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POST-HARVEST VIGOR INDICATORS FOR NATURALLY REGENERATED
BLACK SPRUCE ON PALUDIFIED SOILS

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NATURELLEMENT APRÈS COUPE SUR DES SURFACES PALUDIFIÉES

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PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE LA MAÎTRISE EN BIOLOGIE

PAR
ALEXANDER CAMPBELL

JUIN 2013

UNIVERSITÉ DU QUÉBEC À MONTRÉAL
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"You are what you repeatedly do. Excellence, then, is not an act, but habit."

- Aristotle

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LIST OF ABBREVIATIONS, INITIALS AND ACRONYMS

ANOVA	Analysis of Variance
CLAAG	Careful Logging Around Advance Growth
CPRS	Cutting with Protection of Regeneration and Soil
DBH	Diameter at Breast Height
DGH	Diameter at Ground Height
FM	Fresh Mass
HV	High Vigor
LB	Lateral Branch
LCR	Live Crown Ratio
LDA	Linear Discriminant Analysis
LN	Liquid Nitrogen
LV	Low Vigor
MFA	Multiple Factor Analysis
OM	Organic Matter
PCA	Principal Component Analysis
RDA	Redundancy Analysis
RHI	Relative Height Increment
SD	Standard Deviation
SNW	Specific Needle Weight

RÉSUMÉ/ABSTRACT

Pour continuer à exploiter les épinettes noires de la forêt boréale, il est important que la régénération naturelle dans cette région se fasse adéquatement. Par contre, pour des raisons diverses, plusieurs arbres en régénération dans la forêt boréale ont un taux de croissance stagnant même s'ils se développent en conditions de pleine lumière. Puisque la paludification est un problème récurrent dans le nord-ouest québécois, les conditions de limitation de croissance sont liées au sol et aux processus sous terrains. Des indicateurs de vigueur pourraient déterminer si les arbres reprennent leur croissance ou demeurent en stagnation. Lors de l'été 2011, des données concernant la morphométrie et la physiologie des épinettes noires en régénération naturelle ($n = 390$) ont été recueillies en vue de déterminer lesquelles sont les plus aptes à évaluer la vigueur chez cette espèce. À l'aide d'une analyse discriminante, nous avons essayé de déterminer s'il était possible d'identifier un seuil pour démarquer les arbres vigoureux des arbres peu vigoureux. Des indicateurs morphologiques et physiologiques ont été mesurés pour identifier la vigueur des arbres. Les outils présentement utilisés par les forestiers lors des inventaires forestiers ne sont pas toujours capable d'évaluer correctement les patrons de croissance des épinettes noires en milieu paludifié. Cette étude suggère que le taux de croissance apicale ainsi que la longueur de la flèche terminale, deux indicateurs mesurés présentement, sont les plus aptes à évaluer la vigueur de la régénération des épinettes noire.

Mots-clefs: paludification, morphologie, physiologie, fluorescence, processus sous terrains

To ensure a sustainable exploitation of black spruce in the boreal forest, it is important that natural regeneration grows adequately in this region. For different reasons however, many regenerating black spruce in the boreal forest have weak growth and this even though they grow in full light conditions. Growth stagnation is a recurring problem for pre-established young black spruce trees growing after clearcutting in paludified regions of the boreal forest. Identifying full light post-harvest vigor indicators pertaining to tree growth would help detect trees of high and low vigor. During the summer of 2011, data pertaining to morphological and physiological components of black spruce ($n = 390$) were collected in order to determine which variables were ideal for evaluating vigor. Linear discriminant analysis was used to determine whether a threshold could be identified in order to classify trees as high or low vigor. Morphological and physiological variables were measured for the purpose of relating them to tree vigor. The tools currently implemented by foresters during forest inventories do not always properly evaluate the regeneration success of naturally regenerated post-harvest black spruce trees in paludified regions. This study suggests that height growth rate and leader length however, two indicators currently used, still most aptly evaluate vigor for regenerating black spruce.

Key words: paludification, morphology, physiology, fluorescence, belowground processes

GENERAL INTRODUCTION

The boreal forest is the largest land biome in the world. The North American boreal forest boasts one of the most important tree species for the saw, pulp and paper industry, black spruce (*Picea mariana* (Mill.) BSP), and as such, this forested area has been extensively exploited over the past few decades. As exploitation continues, forest management issues move from planning harvesting mature and overmature natural stands to predicting the development of second growth stands that recruit following clearcutting.

Many tools are useful in making a diagnosis for future regeneration. Basal area measurements aid foresters and researchers alike in gauging stand productivity. Stand density, the quantitative measure of one or more physical characteristics of a forest stand expressed per unit area (Ernst and Knapp, 1985), inform us about tree density, tree volume per unit area or mass. Stocking, describes the spatial distribution of stems (overstocked, understocked or fully stocked) at any level of stand density with respect to a silvicultural goal (Johnson et al., 2002). Stocking, however, should not be estimated without knowing stand basal area in order to get a proper appraisal of stand stocking. As such, a fully stocked stand refers to the point at which both height growth for individual trees and basal area can be maximized for the overall stand (Strobl, 2000). Thus, overstocked stands have too many trees and wood is lost when natural self-thinning occurs whereas understocked stands may generate large sized trees but too few of them to maximize basal area growth rate per unit area. These different measurements can give rise to normal yield tables for individual species, which can predict future yields based on stand age. However, tables, such as stand density management diagrams, are not developed for the early ages of stand development immediately after a disturbance (fire,

outbreak, windthrow, clearcutting). They more commonly shed light on stand development after 20 years of recruitment (Newton, 1997).

Up until now, young stems have been used as indicators to discern whether or not a seedling is growing under good or poor conditions. These seedlings can be described as free-to-grow trees. Different definitions of free-to-grow trees have been developed. Definitions differ depending on the species in question and on forest guidelines set out by the governing jurisdiction. In British Columbia, free-to-grow standards are applied to the area in question and not specifically to the trees such that the British Columbia government states “that an area is considered to be free-to-grow when the regenerating trees are free of reasonably foreseen impediments to growth”. Manitoba has a similar standard but is also more specific towards free-to-grow trees whereby a free-to-grow tree must be well established and at a 1.5 m from any hardwood competition and other free-to-grow trees (Manitoba Conservation, 2010). Hardwood individuals must also not be equal to or exceed 66% of the height of the said free-to-grow tree, otherwise it is deemed a competitor. Contrastingly, Alberta modified their provincial reforestation standards in 2010, moving away from the traditional free-to-grow standards and adopted the Reforestation Standard of Alberta (RSA). The RSA is based on meeting or exceeding forest management requirements developed in the Forest Management Plan (Alberta Environment and Sustainable Resource Development, 2013). In Quebec, however, no definition is given for free-to-grow trees.

Most free-to-grow definitions are developed mainly to assess competitive interactions between stems of similar size, mostly for light. Developing regenerating stands, however, are not always limited by light availability. In some cases, limitation to

regeneration growth comes from soil conditions encountered immediately after clearcutting. The occurrence of less productive soil conditions can limit black spruce growth and contribute to the slow return of merchantable stands. In Quebec's boreal forest, these less productive soil conditions are most commonly associated with paludification.

The slow accumulation of a thick organic matter horizon, partially in response to *Sphagnum* spp. proliferation, is commonly referred to as paludification. Owing to the presence of the Clay Belt, drainage in some zones of northwestern Quebec is poor and the ground surface is prone to *Sphagnum* spp. proliferation, which can lead to a loss of forest productivity (Simard et al, 2007). Paludification decreases soil temperature, nutrient availability and thereby forest productivity (Bernier et al., 2008). Two types of paludification have been described, edaphic and successional. Edaphic paludification occurs when local microtopography retains a high moisture level, resulting in a buildup of sphagnum species and an accumulation of the organic layer (Bernier et al., 2008). Successional paludification on the other hand, typically characterizes surfaces that were exposed to severe fire and have gradually transitioned from hypnaceous mosses to heliophilic sphagnum (Bernier et al., 2008). It has been suggested that sphagnum moss covering the seedbed is a good microclimate for black spruce seedling establishment and germination due to a higher moisture level and increased water supply (Lavoie et al., 2005). Yet, following seedling establishment, growth becomes more dependent on nutrient acquisition than on water availability, and so, sphagnum, which was helpful in the early stages of seedling development, now suppresses seedling growth (Lavoie et al., 2005). Consequently, paludification contributes to the loss of forest productivity in that it

stalls tree growth (St-Denis et. al., 2010). This is especially problematic in paludified areas, such as occur in Scandinavia, Alaska, northern Minnesota, northeastern Ontario and northwestern Quebec where paludification can induce a stagnated growth phase (Groot & Hökkä, 2000).

Moreover, studies (Johnstone and Kasischke, 2005; Moss and Hermanutz, 2009) have shown that even after severe burns in regions that have high organic layers, black spruce establishment is not necessarily optimal. Johnstone and Kasischke (2005) observed that postfire spruce densities were unrelated to prefire spruce basal area, which suggests that predisturbance basal area measurements may be misleading when trying to estimate future yields of post-disturbance stands. Drought and herbivory are also factors that can negatively affect postfire black spruce seedling recruitment (Moss and Hermanutz, 2009).

In many cases, regenerating trees present in northern Quebec could be considered free-to-grow as they are in high light environments without shrub or ericaceous competitors while having stagnated growth. I thus propose that a more biologically meaningful definition should ensure that natural regeneration is considered both free-to-grow and vigorous (Brand and Weetman, 1986). If a vigor indicator were developed, it would help foresters to judge overall stand health. That is to say, with a more precise indicator, foresters, within 10 years of stand initiation, should be able to evaluate when and which type of silvicultural treatment (if any) is needed to ensure adequate development (or growth) for a stand in question.

INTRODUCTION

Black spruce (*Picea mariana* (Mill.) BSP) is the dominant species of the North American boreal forest. This species has important commercial interest as it is the main resource for pulp and paper production and wood transformation, and thus the forest industry depends on a continual and sustainable production of merchantable trees in order to remain profitable. Therefore post-harvest black spruce regeneration needs to be closely followed to ensure optimal stocking and growth on sites to be harvested in the future. Multiple harvest methods have been implemented, however, cutting with protection of advance regeneration and soil (CPRS) is now the dominant harvest method. CPRS was developed to take advantage of advance regeneration and speed the time it takes to recruit a new stand and thus maximize wood production (Harvey and Brais, 2002), though the effectiveness of the method for all forest types is still disputed. On forested peatlands for example, where poor drainage and soil conditions impede tree growth, CPRS has had mixed results (Roy et al., 1999). Studies have mentioned that careful logging around advance growth (CLAAG) and CPRS on forested peatlands may reduce long-term productivity (Lavoie et al., 2005; Lorente et al., 2012) since these harvest methods do not disturb organic layers.

Poor microsite conditions can reduce tree growth and end up lengthening harvest rotation intervals or leading to lower fibre production than anticipated and this even in stands that are fully stocked. Arbitrary minimum stocking estimates of merchantable species are insufficient standards for predicting reliable yields of regeneration success (Brand and Weetman, 1986). In a context in which all young stems share the same potential to generate future mature stems, silviculture based primarily on density control

can be judged acceptable, but in cases where we are faced with large variations in growth microconditions, foresters need to fully consider the difference between promising and non-promising young stems. Counting the number of stems greater than a given height e.g. 1m may be valid for post-harvest sites in which foresters are searching for an evaluation of whether the regeneration is taller than competing species. However, using only stem height needs validation for areas where paludification is problematic as the problem with ensuring forest productivity is below ground and not from above ground competition.

Ruel et al. (2000) reviewed various studies that looked at black spruce response to overstorey removal in relation to morphological indicators of vigor pertaining to growth. Vigor indicators can be defined as morphological characteristics or physiological traits that assess tree health. Physiological vigor indicators could be expected to be manifest before morphological ones and therefore be useful predictors of tree vigor. While physiological vigor indicators seem to be promising tools, few of them have been developed as thoroughly as morphological vigor indicators. Chlorophyll fluorescence however has been used complementarily with root growth potential and stomatal conductance as a means to evaluate field performance of container-grown coniferous seedlings (L'Hirondelle et al., 2007).

Several morphological indicators on the other hand have already been noted as useful tools to predict tree survival and growth rate when measured before canopy removal (Ruel et al., 2000). Combining multiple vigor indicators such as live crown ratio, bole damage and height growth rate can be more practical than using them individually (Ruel et al., 2000). However, though stem diameter has been found to be a useful

predictor of field survival and growth in other systems (Mattsson, 1997), our research suggests that the growth potential of young black spruce individuals on mineral and organic soils is relatively independent of stem size. Relating physiology and morphology could lead to a more complete definition of tree vigor.

At the height of the growing season, energy stored in the tree will first and foremost be used for shoot elongation (Lanner, 1985). As the shoots develop, photochemistry and physiological activity begins within the new needles. Morphologically the tree will respond to increased photosynthetic capacity by producing more foliage which will over time lead to longer live crowns (Messier et al., 1998). In complement to the physiological and morphological data, the information from individual tree components (needle, branch, individual) provides for a more thorough evaluation of the trees characteristics.

Even though black spruce are present and could be deemed free-to-grow in terms of freedom from competition in harvested areas on organic soils, many regenerating stems display poor growth. Foresters need proper tools with which they can estimate tree vigor on sites limited by below ground conditions and not just light. Vigor indicators for young stems will help better understand regeneration success on sites subject to high variation in soil microsite conditions such as soils exposed to paludification. These indicators will be useful in recognizing regenerating stands that need immediate or future silvicultural intervention, whether it is an imminent low scale scarification or a future full-scale silvicultural treatment.

Our main objective is to determine whether full light post-harvest vigor indicators can be developed for black spruce peatland forests that will enable us to determine which regenerating black spruces are likely to grow and which ones will stagnate. Specifically, we evaluate morphological and physiological variables that characterize black spruce seedlings and layers at the individual, branch and needle level. Therefore, this research aims to evaluate vigor related i) physiological characteristics pertaining to the growth of young stems and ii) morphological growth traits in hopes of iii) relating the two. Many studies have looked at post-harvest black spruce growth and physiological responses, here though we seek to link the two and thus expect to obtain a more adequate description of black spruce vigor traits.

1 METHODS

1.1 Site description

The study site is located in the continuous boreal forest of northwestern Quebec between 49°05' N – 50°07' N and 79°08' W – 78°44' W. Glacial movement in northwestern Quebec near the end of the Little Ice Age modified the hydrographic network (Veillette, J., 2002) and left glaciolacustrine clay deposits that prevent proper drainage. These conditions promote sphagnum and moss proliferation which gives rise to highly paludified regions. This region, characterized as the spruce-moss domain, covers more than 412 000 km² (Saucier et al., 2003) and is dominated by black spruce (*Picea mariana* (Mill.) BSP). The regional vegetation is also typified by sub-dominant species such as Jack pine (*Pinus banksiana* Lamb.), larch (*Larix laricina* (Du Roi) K. Koch) and trembling aspen (*Populus tremuloïdes* Michx.), some ericaceous shrubs (mainly *Kalmia angustifolia*, *Rhododendron groenlandicum* (Oeder) Kron & Judd), sphagnum, mosses

and peat bogs. The mean annual temperature is 0° C and mean total precipitation ranges from 800 – 1200 mm per year while more than 1000 mm can fall as snow (Viereck and Johnston, 1990). The growing season begins at the end of May or beginning of June and lasts until mid September. All sites were harvested with protection of regeneration and soil (CPRS) between 1994 and 2000.

