of both *Vaccinium* species at these sites should make them good indicators of poor sites. In this study however, pH was not a major explanatory variable of any growth parameters with the possible exception of survival at DOR5 and MCG5 with PCR coefficients of 0.2 and 0.25 respectively (see Chapter 2). Nonetheless, when its distribution was compared to *G. aparine*, *Fragaria*, *I. capensis* and *T. cordifolia* with a two sample KS test the distribution of *Vaccinium* was found to be on less productive sites. This may be due to competition between *Vaccinium* species and the hybrid poplars. Ericaceous shrubs including *V. angustifolium* and *V. myrtilloides* have also been found to slow the growth of the *Picea mariana* seedlings (Thiffault et al. 2004).

Impatiens capensis is an annual that tends to be found in mesic sites but can be found at sites with variable soil humidity (Mitchellolds and Bergelson 1990; Heschel et al. 2002; Tabak and von Wettberg 2008). Though the genus *Impatiens* is known for an ability to adapt to environmental variation at small scales (Schoen et al. 1986), some characteristics of *I. capensis* predispose it to being a good indicator of soil moisture. At Mont St-Hilaire, Quebec, Lechowicz et al (1988) found that although only *I. capensis*, and not its congener *I. pallida*, grew on the wetter sites, its growth and fecundity decreased when soils became too wet or waterlogged. This is consistent with the two species comparison analysis where *I. capensis* had a higher relative abundance at more productive sites and sites with higher survival when compared to more hydrophyllic species such as *Sphagnum* or *Polytrichum*. Lechowicz et al (1988) also found a relationship between the size of *I. capensis* plants and availability of K in the soil which is consistent with the principal component regression analysis of Chapter2 which found that soil K was an important explanatory variable for basal area at DOR4 and survival at both DOR5 and DOR4.

Only two species of *Fragaria* occur in Quebec, *F. vesca* and *F. virginiana*, and both occurred at the field sites. Both species can tolerate a wide variety of different moisture regimes (Munger 2006), can be found on moderately fertile sites in old fields, meadows and forest openings (Angevine 1983; Kashian et al. 2003; Blatt et al. 2005; USDA-NRCS 2006), are quick colonizers of disturbances including clearcutting and fire (Jurik 1983; Roberts and Gilliam 1995; Penney et al. 2008) and can exist through different successional stages (Jurik 1983) though *F. vesca* occurs more often in mature forests (Angevine 1983; Jurik 1983). *Fragaria* did not demonstrate a relationship to any soil variable but was found on more productive sites at DOR5 and, using the t8wo sample KS test, was found at more productive sites than *Polytrichum* at DOR4, DOR5 and MCG5. Its affinity for more productive sites combined with its ability to colonize disturbances make *Fragaria* a good post-harvest indicator species, particularly when compared to *Polytrichum* which also spreads quickly into disturbances (Penney et al. 2008). The two genera rarely co-occurred and one genus or the other could be found on half to three-quarters of the sites. Even when the species did co-occur, one species was usually dominated the other.

Tiarella cordifolia is a shade-tolerant perennial herb that grows in moist, rich woods (Adam and Kitto 1993; Ford et al. 2000; Rothstein and Zak 2001a) known to have a strong N uptake capacity relative to other deciduous herbs (Rothstein and Zak 2001b). These characteristics combined with its abundance across all four sites and its strong association with more productive sites when compared with *Sphagnum*, *Polytrichum* and *Vaccinium* mean that it has good potential as an indicator. However, its growth habit of accruing 75% of its biomass growth during the spring and autumn (Rothstein and Zak 2001a), when there is less shade, may give it an advantage over less shade tolerant species and thus *T. cordifolia* abundance may be tied to hybrid poplar productivity. Shade tolerance combined with an affinity for moist, rich sites may make it a good potential pre-harvest indicator species.