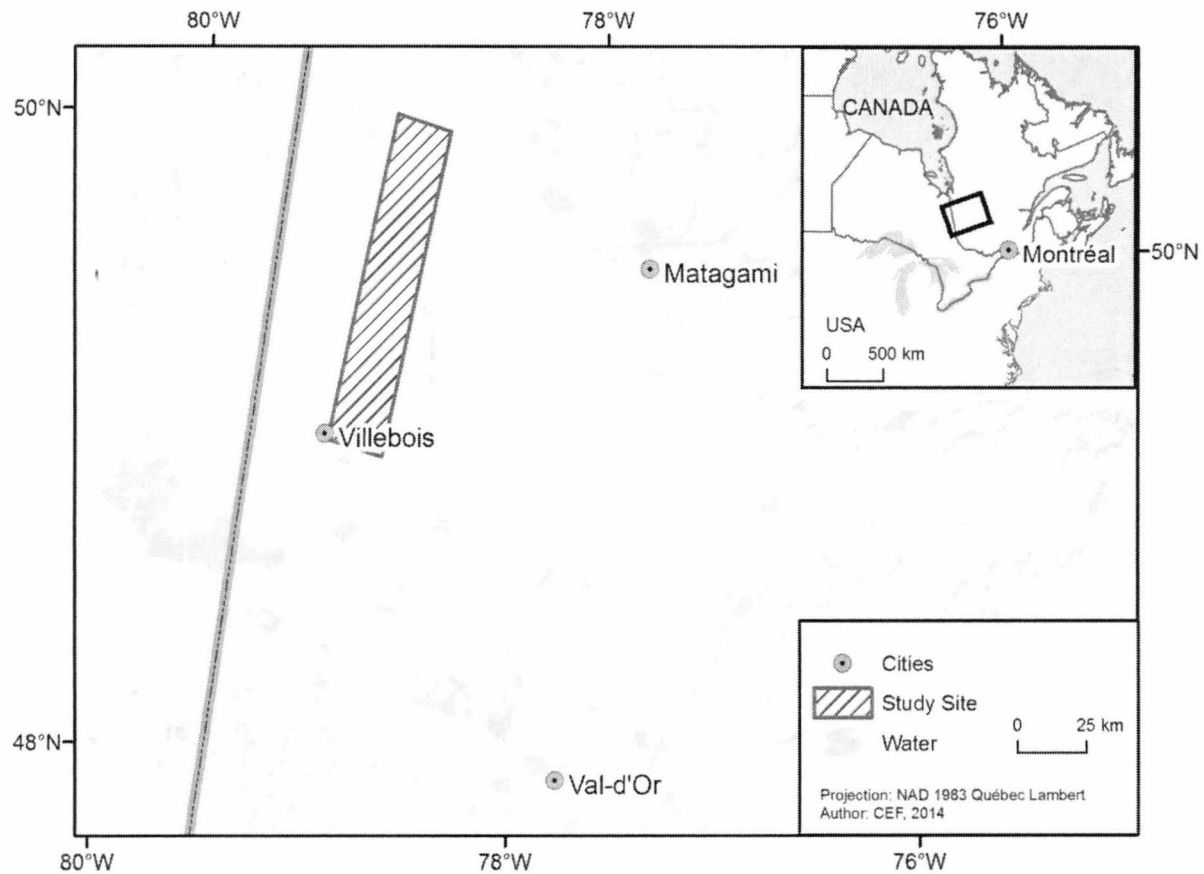


Figure 1. Map of study site

1.2 Sampling design

1.2.1 Selection of study sites and trees

Our sampling design was based on covering a gradient of site conditions from mineral to organic soils. Using a coring device to measure the depth of the organic matter, plots were selected based on the thickness of the organic matter layer. Thirteen

plots were dispersed on sites with different levels of organic matter thickness so as to control for vigor interactions on different substrates. In the summer of 2011, we chose four plots (4,7,8,13) on sites with a high depth of organic matter (> 50 cm), four plots (2,5,6,10) with low levels (< 30 cm) and five plots (1,3,9,11,12) located on an intermediate level of organic matter depth ($30 > 50$ cm). Plots were distributed over the entire study site. All harvested plots were at least 10 years old and less than 20. Trees on younger plots may still present residual effects due to harvesting and for that reason were not considered in this study.

Thirty naturally regenerated trees growing in full sunlight and free from competition ($n = 390$) were selected on each plot. Sample trees were 1 to 3 m in height and also stratified with respect to organic matter thickness. Because there can be a lot of variability in organic matter thickness across a plot, cored soil samples were taken near the stem of each sample tree. Coring near the stem of the tree gives a more accurate measurement of the depth of organic matter at the base of the tree. In this study, black spruce trees were selected relative to their previous years growth increments while covering a large gradient of leader lengths. Individuals bearing continuous and increasing increments were sampled, as were those demonstrating growth stagnation.

1.3 Indicators of tree vigor

Observable traits alone are not sufficient to identify tree growth and stagnation. Therefore, for each regenerated black spruce sampled we measured a number of indicators of vigor that are potentially related to tree health and growth performance. These can be grouped into physiological and morphological indicators.

1.3.1 Physiological indicators

The physiological indicators included total chlorophyll and fluorescence components. Foliar chlorophyll was measured to see if a relationship existed between it and needle color (i.e. foliar hue) where greener needles have a higher concentration of chlorophyll. Green and turquoise colored needles are indicative of healthy, vigorous trees. That is, the root system is able to collect enough water and nutrients to ensure the tree its physiological quota. If however, the needles have a yellow tint, the belowground nutrient supply to leaves is insufficient. The tree then uses up its stored energy and will die when it is depleted unless the root system can reestablish a sufficient nutrient flow to the needles. The fluorescence components were measured to complement the morphological measurements so as to determine whether the two were related. The physiological characteristics are thought to be precursor indicators to the morphological indicators. Fluorescence measurements were taken at the end of August and beginning of September, at the end of the growing season.

1.3.1.1 Chlorophyll determination

Mid crown current year needles (10 – 12) were taken from a single south facing lateral branch on the last whorl of every sample tree. The needles were frozen in liquid nitrogen (LN) and kept in 1.5 ml eppendorf tubes in a freezer (-20°C) for no longer than 72 hours before they were taken to an ultra-low temperature freezer (-80°C) where they were kept until chlorophyll analysis. For the analysis, the samples were cut into 1-2 mm segments, thawed in 95% ethanol (EtOH) and finally incubated at 65°C for 16 hours as described by Minocha et al. (2009). After incubation, samples were vortexed and centrifuged at 13 500g. Next, each extraction was analyzed with a spectrophotometer

(Ultrospec 3100 pro UV/Visible Spectrophotometer, Biochrom) at 649 nm and 664 nm. Finally, total chlorophyll ($\text{mg} \cdot (\text{g FM})^{-1}$) was calculated using Lichtenthaler's (1987) equations:

$$\text{Chlorophyll } a : (13.36 \times A_{664}) - (5.19 \times A_{649})$$

$$\text{Chlorophyll } b : (27.43 \times A_{649}) - (8.12 \times A_{664})$$

$$\text{Total chlorophyll : Chl } a + \text{Chl } b$$

where A is the absorbance value at each wavelength as given by the spectrophotometer.

1.3.1.2 Color determination

Needle color (foliar hue) using digital photographs was determined as an indicator of total chlorophyll concentration (Heiskanen, 2005). Again, a south facing lateral branch segment from the last whorl of each tree's current year growth was cut and bagged. Pictures of the foliage on these harvested branches were taken on the same day (i.e sampling and photos took place on the same day but not all trees were sampled in one day) with a 12.1 mega pixel Canon PowerShot *SD780 IS* Digital Elph. To standardize the lighting, each sample was set inside a white wooden box with the camera set at the same position and angle for every picture. Additionally, white balance was set for every picture as well so that the background color was identical every time. The pictures were subsequently analyzed using Adobe Photoshop CS5 Extended (Version 12.0 x64) software and its eye drop function. This function gives a red, green, blue (RGB) color output for any given selected pixel from a picture. Four pixels on each picture were selected from the needles to characterize the sample after which a mean RGB value was calculated for every tree. The RGB output was then converted to Munsell color notation (hue, value, chroma) with the Munsell Conversion Software (version 11.1.0,

WallkillColor, USA). The Munsell color notation is internationally recognized and widely used for color determination of soil samples. The hue parameter was transformed to hue(100) by removing the GY and Y letters and adding 30 and 40, respectively, to the number values (Heiskanen, J., 2005). Transforming hue parameters to hue(100) creates a continuous series of numbers and therefore facilitates color classification.

1.3.1.3 Quantum efficiency of black spruce needles

Quantum efficiency refers to the effectiveness with which the needles photosynthetic material can convert solar radiation into available energy. This can be determined by measuring the components of fluorescence. Fluorescence measures were taken with a pulse amplitude modulator (PAM-2100, Heinz Walz GmbH, Germany) in the morning before direct sunlight hit the needles. Similarly to previous needle sampling, a single south facing lateral branch from each sample tree was selected. Sample branches were selected in the mid-crown and fluorescence measures were taken on current year needles. To measure light adapted fluorescence traits, needles were exposed to continual actinic light levels of $100 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and to a 0.8 second saturating light every 20 seconds for 4 minutes at which time fluorescence, quantum yield and quenching measurements reached a steady state (Major et al., 2007b). The portable chlorophyll fluorometer PAM-2100 records F_o and F_m (minimal and maximal fluorescence in a dark adapted state respectively), F_o' and F_m' (minimal and maximal fluorescence in an illuminated state respectively), F_t (fluorescence at any given time), F_v/F_m (effective quantum yield of photosystem II) and $\Delta F/F_m'$ (Φ_e , photochemical yield of photosystem II in an illuminated state) where Φ_e is calculated as (Handbook of Operation, Heinz Walz GmbH, 2003):

$$\Phi_e = (Fm' - Ft) / Fm' = \Delta F / Fm'$$

Finally, the PAM-2100 records photosynthetically active radiation (PAR, $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and the apparent electron transport rate (ETR, $\mu\text{mol electron} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). The quantum yield of CO_2 assimilation (Φ_{CO_2} , $\text{mol CO}_2 \cdot \text{mol quanta}^{-1}$) can be calculated from the formula derived by Genty et al. (1989):

$$\Phi_{\text{CO}_2} = \Phi_e \cdot J_a / I_i \cdot 1/k$$

where J_a is the ETR, I_i is the photon flux density incident upon the leaf (PAR) and k is the number of electron equivalents required to reduce 1 mol of CO_2 . There is also an empirical formula used to describe net CO_2 assimilation in terms of the fluorescence emissions:

$$A = I_i \cdot (\Phi_e - 0.0085) / 7.94$$

where A is the net CO_2 assimilation rate measured in $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Keiller and Walker, 1990).

1.3.2 Morphological indicators

1.3.2.1 Plant growth and structure

Finally, morphological vigor indicators related to growth and structure were measured; as following physiological changes, growth and structure would also be expected to change. Height growth rate, measured in cm/y, from previous years was used to predict future (or current) tree growth. Individuals with low growth rates in the past are expected to continue to maintain low growth rates, the same is true for trees with high growth rates. Leader length was measured on each tree from the scar left by the previous apical bud up to the tip of the current year's apical leader. This measure was taken at the

end of the summer, after bud set, to properly estimate the current annual increment. Additionally, past intermodal increments were measured. Measurements were taken down the trunk of the tree until the internodes became indiscernible. Thus, we calculate height growth rate as follows:

$$Gr = (Lt - L_{2004}) / (\Delta_{2004})$$

where L_t is the leader length in year t , L_{2004} is the leader length in 2004 and Δ_{2004} is the number of years between t and 2004. The year 2004 was chosen as the base year since this was as far back as we could go without losing too many data points for leader length as intermodal scars on most trees were indiscernible past 2004. The data for leader length measurements preceding 2004 were too infrequent and did not show significant statistical strength to be incorporated in this study.

We also measured the leader to lateral branch (LB) ratio. The LB ratio is calculated as:

$$LB = L / (\text{mean}[B_1 \dots B_n])$$

where L is the leader length and $B_1 \dots B_n$ are the lengths of the lateral branches produced from the whorl of the leader (Kneeshaw et al., 1998). Though the LB ratio has been used as an index to evaluate seedling response to canopy opening, it was measured here as an indicator of apical growth and growth stagnation. Furthermore, the LB ratio is a quick, simple and easy to measure variable in the field, which is helpful to foresters who intend to use this tools.

Diameter at ground height (DGH) was measured to the nearest centimeter on every tree. Since many sample trees have height less than 1.3 m, measuring the diameter at breast height (DBH) was not possible for every individual. However, when individuals exceed or were equal to 1.3 meters in height, DBH was noted.

Tree height, as well as the height of its live crown, was measured to the nearest centimeter in order to get measurements for the live crown ratio (LCR). The height distribution of buds was also noted if it differed from the live crown. LCR has previously been used as a tool to evaluate growth stress of shade-tolerant conifer species (Ruel et al., 2000). This variable was therefore measured in this study to see how it could be applied as a full-light vigor indicator for black spruce.

One branch sample was taken from the mid-crown section and another from the last whorl of every sample tree for specific needle weight (SNW) determination. To compute SNW, the dry mass of each sample was weighed and then divided by the number of needles in each sample. Multiple needle components (i.e. needle width, needle volume and specific needle area (needle projected area divided by needle dry mass, cm^2/g)) were also measured for each sample tree. These measurements were taken with the WinSeedle software program. Finally, using the WinDendro software program, radial stem increments were measured on each disk after destructive sampling (Regent Instruments Inc. 2012). All sample trees were eventually cut at the root collar where a disk was taken for ring examination in the lab. Radial stem increment measurements were dated back to the first year of growth.

1.4 Statistical analysis

We graphically presented variations in annual internode length and annual radial stem increment. This was used to determine the best growth years as well as to identify the best and worst performing individuals. Based on these results, we used linear regression analysis to determine the relationship between internode length and radial widths. No size effect was detected for internode increments or radial widths during the best growth years (2008, 2009). Next, analysis of variance (ANOVA) was used to test mean organic matter depth, mean tree height and mean DGH across every site and for different harvest years in order to figure out if the independent variables (harvest year and site) have an effect on the dependent variables.

Linear regression was used as well to determine the relationship between foliar color (hue) and chlorophyll concentration as has been previously used for Norway spruce (Heiskanen, 2005). This analysis determines if a relationship exists between green needles and high chlorophyll concentrations. Further, a Pearson correlation matrix was used to link morphometric variables to physiological variables (i.e. fluorescence components). We then implemented multivariate analyses to assess the magnitude of relationships between both sets of variables. Redundancy Analysis (RDA) was used to explore relationship between morphological and physiological data sets.

Once these analyses were completed, linear discriminant analysis (LDA) was then used to determine a vigor classification based on the retained variables (height growth rate and leader length) from the previous results. To predict future tree growth, the leader lengths from 2005, 2006 and 2007 were used to predict height growth rate for 2008 and 2009. Then, several thresholds for leader length were systematically tested. Each

threshold represents a leader length between 10 and 20 cm. The first threshold contrasts stems with leaders less than 10 cm (low vigor) to those with leaders of more than 10 cm (high vigor). These steps increase in 1 cm increments until the final threshold at 20 cm is reached. The threshold levels were then tested using the LDA to identify the optimal vigor threshold for leader length, determined based on LDA percent classification success.