Galium aparine is a semi-self supporting, herbaceous annual (Goodman 2005) that prefers moderate to poor drainage (Auclair et al. 1973; Holmes et al. 2004; Legare et al. 2001). It climbs without twining by using small bristles (Darwin 1891; Puntieri and Pysek 1998) or if no substrate is available can exist prostrate (Mamarot 1996; Puntieri and Pysek 1998). Chen et al. (2004) found that a congener, *Galium trifidum*, occurred almost exclusively on sites with the highest *Populus* site-index class in monodominant stands in British Columbia. Another congener *Galium triflorum* was found to be strongly positively associated to stands of *Populus tremuloides* (Legare et al. 2001). In this study, it was only found on more productive sites relative to *Sphagnum*, *Polytrichum* and *Vaccinium* and not when compared to a neutral species but this finding combined with previous studies indicating an association between *Populus* and *Galium spp.* make *Galium aparine* a potential indicator of productive sites. Also, Small and McCarthy (2002) found that *G. aparine* grew significantly less under low light conditions but there was no significant difference between moderate and high light levels meaning that the association of *G. aparine* with productive sites is not likely due to facilitation due to shading.

Fraxinus only occurred in sufficient abundance at MCG5 but has the potential to be an indicator of fertile sites. Bigelow and Canham (2002) found that *Fraxinus americana* occurred on soils with high Ca and Mg and was found at the higher end of the pH gradient. This is consistent with MCG5 where *Fraxinus* was found in plots with a higher soil pH and Mg content. Also, though the PCR analysis at MCG5 showed no relationship between soil characteristics and any growth parameters variable except survival (see previous chapter), *Fraxinus* was strongly related to volume growth, survival and yield per hectare. *Fraxinus americana* is more productive in high moisture valleys (Frey et al. 2007) and the emergence of seeds has been found to be associated with high soil N and soil moisture (Messaoud and Houle 2006). This may suggest that soil moisture may have been limiting at MCG5 due to the steeper slopes which facilitate overland flow.

3.4.2 *Methodological issues*

The multicollinearity in the data discussed in last chapter can be seen in the EDF analysis. Many plants that responded either positively or negatively to one variable responded in the same manner to collinear variables. For instance, many plants had similar responses to soil Ca, K and Mg because they were closely correlated. This limits EDF in its ability to discriminate between soil variables.

Many of the species that emerged from the analysis were primary successional species and thrive after a disturbance but are not present in suitable quantities before the disturbance to act as pre-harvest indicators (e.g. *Fragaria*, *Polytrichum*). This limits the ability of the indicator species analysis to identify species that could act as indicators pre-harvest. Species such as *V. myrtilloides* and *I. capensis* that can tolerate the heavy shade of a mature forest could be present pre-harvest and therefore could act as a potential pre-harvest indicator species.

A possible source of bias was that no measurements were recorded for plots that could not be located. These plots were most often those where all the trees had died. This has the consequence of underrepresentation of the least productive sites. This may have limited the indicator species analysis' ability to detect species associated with low productivity sites. This technique would be improved with the inclusion of such low productivity sites.

3.5 Conclusion

The EDF analysis suggested *Galium aparine*, *Fragaria*, *Tiarella cordifolia*, and *Impatiens capensis* as potential indicators of productive hybrid poplar sites. *Fraxinus* was also found to be a good indicator of hybrid poplar productivity but only at MCG5. *Polytrichum*, *Vaccinium*, and *Sphagnum* tended to be found more often on less productive sites suggesting they could be indicators of poor sites.

The flexibility of the EDF method means that it can be used to quickly generate a list of species that tend to be found on less or more productive sites. This list can provide information about productivity potential of microsites providing the forester or planter with information at scales that may normally not be accessible. The information can also be used for larger scale decisions such as where to cut, if pre-harvest species can be found to indicate productive or unproductive sites (e.g. *V. myrtilloides*), or which sites will require site preparation or other management interventions. If an indicator species list can be developed for different clones in the same region, there exists the potential that indicator species can suggest which clone is better suited for specific plots or even specific microsites.

Figures and Tables: Chapter 3

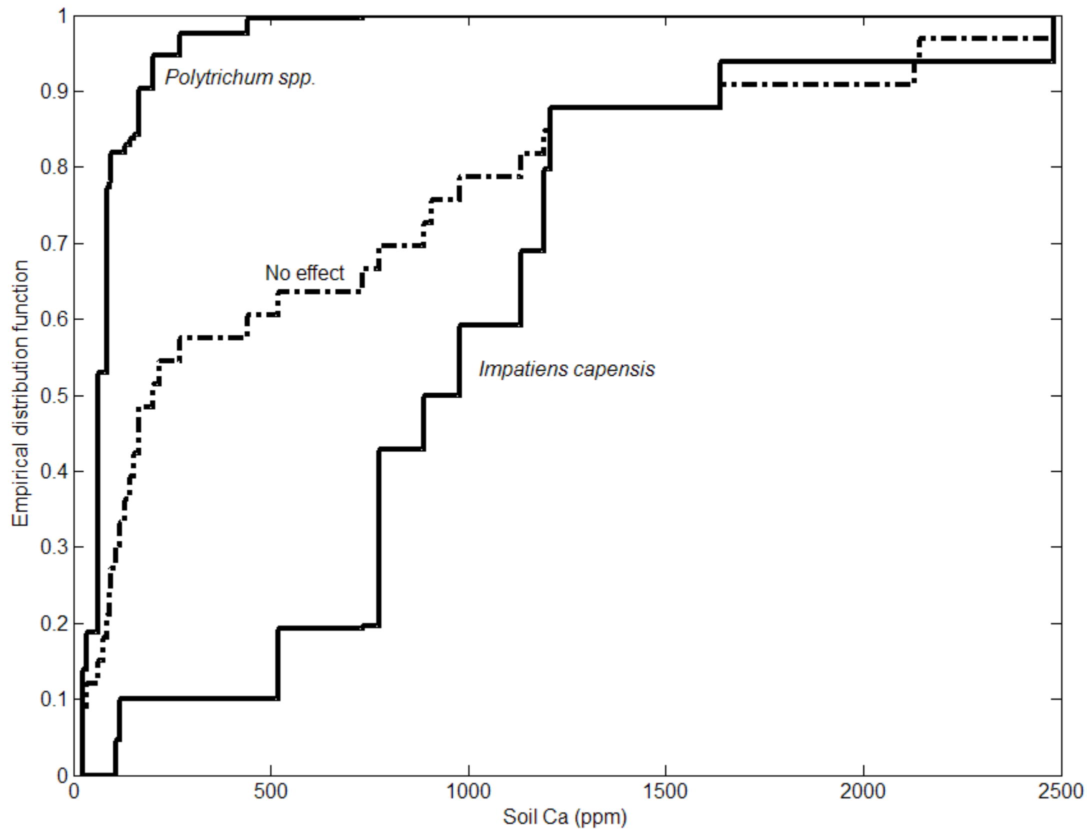

Figure 2 – Example of an EDF plot of *Polytrichum* and *Impatiens capensis* along a soil Ca gradient. The no effect line represents a theoretical neutral species that is not affected by the Ca gradient and therefore appears on every site with equal abundance.