Because not all sites were harvested in the same year, we then looked at how leader length, radial width, tree height, DGH and growth rate (apical and radial) varied with time since harvest. Six figures illustrate these relationships. Each figure detailed 5 curves illustrating different growth patterns. The curves were obtained by taking the median of the percentile rank for each of the growth characteristics listed above. These figures were essential to help illustrate the hidden vigor hierarchy within these growth patterns. All analyses were completed using **R** language software (R Core Team, 2012).

2 RESULTS

2.1 Height relationship to site characteristics

Time since harvest did not seem to affect the mean height of trees on any site (p -value = 0.17) (Table 1). Although sites were widely dispersed and belonged to different OM depth classes (Table 2), mean tree height and DGH were relatively similar across all sites (p -values > 0.2) (Table 1). Sites harvested in the same year are present in all three OM depth classes. Likewise, mean height and DGH were similar regardless of harvest year.

Table 1 Site means for organic matter depth, tree height and diameter at ground height \pm SD

Site	Harvest year	OM depth (cm)	Height (cm)	DGH (mm)
1	2000	45 \pm 33	166.8 \pm 44.73	34.2 \pm 12.2
2	1995	68 \pm 27	176.9 \pm 45.89	35.9 \pm 10.8
3	1994	37 \pm 13	160.8 \pm 37.55	32.0 \pm 7.70
4	1997	28 \pm 15	177.3 \pm 39.84	41.1 \pm 10.9
5	1997	98 \pm 23	166.3 \pm 35.80	34.4 \pm 8.60
6	1997	51 \pm 21	160.5 \pm 41.59	34.1 \pm 10.8
7	1995	28 \pm 16	167.7 \pm 46.23	35.6 \pm 10.9
8	1994	26 \pm 15	178.1 \pm 57.07	34.9 \pm 12.0
9	1997	48 \pm 20	160.7 \pm 40.87	35.5 \pm 11.9
10	1996	55 \pm 23	160.3 \pm 36.55	36.4 \pm 9.90
11	1997	33 \pm 12	163.3 \pm 42.02	36.9 \pm 10.2
12	1997	38 \pm 14	154.7 \pm 34.24	33.2 \pm 10.2
13	1995	21 \pm 15	166.7 \pm 33.66	41.4 \pm 11.6

Table 2 Mean organic matter depth, tree height and diameter at ground height according to the organic matter gradient consolidated from sites 1-13

	OM depth (cm)	Height (cm)	DGH (mm)
Low OM	26	172.45	38.25
Med OM	40	161.26	34.36
High OM	68	166.00	35.20

2.2 Relationship between physiological and morphological variables

Physiological and morphological variables were not well correlated (adjusted $R^2 < 0.001$), a result that is not in accordance with our hypothesis that physiological characteristics should precede and lead to changes in morphological traits. The extremely low value of unbiased variance (unbiased variance represents the explained variance once the adjusted R^2 has been taken into account, results shown in Table 3) confirms the poor relationship between physiological and morphological variables.

Table 3 Redundancy analysis of the physiological variables constrained by the morphological variables

Variable	RDA1	RDA2	PC1 residual eigenvalues	PC2 residual eigenvalues
Eigenvalue	0.38471	0.20133	5.876	2.7982
Proportion explained	0.030	0.015	0.452	0.215
Cumulative proportion	0.030	0.04508	0.513	0.7282
Accumulated constrained	0.4852	0.7391		
Adjusted R^2	< 0.001			
Unbiased variance	< 0.001	< 0.001		

It is possible though to see the morphological trends. For example, vectors identifying needle density and branch length are correlated with total height and the lateral branch ratio, while needle width and needle length have an inversely proportional relationship (Figure 2). These trends are once again visible in the left-hand triplot of Figure 3 where the correlations between morphological traits and tree growth are highlighted. A distance biplot (Scaling 1) and a correlation biplot (Scaling 2) (Borcard et al., 2011) complement each other on the left and right hand side respectively of Figure 2.

Table 4 Redundancy analysis of the growth variables constrained by the morphological and physiological variables

Variable	Morphology		PC1 residual eigenvalues	PC2 residual eigenvalues
	RDA1	RDA2		
Eigenvalue	3.553	0.50094	1.9757	0.7926
Proportion explained	0.4441	0.0626	0.2470	0.0878
Cumulative proportion	0.4441	0.5067	0.7864	0.8742
Accumulated constrained	0.8233	0.9394		
Adjusted R^2	0.5070			
Unbiased variance	0.4174	0.4763		
Variable	Physiology		PC1 residual eigenvalues	PC2 residual eigenvalues
	RDA1	RDA2		
Eigenvalue	0.6505	0.0809	4.7964	1.0233
Proportion explained	0.0813	0.0101	0.5996	0.1279
Cumulative proportion	0.0813	0.0914	0.7018	0.8297
Accumulated constrained	0.7950	0.8939		
Adjusted R^2	0.0534			
Unbiased variance	0.0425	0.0477		

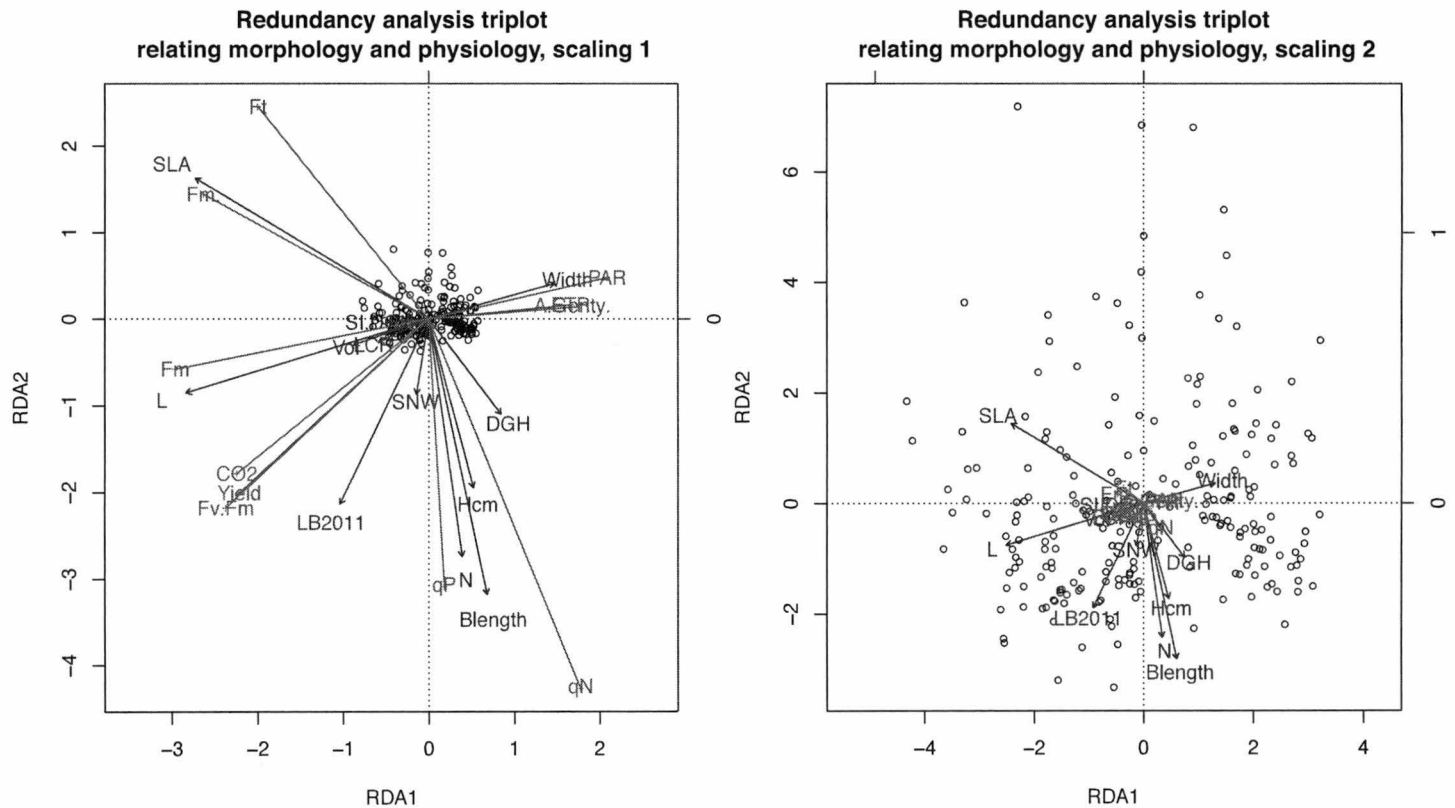


Figure 2. RDA triplots relating physiological (red) and morphological (blue) variables. The bottom and left-hand scales are for the response variables, the top and right-hand scales are for the explanatory variables. (SLA, Specific Leaf Area; Width, needle width; L, needle length; SNW, Specific Leaf Area; DGH, Diameter at Ground Height; LB2011, Lateral Branch ratio in 2011; Hcm, Height in cm; N, number of needles per branch segment; Blength, length of the branch segment; Fv.Fm, maximal quantum yield of photosystem II; Ft, fluorescence yield at any given time; Fm, maximal fluorescence yield; qP, coefficient of photochemical fluorescence quenching; qN, coefficient of non-photochemical fluorescence quenching; Yield, fluorescence yield; CO₂, CO₂ assimilation rate; A.Genty, net photosynthesis)

Physiologically, all of the variables are condensed near the center of the plot showing the lack of a relationship with the morphological variables, so much so that they are indiscernible in the right hand triplot (Figure 2). As evidenced by the accumulated constrained variance, the results from the RDA output suggest the physiological variables are correlated amongst themselves, just like the morphological variables (Table 3). Figure 3 (the right hand triplot) more clearly illustrates the physiological trends. For example, photosynthetically active radiation (PAR) and the electron transport rate (ETR) are well correlated with net photosynthesis and have an inverse relationship with CO₂ assimilation. Similarly to Figure 2 however, these trends are all that is visible as there is a poor relationship between the physiological characteristics and tree growth. Once again, the response variables are indiscernible and condensed towards the center of the triplot.

2.3 Relationships with growth performances

Since there is a poor relationship between the morphological and physiological indicators, we tested the relationship of each of the sets of potentials indicators separately with respect to growth variables. Variables that were highly correlated to growth (e.g. DGH and height) were not kept in the model due to autocorrelation (Table 4). Again, we surprisingly found a poor relationship with the physiological characteristics (adjusted $R^2 = 0.05$) but a good relationship with morphological traits (adjusted $R^2 = 0.51$).

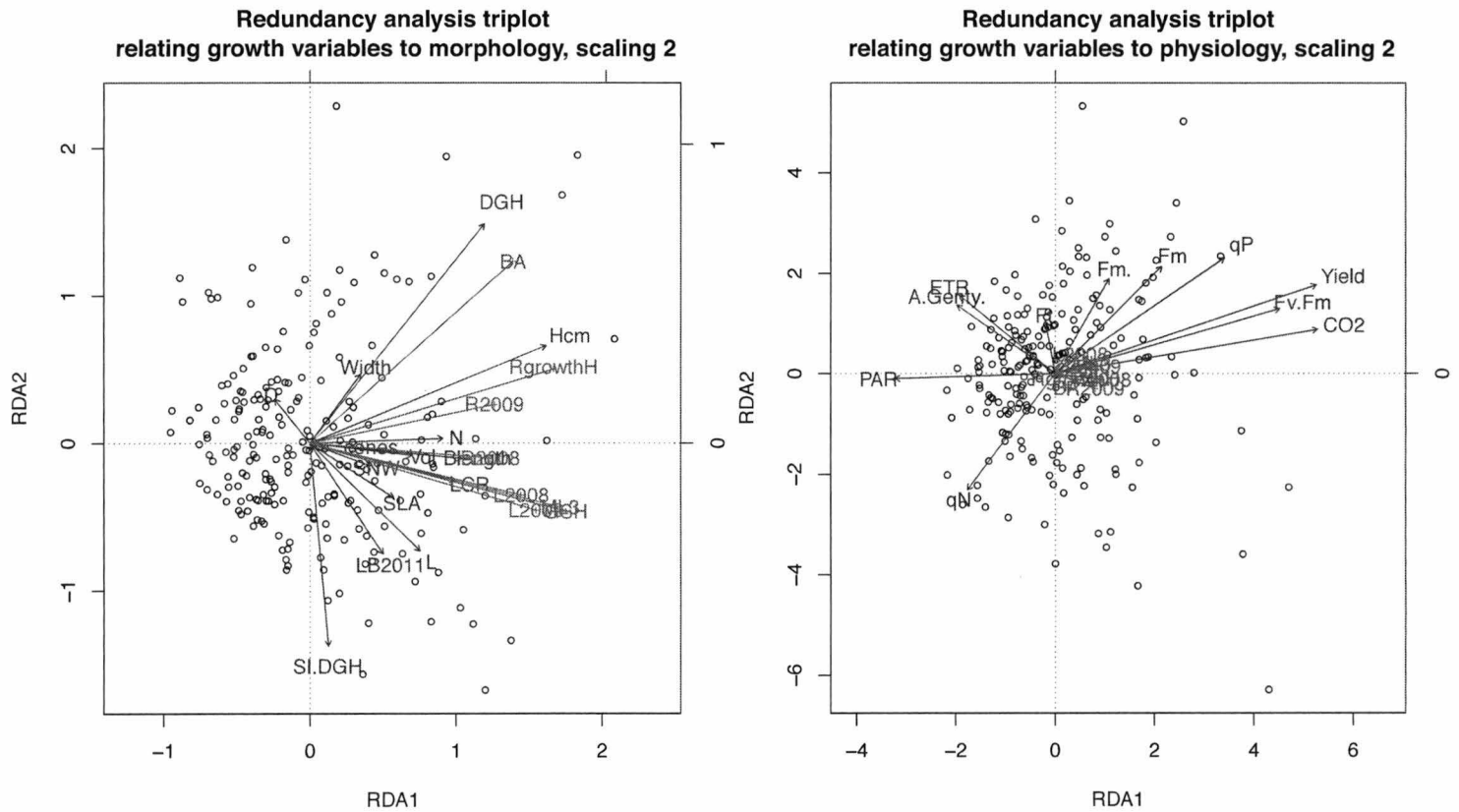


Figure 3. RDA triplots relating growth variables (red) to morphological and physiological variables respectively (blue). The bottom and left-hand scales are for the response variables, the top and right-hand scales are for the explanatory variables. (SI.DGH, Slenderness Index measured with DGH; BA, Basal Area; RgrowthH, radial growth rate since harvest; R2009, radial width in 2009; Fv.Fm, maximal quantum yield of photosystem II; Ft, fluorescence yield at any given time; Fm, maximal fluorescence yield; qP, coefficient of photochemical fluorescence quenching; qN, coefficient of non-photochemical fluorescence quenching; Yield, fluorescence yield; CO₂, CO₂ assimilation rate; A.Genty, net photosynthesis)

2.4 Searching for a vigor threshold

Using all sets of variables (physiological characteristics, morphological traits and past growth performance variables) we tried to identify the best combination of variables allowing us to predict current tree growth rate. Linear discriminant analyses (LDA) were fitted to different threshold levels, as explained in the methods. In all cases, physiological and morphological variables show poor predicting power were discarded from the final models. Only past growth performances in term of leader length and height growth rate were retained. Past leader lengths from 2005, 2006 and 2007 were used to predict future (i.e 2008 and 2009) tree growth rates. Radial growth was not included because classification success was poorer when DGH was included in the model. A vigor threshold that distinguishes HV trees from LV trees could not be found. Instead the relationship is linear with poor past growth being associated with poor future (current) growth and good past growth with good future (current) growth (Figure 4). Though no threshold was found, we observed that past leader length can properly predict future height growth rate with a near 1:1 ratio (Figure 5).

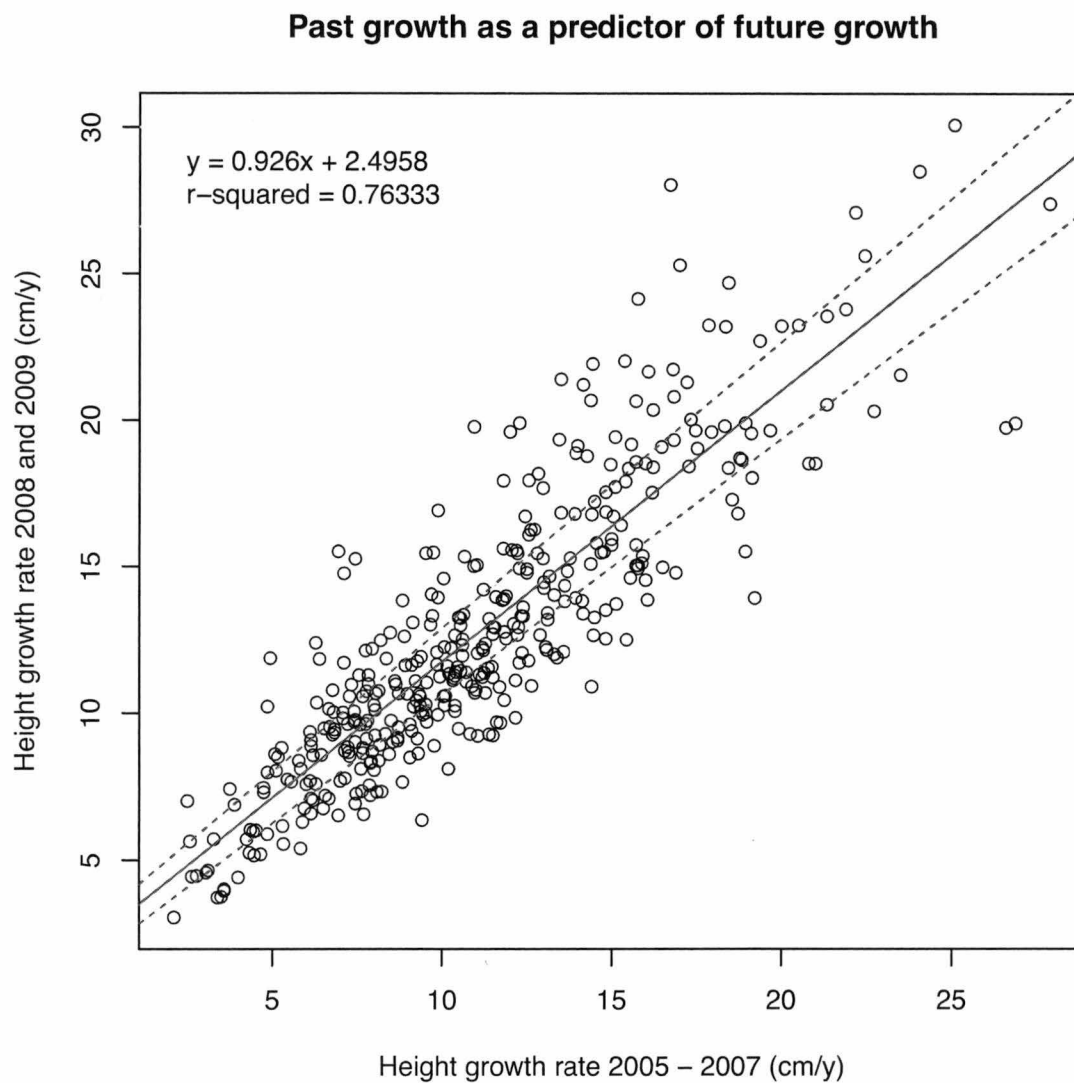


Figure 4. Linear regression with 5% confidence intervals between past height growth (2005-2007) and current height growth (2008 and 2009) to demonstrate the use of past height growth to predict future height growth. ($n = 386$, $RSE = 2.376$, $p\text{-value} < 2.2e^{-16}$)

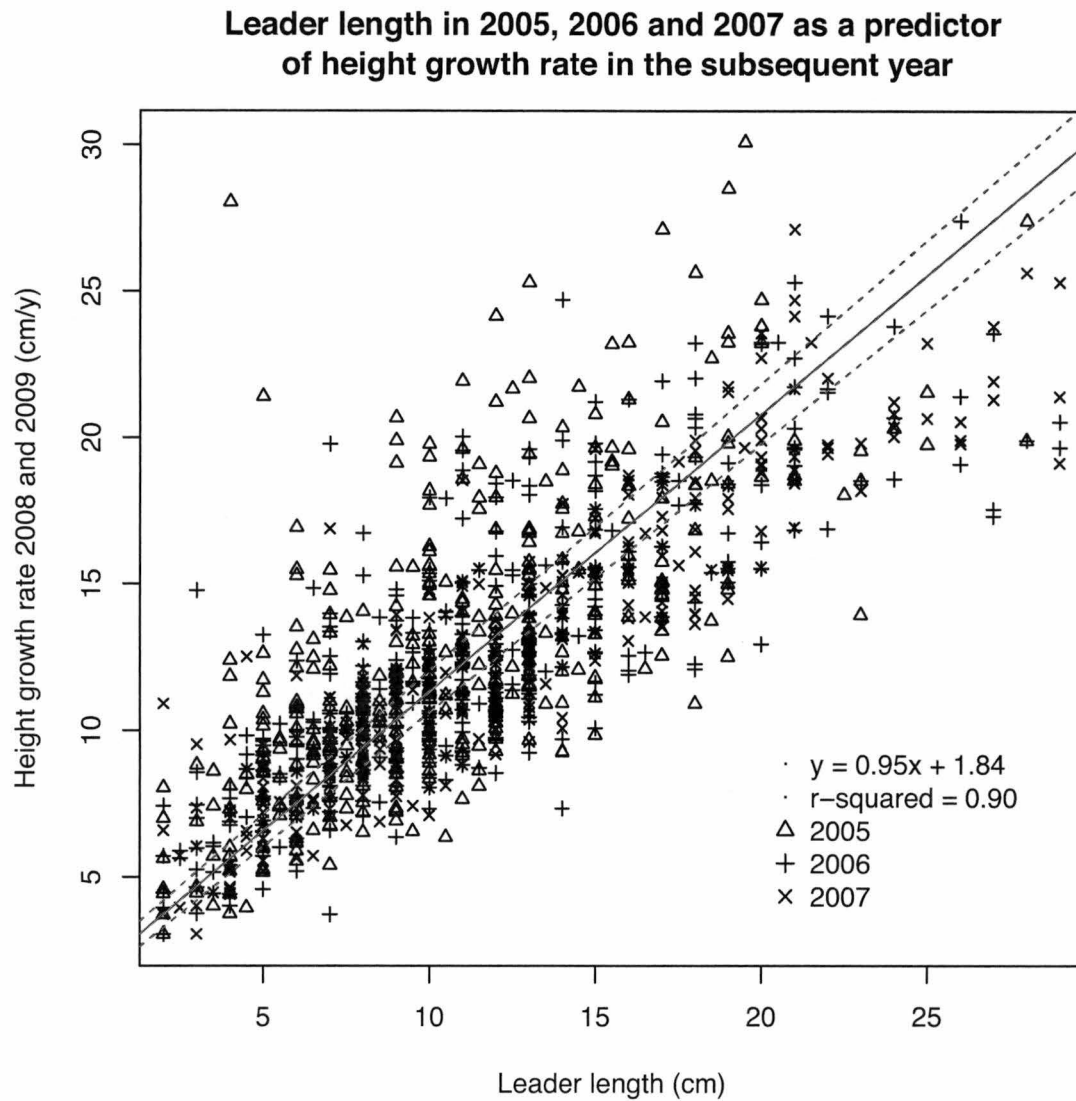
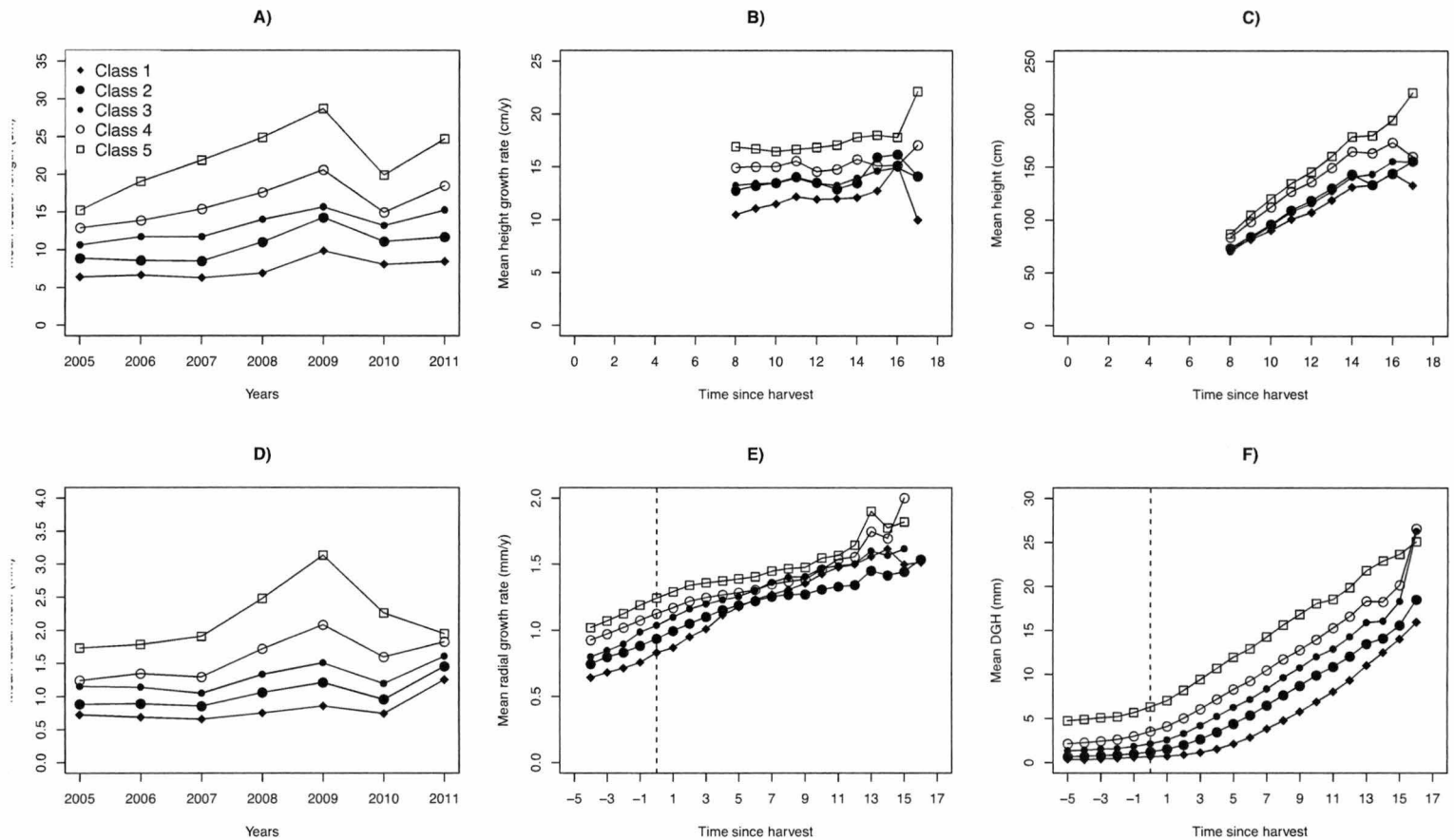


Figure 5. Leader length in 2005, 2006, 2007 as a predictor of height growth in the subsequent year. (\triangle : $n = 386$, $RSE = 3.534$, $p\text{-value} < 2.2e^{-16}$; $+$: $n = 386$, $RSE = 2.763$, $p\text{-value} < 2.2e^{-16}$; \times : $n = 386$, $RSE = 1.981$, $p\text{-value} < 2.2e^{-16}$; overall : $n = 386$, $RSE = 1.545$, $p\text{-value} < 2.2e^{-16}$)



Figures 6A-F. Growth curves obtained from the median of the percentile rank for A) leader length, B) height growth rate, C) tree height, D) radial width, E) radial growth rate and F) diameter at ground height. Class 1: rank 0.0-0.1; Class 2: rank 0.2-0.3; Class 3: rank 0.4-0.5; Class 4: rank 0.6-0.7; Class 5: rank 0.8-0.9. The dotted line represents the time at which harvest took place.

The classes in Table 5 are in increasing order for mean height growth rates. Therefore, class 1 has the lowest height growth rates and class 5 has the highest rates. Though mean height follows the same trend, every class is composed of small trees (<130 cm) and tall trees (>200 cm). Thus, just because a tree is tall does not necessarily mean that it will have a high growth rate. All curves are parallel suggesting that there is no threshold (Figure 6). In Figure 6C though, the curves between what could be high vigor and low vigor individuals seem to diverge.

Table 5 Characteristics of trees in 2011 based on 6,7,8 year post-harvest apical growth classification

Class	n	Mean height (cm)	Median height (cm)	Max height (cm)	Min height (cm)	Mean leader (cm)	Mean growth rate (cm/y)
1	60	144.7	142	232	100	13.0	11.30
2	86	151.6	149.5	246	100	14.6	13.34
3	86	158.6	157.5	245	100	14.9	13.55
4	82	180.4	179	274	111	17.2	15.05
5	54	207.4	208	299	121	17.5	17.24

3 DISCUSSION

We wanted to determine whether full light post-harvest vigor indicators can be developed for black spruce peatland forests that will enable us to determine which regenerating black spruces are likely to grow and which ones will stagnate. We evaluated physiological and morphological variables that characterize black spruce seedlings and layers (though layering dominated black spruce regeneration) at the individual, branch and needle level. Contrary to expectation, only the morphological variables proved to be useful in determining black spruce vigor for trees growing in a full light environment. Logically, physiological characteristics are precursor indicators to morphological traits. However, since physiology was not related to vigor, our ultimate goal of linking physiology and morphology to vigor was impossible. Still, as evidenced by Figure 4 and Figure 5, this study confirmed that the traditional vigor indicators, height growth rate and past leader length, are the most useful tools to evaluate tree vigor as represented by current and future tree growth rate.