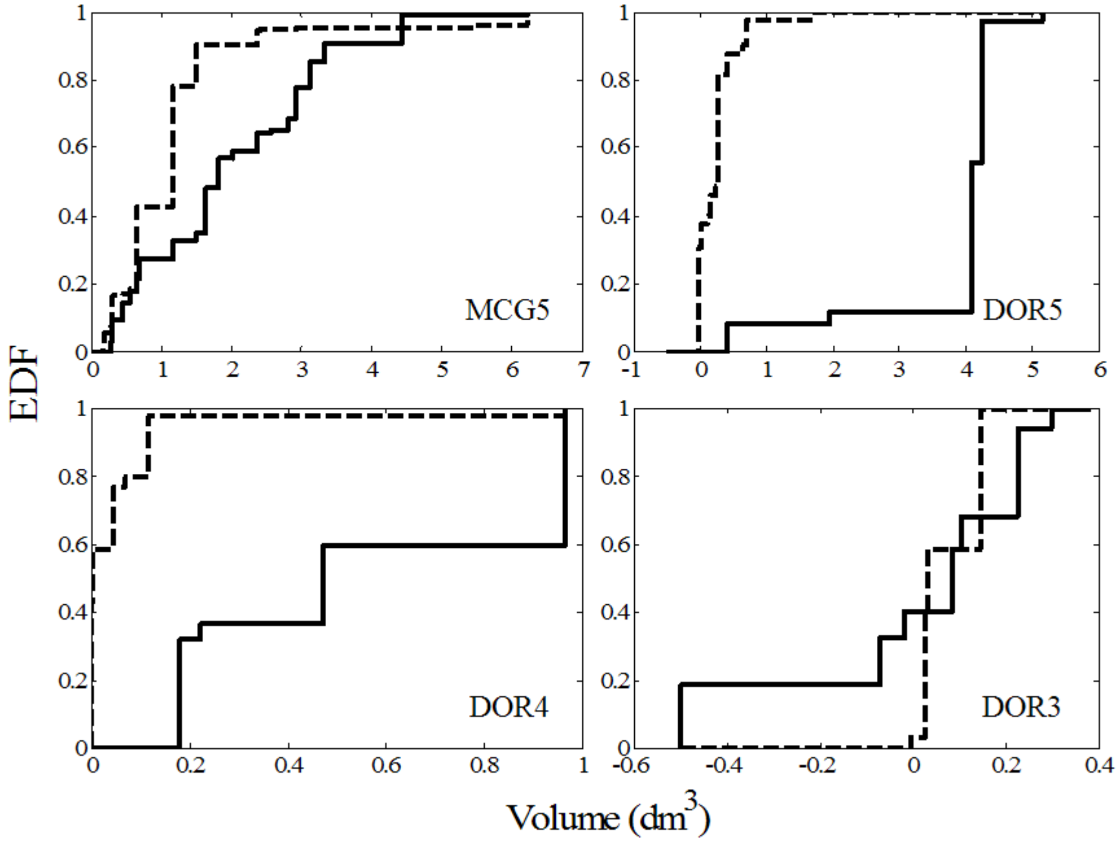

Figure 3 – EDF analysis of two species, *Polytrichum spp.* (dashed line) and *Tiarella cordifolia* (solid line) with stem volume growth as the gradient.

Table 12. List of species that were encountered but not at more than 5% of the plots at least at one of the sites.

Species
Abies balsamea
Acer pensylvanicum
Acer spicatum
Arisaema triphyllum
Carex canescens
Carex debilis
Carex gracillima
Chelone glabra
Clintonia borealis
Coptis groenlandica
Erigeron philadelphicus
Fagus grandifolia
Geum rivale
Gymnocarpium dryopteris
Larix laricina
Linnaea borealis
Lonicera canadensis
Maianthemum canadensis
Malva neglecta
Matteucia Struthiopteris
Oxalis stricta
Picea glauca
Pleurozium sp.
Prunus serotina
Ribes sp.
Sambucus canadensis
Smilacina racemosa
Sorbus americana
Spirea alba
Trillium cernuum
Ulmus sp.
Viburnum alnifolium
Viccia cracca

Table 13. The proportion of plots in which each plant species was present at each site. 'A' indicates the plant species was absent at that site.