We define a vigorous tree as an individual that seasonally sustain a good height growth rate and a long apical leader. Here, good height growth rate is relative to the

entire tree such that there is no specific numerical threshold for all trees at which point they become vigorous. We argue thus that height growth rate and leader length need to be evaluated by foresters as well as total tree height when judging post-harvest stand productivity on paludified sites. These two variables in tandem lend more confidence than tree height alone. Total height, which is often used, can be a misleading tool for proper regeneration assessment since taller seedlings can be old and now have stagnate growth. Currently, leader length is a common and obvious indicator of tree vigor. However, using a predetermined leader length to define vigorous individuals can create a bias towards taller trees.

Though tree age was not specifically investigated, it does not seem to play a role in determining tree height or growth rate on paludified microsites (Paquin & Doucet, 1992, Ruel et al., 2000). Advance regeneration as well as trees originating following harvest can both have poor growth or good growth. The two oldest sampled trees were 76 and 78 years old, situated only a few meters apart and demonstrated poor growth (11.83 cm/y) and good growth (18.75 cm/y) respectively. Still in the vicinity of the two oldest trees, two of the youngest sampled trees, both 11 years old, also showed poor growth (12.83 cm/y) and good growth (16 cm/y). Despite being a sub-sample, these 4 trees illustrate that age is not a good predictor of tree growth on paludified sites. Local belowground processes for individual microsites may therefore play an important role in determining the growth of black spruce trees on paludified sites and future research could investigate factors such as root zone saturation and duration of aeration. St-Denis et al. (2010) report similar accounts of age not being a limiting factor for growth of black spruce advance regeneration after canopy opening. A more extensive analysis between

tree age and vigor is required in order to determine whether this lack of relationship with age occurs consistently.

3.1 Physiological indicators

In contrast to morphology, physiology can explain relationships mechanistically. Energy production in higher plants is restricted to the leaves (needles) and therefore a proper understanding of a plant's physiological response to differing microconditions should be useful for a complete description of plant growth. However, as with other physiological indicators in our study, foliar color was not useful for determining the vigor of black spruce regeneration. Both high and low vigor trees have similar foliar complexions and therefore vigor cannot be distinguished based solely on needle coloration. For pines, Viro (1959) also determined that the chlorophyll content of pine needles was not a good vigor indicator of the growth of saplings. Other researchers have, however, found that foliar color was a good indicator of nutrient composition (nitrogen, phosphorus, potassium and chlorophyll) in needles in unfertilized stands (Heiskanen, 2005; Hytonen and Wall, 2006) yet was not related to root or height growth and therefore not to tree vigor. That being said, trees with chlorotic needles suffer from malnutrition of some kind and thus should not be considered vigorous. Despite its lack of usefulness in evaluating vigor, other than for the most severely chlorotic trees, colorimetry can be a useful tool to evaluate foliar nutrient compositions though results vary between species and areas. Biotic and abiotic factors such as nutrient leaching from nearby allelopathic ericaceous shrubs or water logged stands, have also been identified as elements that can affect needle color and induce chlorosis (Viro, 1959; Hytonen and Wall, 2006). Physiological characteristics then are not completely uninformative indicators. They

should though, for example, be used as indicators of nutrient composition and not for vigor determination.

Chlorophyll concentration and chlorophyll fluorescence components were also unrelated to vigor. Though we found similar values for foliar color and chlorophyll concentrations as measured for Norway spruce by Heiskanen (2005), we were unsuccessful at reproducing the relationship between the two variables or in establishing a relationship with any other measured variables in our study. Though this approach is innovative (Heiskanen, pers. com.), the discrepancy in the results between our study and Heiskanen's might be due to the method used for color evaluation. Future evaluations of black spruce needle color using a chroma meter as in Heiskanen's (2005) study may yield results for black spruces that are more similar to the relationship found for Norway spruces in Scandinavia.

3.2 Morphological indicators

As with the physiological indicators, most of the morphological traits evaluated in this study were not useful in determining tree vigor. Past height growth rate and leader length were the only morphological indicators that provided an evaluation of current tree vigor. Though the traditional indicators proved to be the only accurate way to estimate tree vigor, we note that combining the indicators, as previously done with other morphological indicators (Ruel et al., 2000), as opposed to using them independently, may provide a better evaluation of tree vigor.

More precisely, by combining measurements of past height growth rate and past leader length, we were able to predict future (current) height growth rate and leader length. We originally thought that a threshold would occur where we could classify trees

into high vigor (HV) and low vigor (LV) groups. Instead such groups are arbitrary as growth occurs along a continuum in this system. A similar analysis however, that compares tree vigor for individuals growing in an environment in which above ground competition is important to those in a full light environment, may reveal that a threshold exists between the two. In our case however, the transition from low vigor (poor growth) to high vigor (good growth) individuals is much more gradual.

In some cases, trees with low growth rates show no apical growth for a given year. These occurrences though are rare. Therefore, a stagnated phase can be represented by small increments in apical growth as opposed to complete stoppage of apical growth. Trees qualified as such however may not necessarily be doomed to remain in this state and never reach a more vigorous growth phase. The mean height growth rates recorded in 2011 for trees with poor growth and those with good growth was 10.93 cm/y and 19.39 cm/y respectively. Given the linear relationship that was observed, this 19.3 cm per year growth rate is close to the 20 cm/y rate (Mailly & Goudreault, 2005) that is necessary in order to reach an optimal tree size by the time the next harvest rotation arrives. Our data however accounts for only the first 17 years post-harvest. For other peatland black spruces, maximum height growth occurred between 20 – 25 years post-harvest (Groot & Hökkä, 2000; Paquin & Doucet, 1992; Pothier et al., 1995) at which point it begins to decrease. Thus, peak height growth for all the trees in this study has probably not been reached. No matter whether a tree has good growth or poor growth, tree height is relatively similar for all trees in the few years following harvest. After about 10 years however, a slight distinction can be made between trees with good growth (i.e. growth above the mean) and those with poor growth (Figure 6C).

Ruel et al. (2000) mention that trees with a live crown ratio (LCR) of 66% or more have a high survival rate while those with less than 33% live crown have a poor chance of surviving. Nearly 95% of the sampled trees in this study had a LCR of at least 70% but they belonged to both the HV and LV groups. This suggests that, even though a tree is identified as a low vigor individual, it does not mean that it will not survive. Incidentally, there are many trees that support a LCR >70% and should not be considered vigorous individuals. Nearly 20 years after harvest, stagnated black spruces were still surviving and supporting an LCR well above the values recorded 10 years post-harvest for other trees (Solarik et al., 2011). All but one of the remaining trees from this study with a live crown less than 70% were LV individuals and the lowest ratio recorded in this study was 46%, still much higher than the 33% threshold that was suggested as being needed for survival. Tree vigor and survival are thus not necessarily synonymous.

CONCLUSION

Vigor indicators should be simple tools that are measurable in the field and provide relevant information on future growth and thus success of regenerating areas. Aside from height growth rate and leader length, we found that morphological and physiological indicators are not related to vigor (or only weakly) for natural black spruce regeneration growing on clay belt soils. Although we expected there to be a relationship between vigor, morphology and physiology, other authors also found it difficult to relate these elements (Viro, 1959; Heiskanen, 2005). Equally, we did not find significant evidence for a relationship between foliar hue and foliar chlorophyll concentration even though they have previously been related for Norway spruce (Heiskanen, 2005).

Our study showed that, leader length and height growth rate, are still the most useful at evaluating vigor for naturally regenerated black spruce trees. As these measurements can be taken during the first regeneration survey, foresters should get an idea of natural regeneration success. This information can then be used to determine whether a silvicultural intervention on surveyed sites is needed to reestablish vigorous tree growth.

GENERAL CONCLUSION

Though paludification is a well know problem, the forest industry still struggles to find ways to harvest and manage paludified stands. Post-harvest vigor indicators can be used to evaluate black spruce regeneration growth on these problematic sites. Leader length and height growth rate are two full-light vigor indicators that can accurately determine tree vigor on such sites. Implementing these measurements during post-harvest forest inventories may take longer than traditional inventories of stocking and density but the final assessment will be more insightful into evaluating the potential future success of black spruce regeneration. High vigor trees on paludified sites could become merchantable products whereas an abundance of low vigor trees will require silvicultural interventions to improve tree success.

By only taking into account the number of trees taller than 1 m 8 years post-harvest, foresters can encounter two major problems. The first is that it is highly possible that they will overestimate the quality of the trees regenerating on paludified sites. Though sites may be fully stocked, some trees could be in a stagnated phase of growth. Foresters concluding that trees on the site will produce a future harvest in a given rotation may eventually be surprised to find that tree growth was mediocre since the trees were not vigorous. Had the forest inventory taken into account leader length and height growth rate, a silvicultural treatment could have been planned to reengage tree growth and thus save money in the long term.

The other oversight that can be made by foresters is an underestimation of the forest's future merchantable trees. Seemingly under stocked stands can eventually become profitable although not always within the preferred time delay. Measuring leader

length and height growth rate may keep foresters from disregarding stands that might otherwise have been considered not satisfactorily restocked.

Including height growth rate and leader length for a stand regeneration survey though is more time consuming. It is our contention however that the little extra time and expenses carried out while inventorying can lead to sizable profits if the stand is well stocked with vigorous trees. The long-term payout could be worthwhile if the forest industry is willing to sacrifice a few weeks of field work so as to properly evaluate tree regeneration within the harvested stands.

Future studies looking at black spruce vigor indicators should consider further evaluation of belowground processes. Notably, measurements regarding soil nutrients (nitrogen, phosphorus and potassium), root depth as well as measuring the height of the water table at each sample tree. What is more, using fresh needles samples as oppose to drying them may lend different results. Logistically, this is a more difficult and time-consuming approach. Nevertheless, the characteristics of green needles give more exact measurements than dry needles.

Lastly, a look at biomass and energy allocation throughout the entire tree may reveal more about tree vigor. This could be especially interesting given the heterogeneous microtopography of paludified microsites. Even though most black spruces on a site may share similar genetic makeups owing to layering, biomass allocation tends to be environmentally determined as opposed to genetically determined (Rweyongeza et al., 2005). A study broaching this topic may reveal more about black spruce physiological and morphological plasticity and their relation to vigor.

REFERENCES

- Alberta Sustainable Resource Development. (2008) Alberta Regeneration Survey Manuel [online]. Government of AB. Available at <http://srd.alberta.ca/forest/managing/manual/aspx>.
- Arnon D (1949) Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris*. *Plant Physiology* 24(1):1.
- Bannan M (1942) Notes on the origin of adventitious roots in the native Ontario conifers. *American Journal of Botany* 29(8):593-598.
- Berninger K, Adamowicz W, Kneeshaw D, & Messier C (2010) Sustainable forest management preferences of interest groups in three regions with different levels of industrial forestry: An exploratory attribute-based choice experiment. *Environmental management* 46(1):117-133.
- Boily J & Doucet R (1993) Young growth of black spruce layers in regeneration after harvesting of the main stand. *Croissance juvenile de marcottes d'épinette noire en régénération après récolte du couvert dominant* 23(7):1396-1401.
- Bond-Lamberty B, Wang C, & Gower ST (2002) Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. *Canadian Journal of Forest Research* 32(8):1441.
- Brand D & Weetman G (1986) Standards for regeneration establishment in Canada: a case study for Douglas-fir. *For. Chron* 62(2):84-90.
- Borcard D, Legendre, P & Gillet, F (2011) *Numerical Ecology with R*, Use R. Springer, New York, Dordrecht, London, Heidelberg. Chap 6, p153-225.
- Chen J, Rich P, Gower S, Norman J, & Plummer S (1997) Leaf area index of boreal forests: theory, techniques, and measurements. *Journal of Geophysical Research* 102(D24):29429.
- Cleland T (1937) *A practical description of the Munsell color system: with suggestions for its use* (Munsell Color Co.).
- Doucet R (1990) Long term development of black spruce advance growth released by cutting. *The silvics and ecology of boreal spruces*:05-12.
- Duchesneau R, Lesage I, Messier C & Morin H (2001) Effect of light and intraspecific competition on growth and crown morphology of two size classes of understory balsam fir saplings. *Forest Ecology and Management* 140:215-225.

- Eastham A & Jull M (1999) Factors affecting natural regeneration of *Abies lasiocarpa* and *Picea engelmannii* in a subalpine silvicultural systems trial. *Canadian Journal of Forest Research* 29(12):1847-1855.
- Ernst, R.L. and Knapp, W.H. (1985) Forest stand density and stocking: concepts, terms and the use of stocking guides. *USDA Forest Service General Technical Report WO WO-44*.
- Fraser D.A. (1962) Apical and radial growth of white spruce (*Picea glauca* (Moench) Voss) at Chalk river, Ontario, Canada. *Canadian Journal of Botany* 40: 659-668.
- Genty B, Briantais J-M & Baker R. N (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochimica et Biosophysica Acta* 990:87-92.
- Groot A, & Hökkä H (2000) Persistence of suppression effects on peatland black spruce advance regeneration after overstory removal. *Canadian Journal of Forest Research* 30(5):753-760.
- Heiskanen J (2005) Foliar color as an indicator of foliar chlorophyll and nitrogen concentration and growth in Norway spruce seedlings. *Scandinavian Journal of Forest Research* 20:329-336.
- Humbert L, Gagnon D, Kneeshaw DD, & Messier C (2007) A shade tolerance index for common understory species of northeastern North America. *Ecological Indicators* 7(1):195-207.
- Johnson, P.S., Shifley, S.R. and Rogers R. (2009) *The ecology and silviculture of oaks*. (CABI publishing).
- Johnstone J & Kasischke E (2005) Stand-level effects of soil burn severity on postfire regeneration in a recently burned black spruce forest. *Canadian Journal of Forest Research* 35(9):2151-2163.
- Keiller R. D & Walker A. D (1990) The use of chlorophyll fluorescence to predict CO₂ fixation during photosynthetic oscillations. *Proceeding of the Royal Society of London* 241:59-64.
- Klinka K, Green R.N., Trowbirdge R.L. & Lowe L.E. (1981) Taxonomic humus classification forms in ecosystem of British Columbia. Province of British Columbia, Ministry of Forests, Land Management Report 8, pp 61.
- Kneeshaw D, Williams H, Nikinmaa E, & Messier C (2002) Patterns of above-and below-ground response of understory conifer release 6 years after partial cutting. *Canadian Journal of Forest Research* 32(2):255-265.

- Lanner M. R (1985) On the intensity of height growth to spacing. *Forest Ecology and Management* 13:143-148.
- Lafleur B, Pare D, Fenton N, & Bergeron Y (2010) Do harvest methods and soil type impact the regeneration and growth of black spruce stands in northwestern Quebec? *Canadian Journal of Forest Research* 40(9):1843-1851.
- Lavoie M, Paré D, Fenton N, Groot A, & Taylor K (2005) Paludification and management of forested peatlands in Canada: a literature review. *Environmental Reviews* 13(2):21-50.
- L'Hirondelle SJ, Simpson DG, & Binder WB (2007) Chlorophyll fluorescence, root growth potential, and stomatal conductance as estimates of field performance potential in conifer seedlings. *New Forests* 34:235-251.
- Li C, Liu S, & Berninger F (2004) *Picea* seedlings show apparent acclimation to drought with increasing altitude in the eastern Himalaya. *Trees-Structure and Function* 18(3):277-283.
- Lichtenthaler HK. (1987) Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes, in *Methods in Enzymology*, edited by R.D. Lester Packr, pp. 350-382, Academic Press.
- Mailly D & Gaudreault M. (2005) Growth intercept models for black spruce, jack pine and balsam fir in Quebec. *Forestry Chronicle* 81(1):104-113.
- Major J, Barsi D, Mosseler A, Rajora O, & Campbell M (2007a) Predominant paternal inheritance pattern of light-energy processing adaptive traits in red and black spruce hybrids. *Canadian Journal of Forest Research* 37(2):293-305.
- Major J, Mosseler A, Barsi D, & Campbell M (2007b) Comparative nutrient economy, stable isotopes, and related adaptive traits in *Picea rubens*, *Picea mariana* and their hybrids. *Trees - Structure and Function* 21(6):677-692.
- Mallik A.U. (1987) Allelopathic potential of *Kalmia angustifolia* to black spruce (*Picea mariana*). *Forest Ecology and Management* 20(1-2):43-51.
- Manitoba Conservation. (2010) Manitoba free-to-grow survey manual [online]. Government of Manitoba. Available at http://gov.mb.ca/conservation/forestry/pdf/renewal/ftg_2010.pdf.
- Marshall JD, Rehfeldt GE, & Monserud RA (2001) Family differences in height growth and photosynthetic traits in three conifers. *Tree Physiology* 21(11):727-734.
- Mattsson A (1997) Predicting field performance using seedling quality assessment. *New Forests* 13(1):227-252.

- Messier C., Doucet R., Ruel J-C., Claveau Y., Kelly C. and Lechowicz J.M. (1999) Functional ecology of advance regeneration in relation to light in boreal forests. *Canadian Journal of Forest Research* 29(6):812-823.
- Messier C., Parent S. & Bergeron Y (1998) Effect of overstory and understory vegetation on the understory light environment in mixed boreal forests, *Journal of Vegetation Science*, 9(4):511-520.
- Ministry of Forests, Lands and Natural Resource Operations. (2010) Silviculture [online]. Government of British Columbia. Available at <http://for.gov.bc.ca/dqc/Silviculture.htm>
- Minocha, R., G. Martinez, B. Lyons and S. Long (2009) Development of a standardized methodology for quantifying total chlorophyll and carotenoids from foliage of hardwood and conifer tree species, *Canadian Journal of Forest Research*, 39, 849-861.
- Mitchell R, Waring R, & Pitman G (1983) Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science* 29(1):204-211.
- Morin H & Gagnon R (1991) Structure et croissance de peuplements d'épinette noire issus de régénération préétablie une quarantaine d'années après coupe au Lac-Saint-Jean. *Québec. For. Chron* 67:275-283.
- Morin H & Gagnon R (1992) Comparative growth and yield of layer-and seed-origin black spruce (*Picea mariana*) stands in Quebec. *Canadian Journal of Forest Research* 22(4):465-473.
- Moss, M. & L. Hermanutz (2009) Postfire seedling recruitment at the southern limit of lichen woodland, *Canadian Journal of Forest Research*, 39(12), 2299-2306.
- Muller H. W (1967) Botany: A Functional Approach. The Macmillan Company, New York, 486 pp.
- Munster-Swendsen M (1987) Index of vigor in Norway spruce (*Picea abies* Karst.). *Journal of Applied Ecology* 24(2):551-561.
- Paludification des sites forestiers sur les basses terres de la Baie James: un phénomène à gérer. 2008. Bernier, P.Y.; Simard, M; Paré, D.; Bergeron, Y. Pages 1-2 (Vol. Fiche technique no7) dans Chaire en aménagement forestier durable. Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Québec. p.
- Paquin R & Doucet R (1992a) Productivité de pessières noires boréales régénérées par marcottage à la suite de vieilles coupes totales au Québec. *Canadian Journal of Forest Research* 22(4):601-612.

- Paquin R & Doucet R (1992b) Croissance en hauteur à long terme de la régénération préétablie dans des pessières noires boréales régénérées par marcottage, au Québec. *Canadian Journal of Forest Research* 22(4):613-621.
- Paquin R, Margolis H, Doucet R, & Coyea M (1999) Comparison of growth and physiology of layers and naturally established seedlings of black spruce in a boreal cutover in Quebec. *Canadian Journal of Forest Research* 29(1):1-8.
- Remphrey W.R. & Powell G.R. (1984) Crown architecture of *Larix laricina* saplings: shoot preformation and neoformation and their relationship to shoot vigor. *Canadian Journal of Botany* 62: 2181-2192.
- R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>
- Richardson AD, Duigan SP, & Berlyn GP (2002) An evaluation of noninvasive methods to estimate foliar chlorophyll content. *New Phytologist* 153(1):185-194.
- Robichaud E & Methven I (1991) Tree vigor and height growth in black spruce. *Trees-Structure and Function* 5(3):158-163.
- Rossi S, Tremblay M, Morin H, & Levasseur V (2009) Stand structure and dynamics of *Picea mariana* on the northern border of the natural closed boreal forest in Quebec, Canada. *Canadian Journal of Forest Research* 39(12):2307.
- Roy V, Bernier P, Plamondon A, & Ruel J (1999) Effect of drainage and microtopography in forested wetlands on the microenvironment and growth of planted black spruce seedlings. *Canadian Journal of Forest Research* 29(5):563-574.
- Ruel J, Messier C, Doucet R, Claveau Y, & Comeau P (2000) Morphological indicators of growth response of coniferous advance regeneration to overstorey removal in the boreal forest. *Forestry Chronicle* 76(4):633-642.
- Ruel JC, Horvath R, Ung CH, & Munson A (2004) Comparing height growth and biomass production of black spruce trees in logged and burned stands. *Forest Ecology and Management* 193(3):371-384.
- Rweyongeza M. D, Yeh C. F, & Dhir K. N (2005) Heritability and correlations for biomass production and allocation in white spruce seedlings. *Silvae Genetica* 54:228-235.
- Salemaa M & Jukola-Sulonen E-L (1990) Vitality rating of *Picea abies* by defoliation class and other vigor indicators. *Scandinavian Journal of Forest Research* 5(1):413 - 426.

- Saucier, J-P., Grondin, P., Robitaille, A. & Bergeron, J-F., (2003) Vegetation zones and bioclimatic domains in Quebec [online]. Available from <http://www.mrnfp.gouv.qc.ca/english/publications/forest/publications/zone-a.pdf>.
- Seaton G. R. G & Walker A. D (1990) Chlorophyll fluorescence as a measure of photosynthetic carbon assimilation *Proceeding of the Royal Society of London* 242:29-35.
- Simard M, Lecomte N, Bergeron Y, Bernier PY, & Paré D (2007) Forest productivity decline caused by successional paludification of boreal soils. *Ecological Applications* 17(6):1619-1637.
- Solarik A. K, Volney Jan A. W, Lieffers J. V, Spence R. J & Hamann A (2011) Factors affecting white spruce and aspen survival after partial harvest. *Journal of Applied Ecology* 49(1):145-154.
- Startsev N, McNabb D, & Startsev A (1998) Soil biological activity in recent clearcuts in west-central Alberta. *Canadian Journal of Soil Science* 78(1):69-76.
- St-Denis A, Kneeshaw D, & Bergeron Y (2010) The role of gaps and tree regeneration in the transition from dense to open black spruce stands. *Forest Ecology and Management* 259(3):469-476.
- Stenberg P (1996) Simulations of the effects of shoot structure and orientation on vertical gradients in intercepted light by conifer canopies. *Tree Physiology* 16(1-2):99.
- Stevenson A, Muzika R, & Guyette R (2008) Fire scars and tree vigor following prescribed fires in Missouri Ozark upland forests. p 525.
- Veillette J (1994) Evolution and paleohydrology of glacial lakes Barlow and Ojibway. *Quaternary Science Reviews* 13(9-10):945-971.
- Viro PJ (1959) Estimation of the Effect of Fertilization from Needle Color. *Oikos* 10(2):183-189.
- Walker G & Mallik A (2009) Black spruce reforestation in Kalmia heath: seedling response to forest floor mixing and mycorrhizal inoculation with *Paxillus involutus*. *Canadian Journal of Forest Research* 39:2007-2020.
- Waring R, Thies W, & Muscato D (1980) Stem growth per unit of leaf area: a measure of tree vigor. *Forest Science* 26(1):112-117.

- Yamasaki S, Fyles J, & Titus B (2002) Interactions among *Kalmia angustifolia*, soil characteristics, and the growth and nutrition of black spruce seedlings in two boreal Newfoundland plantations of contrasting fertility. *Canadian Journal of Forest Research* 32(12):2215-2224.
- Zeng R & Mallik A (2006) Selected ectomycorrhizal fungi of black spruce (*Picea mariana*) can detoxify phenolic compounds of *Kalmia angustifolia*. *Journal of Chemical Ecology* 32(7):1473-1489.

APPENDIX

Here we present tables and figures that complement this research. These elements help to clarify certain aspects of this study.

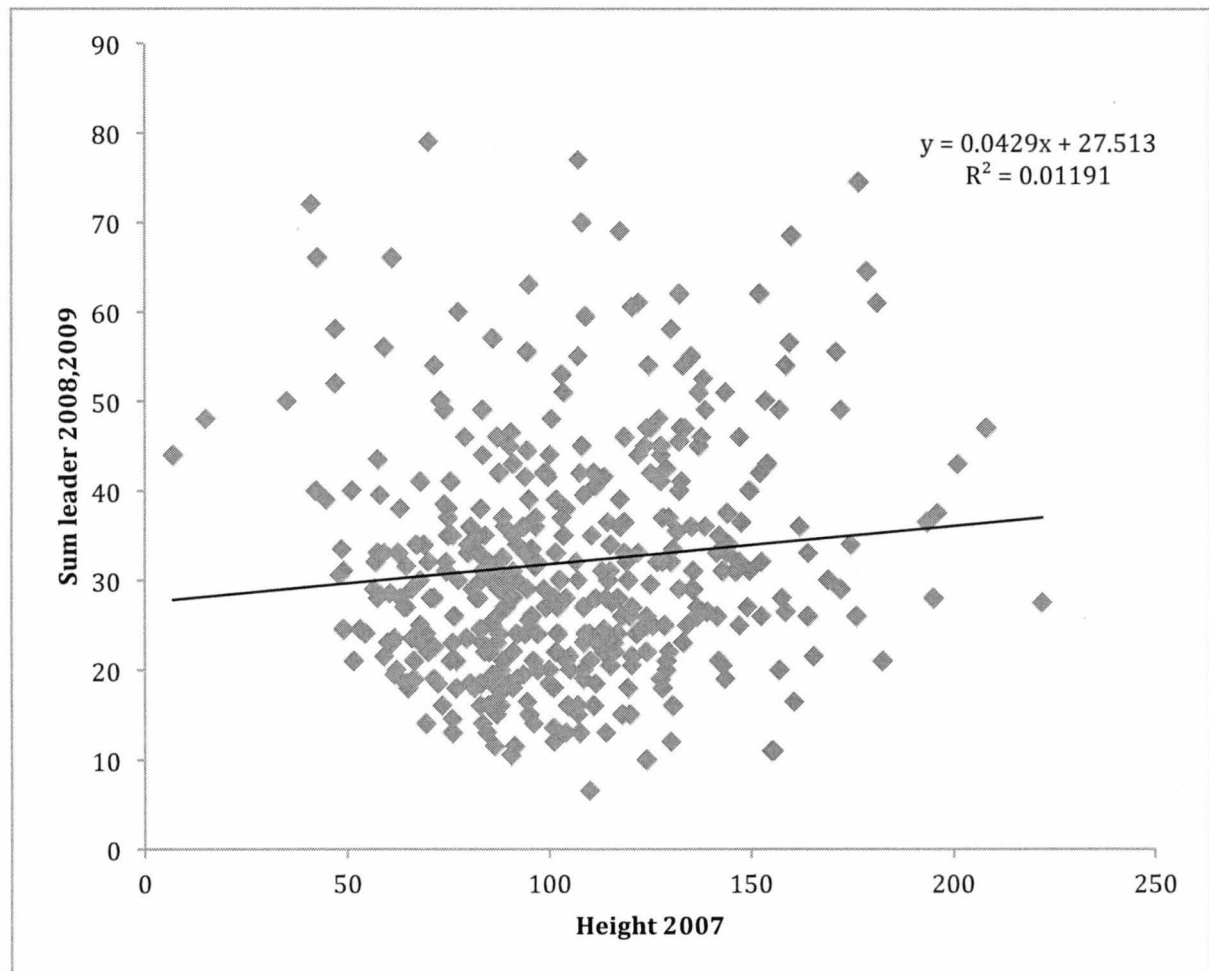


Figure 1A. Black spruce size effect used to determine if past height has an effect on future leader length.

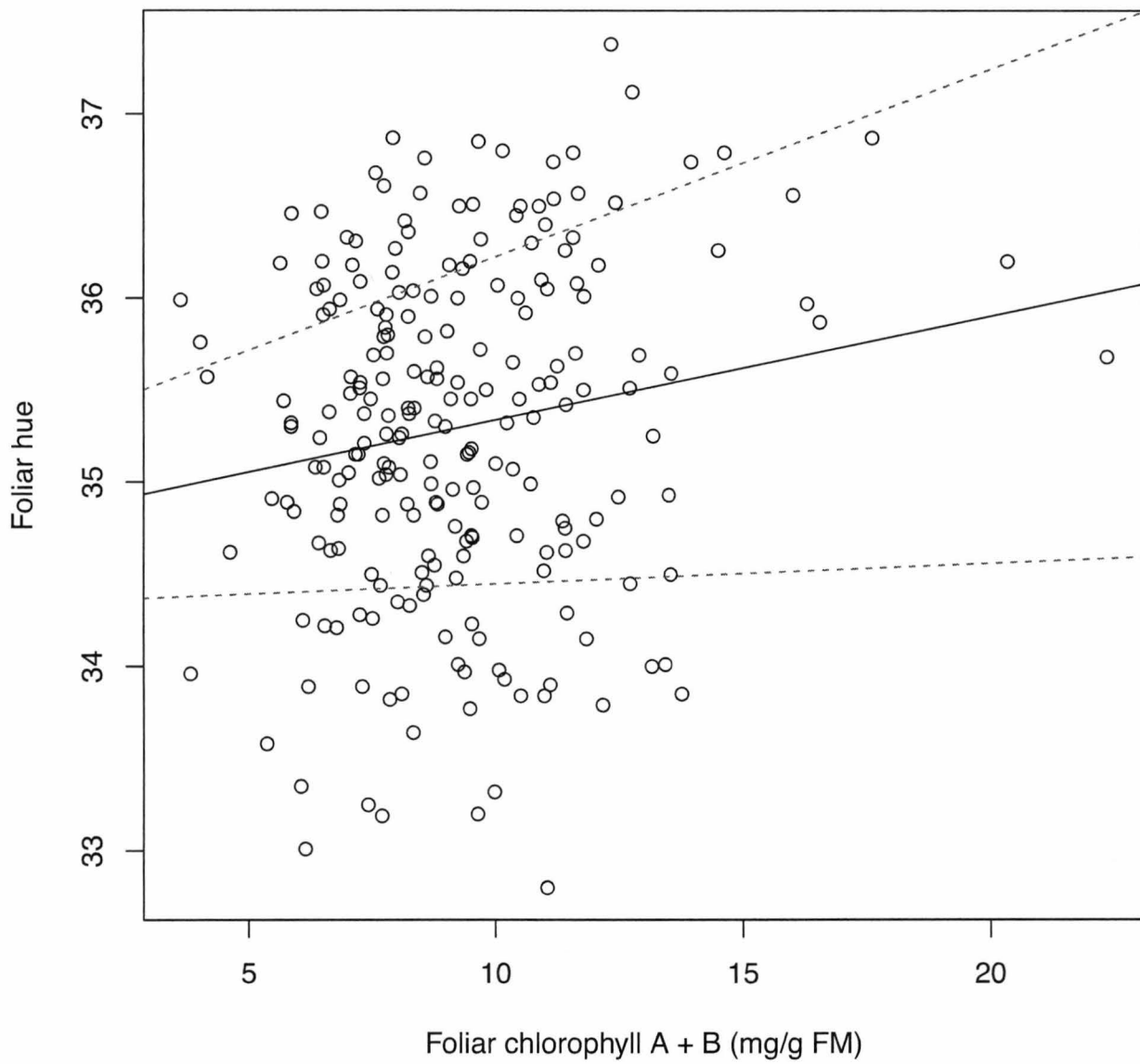


Figure 2A. Relationship between foliar hue and total chlorophyll ($n = 130$, $\text{Adj. } R^2 = 0.02225$, $\text{RSE} = 0.9053$, $y = 0.06x + 34.77$).