Species name	MCG5	DOR5	DOR4	DOR3
Acer rubrum	0.48	0.36	0.70	0.76
Acer saccharum	0.42	A	A	A
Alnus spp.	0.03	0.28	0.15	0.19
Anaphalis margaritacea	0.48	0.08	0.50	0.24
Aralia nudicaulis	0.15	0.19	0.45	0.05
Aster puniceus	0.12	0.58	0.65	0.38
Aster umbellatus	0.09	0.42	A	A
Athyrium felix-femina	0.36	0.25	0.45	0.05
Bare soil	0.91	0.97	1.00	1.00
Betula alleghaniensis	0.33	0.03	A	0.05
Betula papyrifera	A	0.19	0.10	0.05
Betula populifolia	0.12	0.03	0.25	0.29
Carex arctata	0.03	0.17	0.20	0.10
Carex echinata	0.06	0.03	0.05	0.29
Carex gynandra	0.36	0.42	0.35	0.33
Carex intumescens	0.21	0.53	0.75	0.81
Carex sect. ovales	0.33	0.69	0.60	0.81
Carex stipata	0.15	0.36	0.40	0.48
Cirsium spp.	0.31	A	A	A
Clematis virginiana	0.21	0.39	0.20	A
Cornus canadensis	0.15	0.19	0.40	0.33
Corylus cornuta	0.03	0.19	A	A
Dennstaedtia punctilobula	0.18	0.03	A	A
Dryopteris spp.	0.33	0.36	0.25	0.24
Epilobium angustifolium	0.24	0.06	0.10	0.38
Epilobium leptophyllum	0.09	0.22	0.10	0.24
Equisetum spp.	0.15	0.25	0.40	0.33
Eupatorium maculatum	0.06	0.19	0.15	0.24
Euthamia graminifolia	0.91	0.72	0.90	0.76
Fragaria spp.	0.48	0.56	0.55	0.38
Fraxinus spp.	0.30	0.03	A	0.05
Galium aparine	0.12	0.22	0.20	0.14
Hieracium spp.	0.48	0.08	0.40	0.24
Impatiens capensis	0.36	0.33	0.25	0.10
Juncus spp.	0.67	0.44	0.75	0.95
Nemopanthus mucronatus	A	0.08	A	0.10
Onoclea sensibilis	0.52	0.28	0.20	0.29
Osmunda spp.	0.27	0.25	0.20	0.10
Panicum spp.	0.39	0.69	0.75	0.76
Phalaris arundinacea	0.12	0.44	0.10	0.43
Polygonum sagittatum	A	0.22	0.15	0.29
Polytrichum spp.	0.48	0.31	0.30	0.19
Populus balsamifera	A	0.03	A	A

Table 13 - continued

Species name	MCG5	DOR5	DOR4	DOR3
Populus tremuloides	0.48	0.67	0.45	0.24
Potentilla norvegica	0.42	0.03	0.15	0.29
Prunus virginiana	0.03	0.22	0.10	A
Pteridium aquilinum	0.48	0.25	0.15	A
Rubus allegheniensis	0.15	A	A	0.14
Rubus hispidus	0.12	0.19	0.35	A
Rubus idaeus	0.09	0.97	1.00	0.95
Rubus pubescens	0.36	0.72	0.95	0.76
Salix spp.	0.91	0.39	0.50	0.71
Scirpus spp.	0.33	0.83	0.95	0.90
Seneccio schweinitzianus	A	A	0.15	0.10
Solidago canadensis	0.12	0.44	0.85	0.57
Solidago rugosa	0.03	0.94	0.90	1.00
Sphagnum spp.	0.06	0.17	0.25	0.24
Spirea tomentosa	0.36	0.03	0.15	0.05
Thalictrum spp.	0.21	0.08	A	A
Thelypteris noveboracensis	0.33	A	0.15	0.33
Tiarella cordifolia	0.15	0.14	0.25	0.38
Tussilago farfara	0.31	0.03	A	0.05
Vaccinium spp.	0.21	0.22	0.15	0.05
Viburnum cassinoides	0.15	0.39	0.20	0.05

Table 14. EDF analysis comparing each species to a theoretical neutral species. '+++', '++' and '+' represent an association with higher levels of a soil variable at the 0.01, 0.05 and 0.1 significance levels respectively. '---', '--' and '-' represent an association with lower levels of a soil variable at the 0.01, 0.05 and 0.1 significant levels respectively. 'A' indicates the plant species was absent at that site.

	pH			C:N			Ca			K			Mg			P:Al			clay			sand		
	M5	D5	D4	M5	D5	D4	M5	D5	D4	M5	D5	D4	M5	D5	D4	M5	D5	D4	M5	D5	D4	M5	D5	D4
Acer rubrum		--						-																
Acer saccharum		A	A		A	A		A	A		A	A		A	A		A	A		A	A		A	A
Alnus spp.		-									--									--				
Anaphalis margaritacea																								
Aralia nudicaulis	+												+											
Aster puniceus																								
Aster umbellatus	--		A			A			A			A			A			A			A		+	A
Athyrium felixfemina	+																							
Betula alleghaniensis			A			A			A			A			A			A			A			A
Betula papyrifera	A	-		A			A	-		A			A			A			A			A		
Betula populifolia																								
Carex arctata																								
Carex echinata																								
Carex gynandra				-																				
Carex intumescens																								
Carex sect. ovales																								
Carex stipata	+						+			+			+											
Cirsium spp.		A	A		A	A		A	A		A	A		A	A		A	A		A	A		A	A
Clematis virginiana		++						++			++			+									--	
Cornus canadensis	++		-				+		--	-		-	+		--	+			-			++		
Corylus cornuta			A			A			A			A			A			A			A			A
Dennstaedtia punctilobula	--		A			A	--		A			A	-		A			A			A			A
Dryopteris spp.																								
Epilobium angustifolium																								
Epilobium leptophyllum																					+			
Equisetum spp.	+	-						-		+				-										
Eupatorium maculatum								++			++			++						++			--	
Euthamia graminifolia																								
Fragaria spp.													+											
Fraxinus spp.	++		A			A			A			A	+		A			A			A			A
Galium aparine								+			+		+							+				
Hieracium spp.																								
Impatiens capensis	++						++	++			++		++	++			--			+++				
Juncus spp.								++						++		M5								