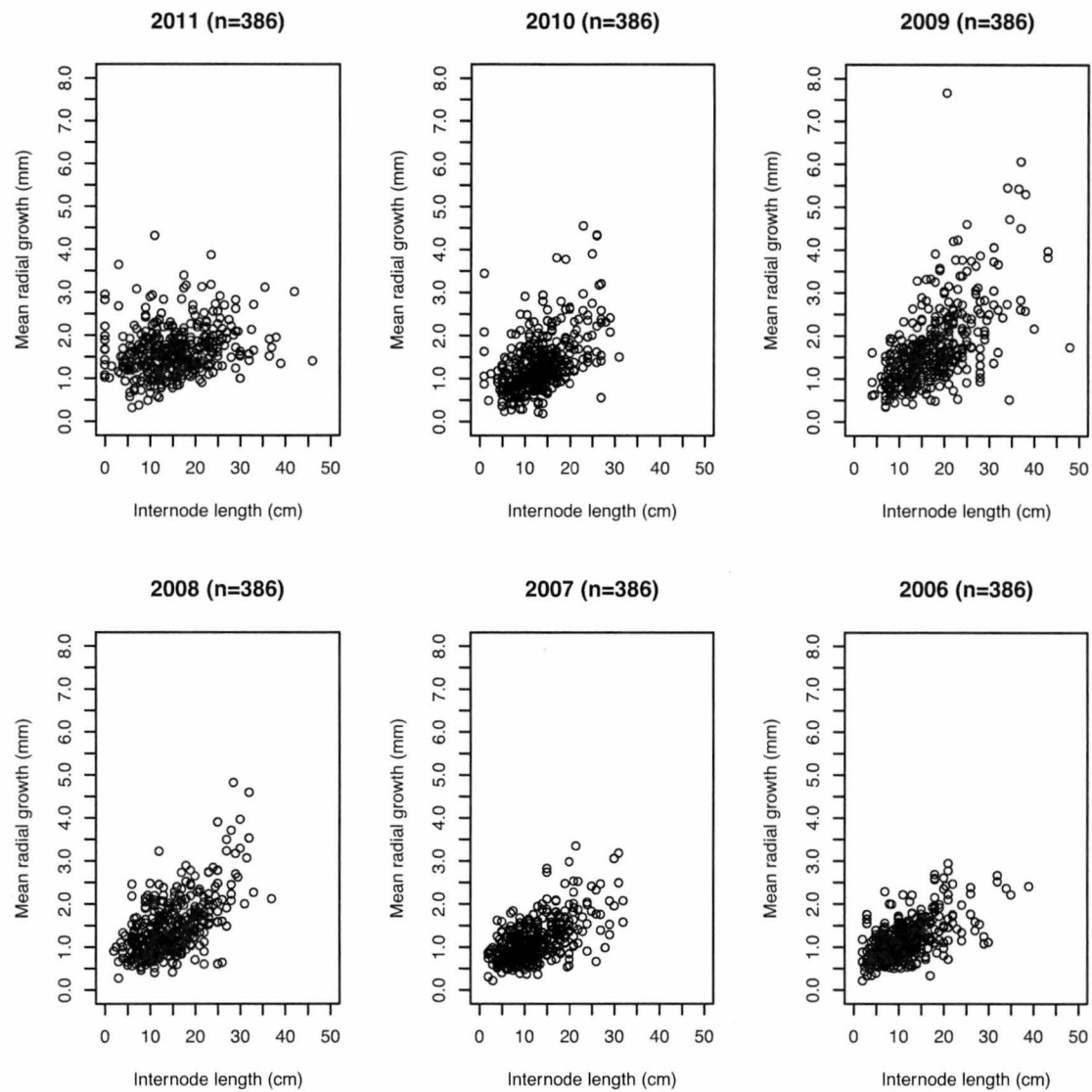


Figure 3A. Mean radial growth as a function of internode length for 2006-2011. Mean radial growth is set up as a function of internode length in order to highlight 2008 and 2009 as they demonstrate the two best growth years.

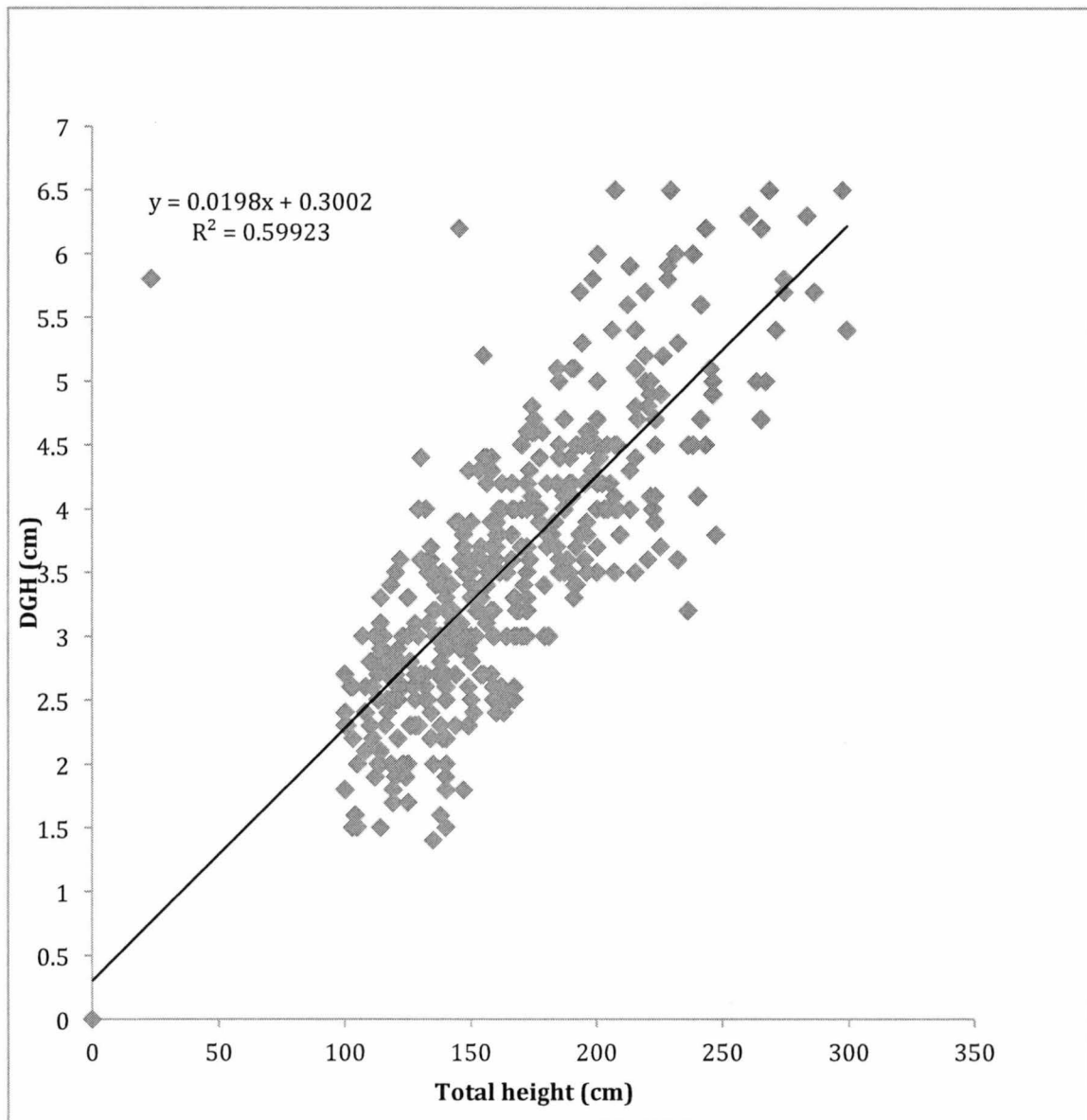


Figure 4A. Diameter at ground height (DGH) with respect to total height.

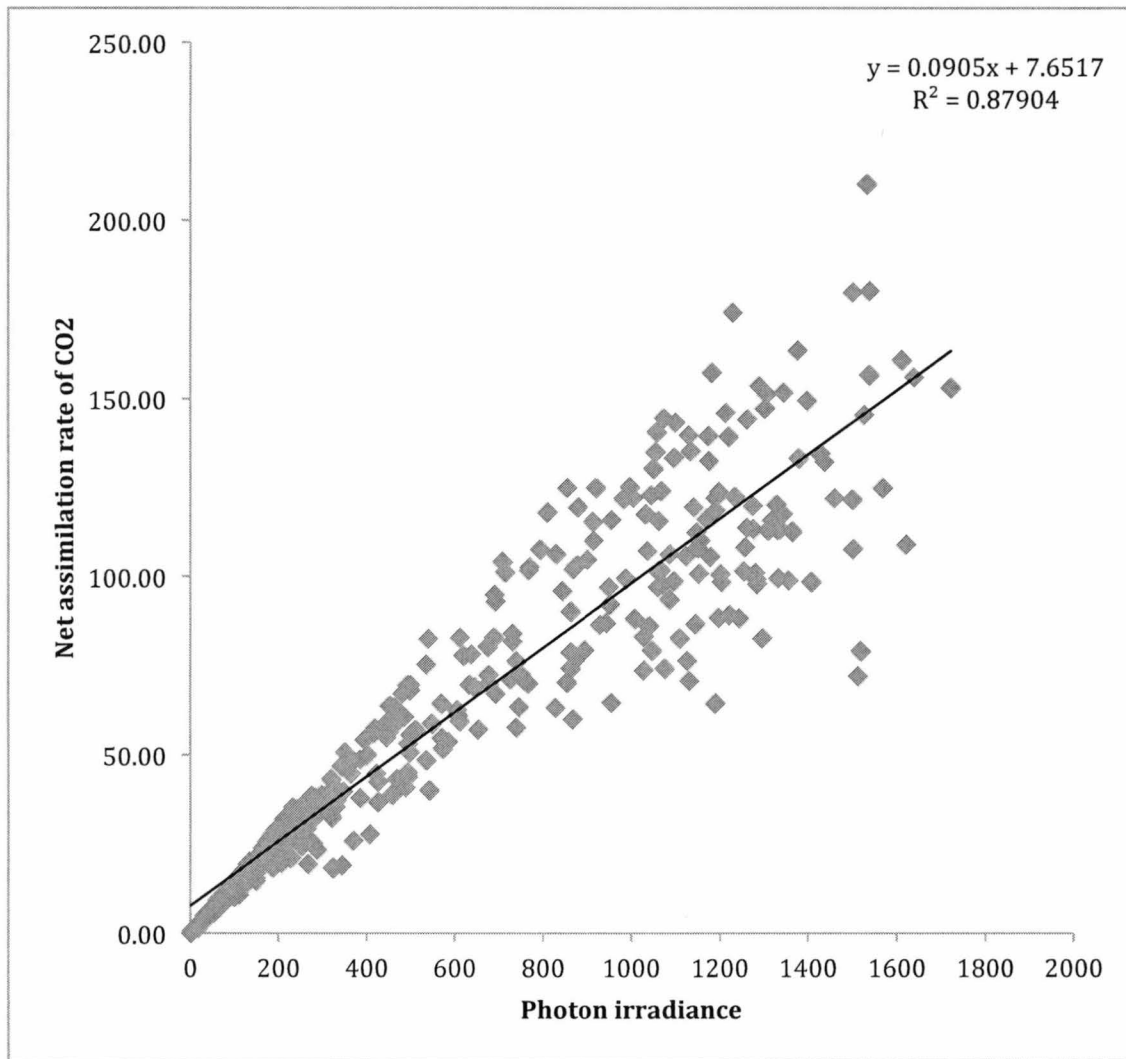


Figure 5A. Changes in the rate of CO₂ assimilation.

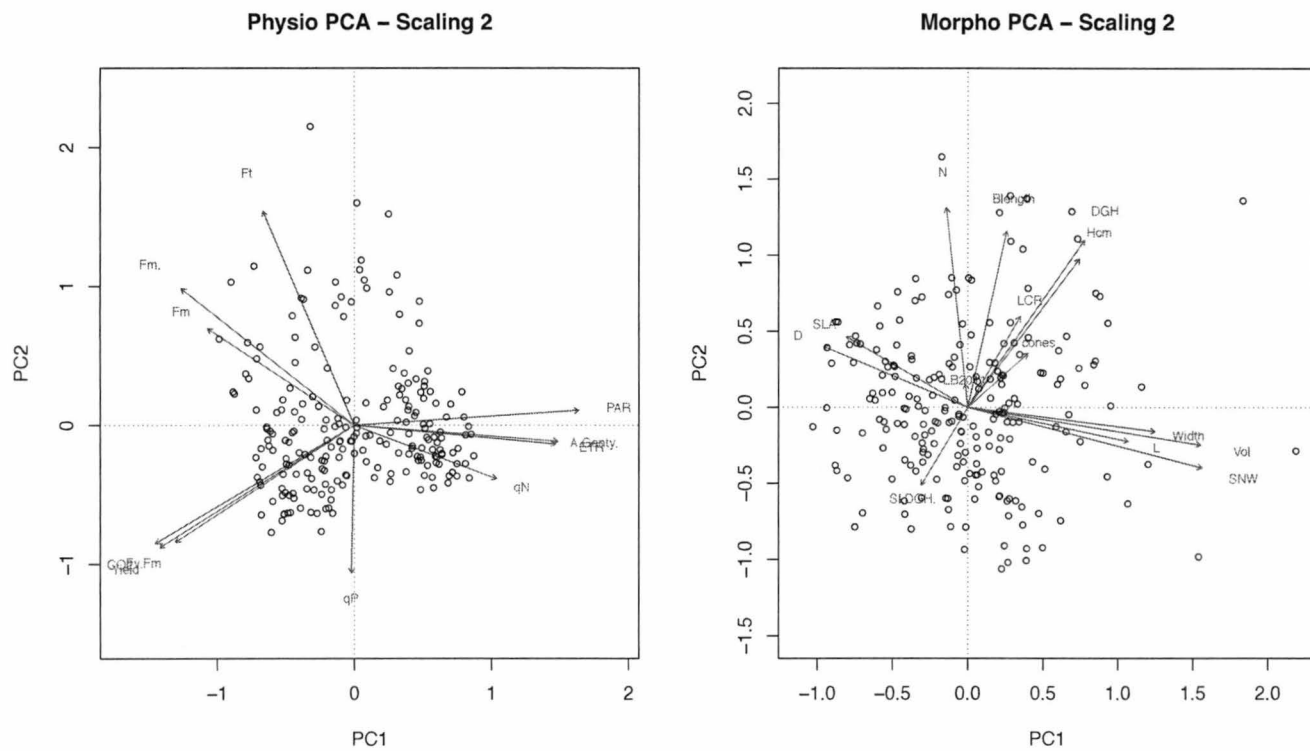


Figure 6A. PCA biplots for physiological and morphological variables.

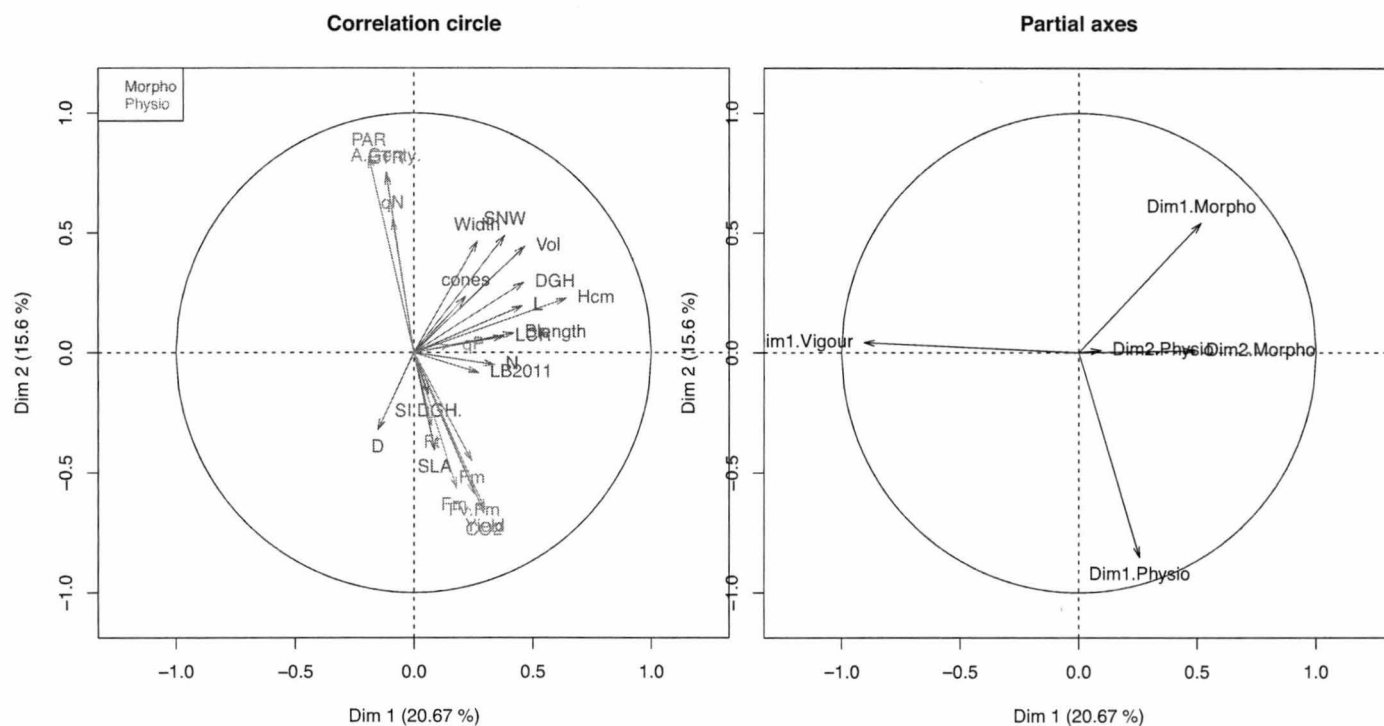
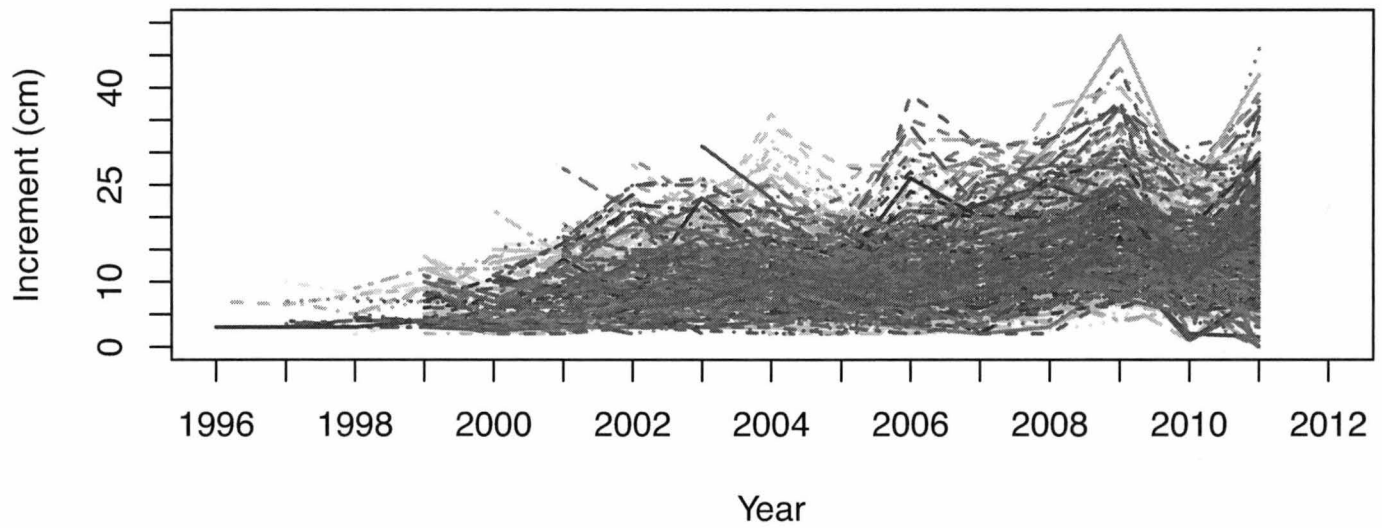


Figure 7A. Multiple Factor Analysis (MFA): correlation circle and partial axes between physiology, morphology and vigor. The figure on the left entitled “Correlation circle” shows the normalized physiological and morphological vectors and their relationship to one another. The figure on the right shows the partial axes of the MFA analysis.

Variation in internode increments (n=386)



Variation in ring width (n=386)

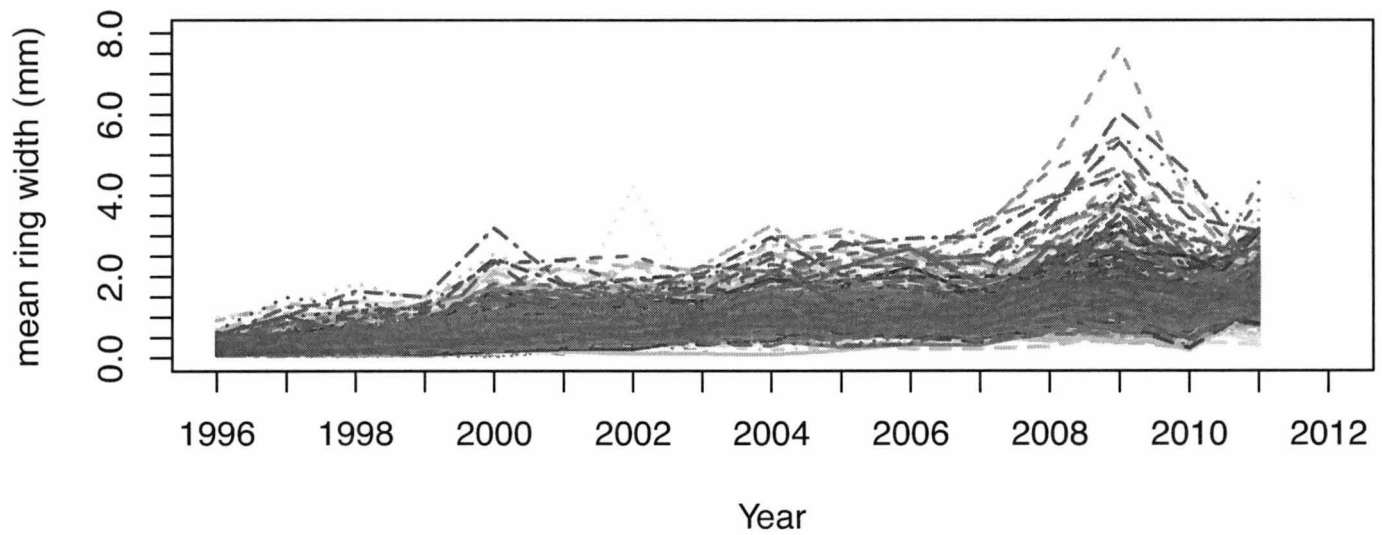


Figure 8A. Variations in internode increments and ring widths respectively. Each sample tree is represented by a color.

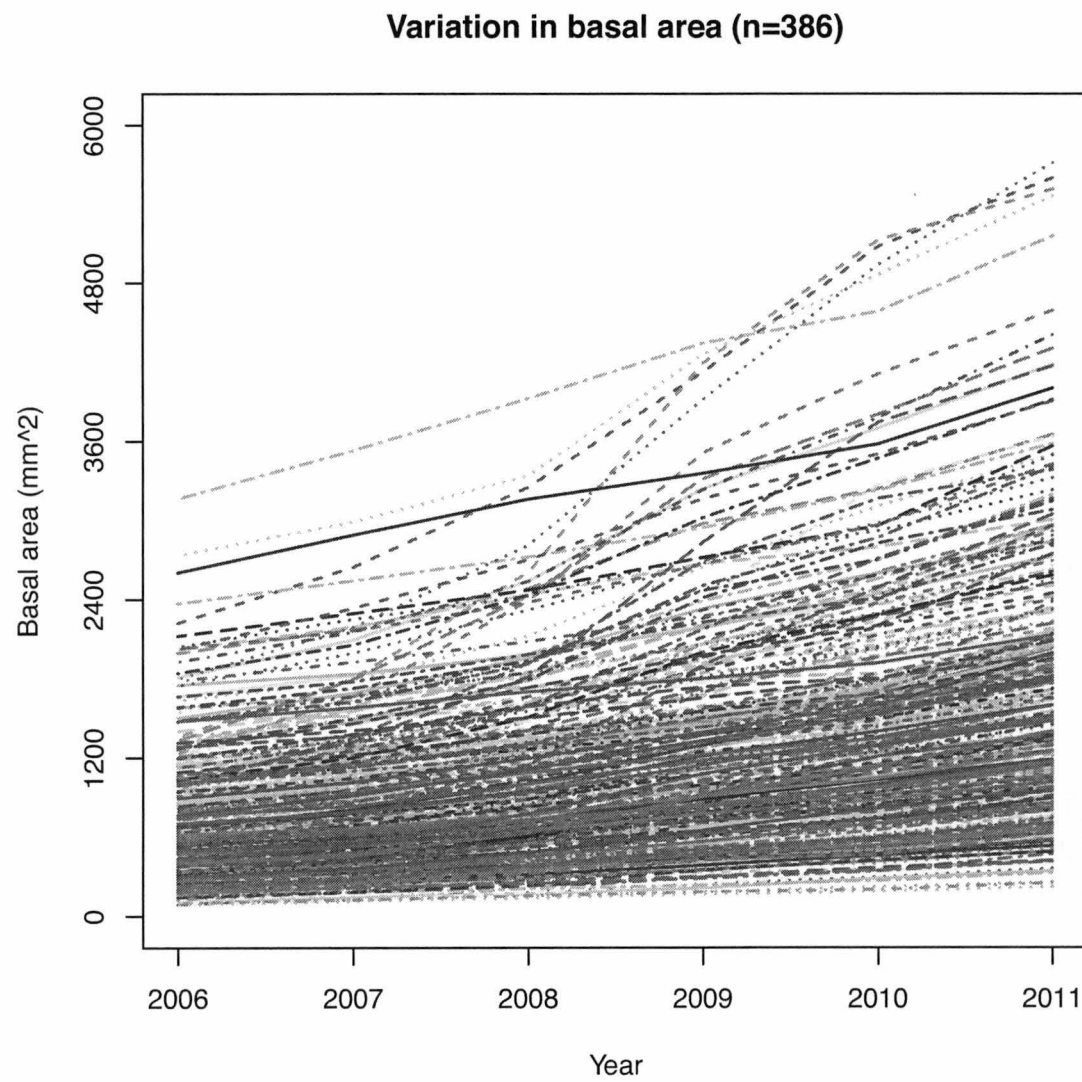


Figure 9A. Variation in basal area. Each sample tree is represented by a color.

Table 1A Pearson correlation matrix, ρ

	Tree height	SLA	SNW	L	W	V	D	DGH	SI	PAR	ETR	Yield	A	CO ₂
Tree height	1.000													
SLA	-0.026	1.000												
SNW	0.210	-0.577 ***	1.000											
L	0.087	-0.080 ***	0.734 ***	1.000										
W	0.355	-0.323 **	0.633 *	0.128 ***	1.000									
V	0.302	-0.274 ***	0.903 ***	0.673 ***	0.802 ***	1.000								
D	0.011	0.291	-0.543	-0.469	-0.250	-0.468	1.000							
DGH	0.753 ***	-0.127	0.193	0.001	0.346	0.256	0.012	1.000						
SI	0.011 ***	0.180	-0.052	0.101	-0.108	-0.033	-0.016	-0.622 ***	1.000					
PAR	0.004	-0.114	0.076	-0.019	0.118	0.054	-0.070	0.034	-0.04 .	1.000				
ETR	0.013	-0.101	0.089	0.025	0.095	0.062	-0.089	0.028	-0.019	0.940	1.000			
Yield	0.029	0.084 *	0.020	0.124	-0.051	0.045	-0.040	-0.039	0.078	-0.665 ***	-0.444 *	1.000		
A	0.025	-0.101	0.093	0.023	0.105	0.070	-0.087	0.032	-0.013	0.944 ***	0.993 ***	-0.460 ***	1.000	
CO ₂	0.017	0.090	0.023	0.130	-0.048	0.049	-0.043	-0.042	0.071	-0.681 ***	-0.484 ***	0.987 ***	-0.506 ***	1.000

*** significant at 0.001

** significant at 0.01

* significant at 0.05

SLA, Specific Leaf Area; SNW, Specific Needle Weight; L, needle length; W, needle width; V, needle volume; D, branch density; SI, Slenderness Index; PAR, Photosynthetically Active Radiation; ETR, Electron Transfer Rate; A, Photosynthesis; CO₂, CO₂ assimilation rate