Table 14 continued

	pH			C:N			Ca			K			Mg			P:Al			clay			sand		
	M5	**D5**	**D4**	**M5**	**D5**	**D4**	**M5**	**D5**	**D4**	**M5**	**D5**	**D4**	**M5**	**D5**	**D4**	**M5**	**D5**	**D4**	**M5**	**D5**	**D4**	**M5**	**D5**	**D4**
Nemopanthus mucronatus			A			A			A		--	A			A			A			A			A
Onoclea sensibilis	+					-		+					+	+										
Osmunda spp.												+												+
Panicum spp.																+								
Phalaris arundinacea		++		--															--				-	
Polygonum sagittatum	A			A			A	+		A			A	+		A			A			A		
Polytrichum spp.	--						---	-		--	-	-	--	-			--					-		
Populus balsamifera	A		A	A		A	A		A	A		A	A		A	A		A	A		A	A		A
Populus tremuloides													-											
Potentilla norvegica				+																				
Prunus virginiana	A			A			A			A			A			A			A			A		
Pteridium aquilinum	A	-	-	A			A	-		A			A	-		A			A			A		
Rubus allegheniensis		A	A		A	A		A	A		A	A	-	A	A		A	A		A	A	+	A	A
Rubus hispidus	A			A			A			A			A			A			A	+		A	-	
Rubus idaeus																								
Rubus pubescens	+												+											
Salix spp.																								
Scirpus spp.																								
Seneccio schweinitzianus		A			A			A			A			A			A			A			A	
Solidago canadensis																								
Solidago rugosa																								
Sphagnum spp.		--	--		--			--	--		-	-		--			--	+						
Spirea tomentosa				+																	+			-
Thalictrum spp.		+	A			A			A			A			A			A			A			A
Thelypteris novaboracensis		A			A			A			A			A			A		+	A		-	A	
Tiarella cordifolia																								
Tussilago farfara	++		A			A	+		A	+		A	++		A			A			A			A
Vaccinium spp.	A	-		A			A	--		A	-		A	--		A	--		A			A		
Viburnum cassinoides	A	-		A			A	--		A	--		A	--		A			A	--		A		

Table 15. EDF analysis comparing each species to a theoretical neutral species along a gradient of hybrid poplar productivity. '+++', '++' and '+' represent an association with higher levels of a soil variable at the 0.01, 0.05 and 0.1 significance levels respectively. '---', '--' and '-' represent an association with lower levels of a soil variable at the 0.01, 0.05 and 0.1 significant levels respectively. 'A' indicates the plant species was absent at that site.

	2006 leader growth				Volume growth				Survival				Yield per hectare			
	M5	D5	D4	D3	M5	D5	D4	D3	M5	D5	D4	D3	M5	D5	D4	D3
Acer rubrum																
Acer saccharum		A	A	A		A	A	A	+	A	A	A		A	A	A
Alnus spp.										-						
Anaphalis margaritacea	-															
Aralia nudicaulis					+					++						
Aster puniceus																
Aster umbellatus			A	A			A	A	+	+	A	A			A	A
Athyrium felixfemina																
Betula alleghaniensis			A				A				A				A	
Betula papyrifera	A				A	-			A				A	-		
Betula populifolia																
Carex arctata																
Carex echinata																
Carex gynandra																
Carex intumescens																
Carex sect. ovales																
Carex stipata																
Cirsium spp.		A	A	A		A	A	A		A	A	A		A	A	A
Clematis virginiana		+		A		++		A		+		A		++		A
Cornus canadensis					+		--		+				+		--	
Corylus cornuta			A	A			A	A			A	A			A	A
Dennstaedtia punctilobula			A	A			A	A			A	A			A	A
Dryopteris spp.	+															
Epilobium angustifolium																
Epilobium leptophyllum																
Equisetum spp.																
Eupatorium maculatum																
Euthamia graminifolia																
Fragaria spp.		+				+				+				++		
Fraxinus spp.	+		A		++		A		+++		A		++		A	
Galium aparine											++					
Hieracium spp.																
Impatiens capensis											+					
Juncus spp.									+							

Table 15. continued

	2006 leader growth				Volume growth				Survival				Yield per hectare			
	M5	D5	D4	D3	M5	D5	D4	D3	M5	D5	D4	D3	M5	D5	D4	D3
Nemopanthus mucronatus			A			--	A			--	A			--	A	
Onoclea sensibilis																
Osmunda spp.	+															
Panicum spp.											+					
Phalaris arundinacea						+								++		
Polygonum sagittatum	A				A				A		+		A		+	
Polytrichum spp.	--	--				-	-		--				--		-	
Populus balsamifera	A		A	A	A		A	A	A		A	A	A		A	A
Populus tremuloides	-				-											
Potentilla norvegica																
Prunus virginiana	A			A	A			A	A		+	A	A			A
Pteridium aquilinum	A			A	A			A	A			A	A			A
Rubus allegheniensis		A	A			A	A			A	A			A	A	
Rubus hispidus	A			A	A			A	A			A	A			A
Rubus idaeus																
Rubus pubescens	+															
Salix spp.																
Scirpus spp.																
Seneccio schweinitzianus		A				A				A				A		
Solidago canadensis												++				
Solidago rugosa																
Sphagnum spp.		--	++			--	--			-	--			--	--	
Spirea tomentosa																
Thalictrum spp.			A	A			A	A			A	A			A	A
Thelypteris novaboracensis		A				A				A	+			A		
Tiarella cordifolia		++				++								++		
Tussilago farfara			A				A		++		A				A	
Vaccinium spp.	A	-			A	--	-		A				A	--	-	
Viburnum cassinoides	A				A				A				A			

Table 16. Kolmogorov-Smirnov two sample tests of species associated with high productivity to species associated with low productivity across volume growth (V), survival (S) and volume yield (VY) gradients. '+' indicates significant at 0.1, '++' indicates significant at 0.05, '+++' indicates significant at 0.01, 'NS' indicates not significant and 'A' indicates one of the species was not present on that site.

		MCG5			DOR5			DOR4			DOR3		
High productivity	**Low productivity**	**V**	**S**	**VY**	**V**	**S**	**VY**	**V**	**S**	**VY**	**V**	**S**	**VY**
Gallium aparine	*Polytrichum sp.*	+	++	++	+++	NS	+++	+++	++	+++	NS	NS	NS
Fragaria sp.	*Polytrichum sp.*	++	+++	+++	+++	NS	+++	+++	+	+++	NS	NS	NS
Impatiens capensis	*Polytrichum sp.*	+++	+++	+++	++	NS	NS	+++	+++	+++	NS	NS	NS
Tiarella cordifolia	*Polytrichum sp.*	+++	+++	+++	+++	NS	+++	+++	+++	+++	NS	NS	NS
Fraxinus sp.	*Polytrichum sp.*	+++	+++	+++	NS	NS	NS	NS	NS	NS	NS	NS	NS
Gallium aparine	*Vaccinium sp.*	A	A	A	+++	++	+++	++	++	++	NS	NS	NS
Fragaria sp.	*Vaccinium sp.*	A	A	A	+++	++	+++	+++	++	+++	NS	NS	NS
Impatiens capensis	*Vaccinium sp.*	A	A	A	+++	++	+++	+++	+++	+++	NS	NS	NS
Tiarella cordifolia	*Vaccinium sp.*	A	A	A	+++	+	+++	+++	++	+++	NS	NS	NS
Gallium aparine	*Sphagnum sp.*	NS	NS	NS	+++	+++	+++	+++	+++	+++	NS	NS	NS
Fragaria sp.	*Sphagnum sp.*	NS	NS	NS	+++	+++	+++	+++	+++	+++	NS	NS	NS
Impatiens capensis	*Sphagnum sp.*	NS	NS	NS	+++	+	+++	+++	+++	+++	NS	NS	NS
Tiarella cordifolia	*Sphagnum sp.*	NS	NS	NS	+++	+++	+++	+++	+++	+++	NS	NS	NS

Chapter 4:

Conclusion

Unimproved plantations (i.e. unfertilized or limed) of different hybrid poplar clones on forest sites have met with limited amounts of success in southern Quebec. In order to achieve levels considered average for Quebec, some plantations may require improved drainage, the addition of lime or fertilizer application to increase soil pH and nutrient levels.

The difference between the productivity of the McGill plantation relative to Dorset plantations in terms of survival and volume growth demonstrates that sites with relatively similar concentrations of soil nutrients can behave very differently. On smaller scales, the variance component analysis indicates that even within one site, microsite difference on a scale of 3-9 m may be more important that larger scale variation (100-1000 m). Both these results can complicate site selection for hybrid poplars and how foresters make decisions about these plantations.

The challenge in selecting sites that have a high potential to promote hybrid poplar production could be addressed, in part, using indicator species. This study found that species such as *Galium aparine*, *Fragaria*, *Fraxinus*, *Impatiens capensis* and *Tiarella cordifolia* tended to associate with more productive sites while species such as *Polytrichum*, *Sphagnum* and *Vaccinium* associated with low productivity sites. The presence of these species, particularly when in high abundance, provides some information about the potential productivity of a given microsite. The relationship between *Polytrichum* and species associated with high productivity was particularly strong across all sites except DOR3 making them good potential indicator species for the establishment of new plantations.

These indicator species could be used for plantations in southeastern Quebec and possibly other regions with similar climates and flora. It would preferable, however, for the EDF analysis to be tailored to different regions when young plantations already exist. A large quantity of data on tree height, dbh and survival along with relative abundance data can be gathered within a day. Because the EDF analysis is not mathematically complex, a list of indicator species can quickly be generated and used to make site selection or other site management decisions within a short period of time providing foresters with regional or site specific indicator species lists relatively easily. If the EDF indicator species analysis was applied broadly, lists of indicator species could be developed for different clones which could aid in clone allocation.

Indicator species can provide information on small scale variation allowing the planter to make quick, on-site decisions about preferred microsites. For instance, if a patch of *Fragaria* is next to a patch of *Polytrichum* it would preferable to plant a tree in the former. The indicator species list can be tailored to the level of botanical knowledge of the forester performing the EDF analysis or the planter applying the list. In this study, the indicator species are quite distinct and easily identifiable demonstrating that specialized knowledge of botany is not a prerequisite of the analysis.

The next step in this research would be to test the indicator species by finding places where indicator species from this analysis are located and plant trees. Given sufficient resources, one could plant a number of trees in a locations dominated by different plants with the plots being as close together as possible so as to the limit the number of confounding factors. The difference in volume between the plots would be an indication of the increased productivity using indicators species could give.

One drawback is that the area of productive ground would be limited by the abundance of indicator species. If the indicators of productive sites are few and the indicators present suggest a wet, therefore poor site, one could plant a hybrid better suited to wet conditions. Another drawback is that a customized indicator species list for a region cannot be obtained for the first plantations established. In this case, indicator species from this study or nearby regions could be used and the site selection guidelines could be adjusted when the first plantations are old enough that an EDF analysis can be performed on them. Ideally, these lists would be generated from four or five year old plantations that are beyond the dieback stage but have not grown sufficiently to close the canopy so site specific indicators species lists could only be generated after that period of time.

Overall, using the EDF analysis to identify plant species that tend to grow on productive sites provides a quick method of assessing the potential productivity of sites on both small, microsite scales and on larger, landscape scales.

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