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Permanent site characteristics exert a larger influence than atmospheric conditions on leaf mass, foliar nutrients and ultimately aboveground biomass productivity of *Salix miyabeana* 'SX67'

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ABSTRACT

Salix species are widely used for wood production, but the interactive effects of soil types and atmospheric conditions on *Salix* foliar nutrients and aboveground biomass productivity have not yet been elucidated. The objectives of this study were fourfold: (1) to assess the variation in foliar nutrients and leaf mass of *Salix miyabeana* 'SX67' grown as short rotation coppice (SRC) across three growing seasons and nine locations in Quebec with different permanent site characteristics and atmospheric conditions, (2) to test if atmospheric conditions and permanent site characteristics could explain the variation in foliar nutrients and leaf mass, (3) to develop models that consider foliar traits and nutrient interactions to produce more robust predictions of annual aboveground biomass yields, and (4) to compare nutritional requirements of 'SX67' to other *Salix* cultivars used for SRC. Leaf samples were collected over three growing seasons at all sites. For each site, atmospheric conditions were simulated and foliar nutrient levels were measured to perform centered log ratio (clr) transformations for each foliar nutrient. This approach considered foliar nutrient interactions and dealt with clr scores as linearly independent. The clr scores were more largely influenced by permanent site characteristics than by atmospheric conditions, despite large variations in degree-days. However, some foliar nutrients and leaf mass were linearly related to atmospheric variables within sites. Strong relationships between annual aboveground biomass yields and leaf mass were computed (e.g. adjusted $R^2 = 0.62$), likely due to a proportional allocation between foliage and wood. Although significant linear relationships between clr scores (i.e. N, Ca and Mn) and annual aboveground biomass yields were detected, yields were more robustly explained non-linearly by thresholds (i.e. N, Ca and P) (e.g. $R^2 = 0.85$), likely due to permanent characteristics specific to each of the sites and climatic limitations during the growing seasons studied. The thresholds detected by non-linear models suggested high N and P use efficiencies and a large Ca requirement of 'SX67'.

1. Introduction

Species of *Salix* exhibit high physiological and growth plasticity (He and Dong, 2003). They can be grown under a wide range of soil and climatic conditions (Tahvanainen and Rytkönen, 1999; Sannervik et al., 2006; Aylott et al., 2008; Ens et al., 2013), but yields of a species or genotype can be dramatically influenced by soil nutrients and thus, they can vary substantially among sites. Genotypes of *Salix* grown as short rotation coppice (SRC) are more nutrient-demanding than those growing in the wild (Weih, 2001) and are capable of building very high contents of N, P, K, Ca and Mg (Adegbidi et al., 2001). Soil N

availability influences foliar N and aboveground yields (Ens et al., 2013; Toillon et al., 2013). Ericsson (1981a) also demonstrated strong causal relationships between nutrient availability (including N, P, K, Ca and Mg), foliar nutrients and aboveground biomass yields for three *Salix* cultivars grown hydroponically. Various studies have also showed the benefits of fertilization on foliar nutrients such as N, P or K and aboveground biomass yields of *Salix* (Marmiroli et al., 2012; Quaye et al. 2015; Labrecque and Teodorescu, 2001; Labrecque and Teodorescu, 2003).

Monitoring of foliar nutrients over successive years following the fertilization of forests or plantations has often been done (Huettl et al.,

1990; Wilmot et al., 1996), including *Salix* (Labrecque et al., 1998), but very few studies have established a relationship between year-to-year variations in atmospheric conditions and foliar nutrients (or other leaf traits). A better understanding of the year-to-year variation in foliar nutrients and other leaf traits of woody crops such as willow SRC could provide valuable information to support nutrient and water management in the context of climate change. Duquesnay et al. (2000) showed that foliar N, P, K, Ca and Mn of European beech (*Fagus sylvatica* L.) varied over several growing seasons within the same plots. The combined year-to-year and plot effects explained more than 70% of the variation in foliar nutrients. Kudo (2003) observed lower N concentrations in leaves of Miyabe willow (*Salix miyabeana* 'Seemen') during warm summers compared to cooler ones, suggesting that year-to-year atmospheric variations influenced *Salix* nutrition. In Mediterranean Italy, year-to-year atmospheric variations and soil conditions influenced leaf traits of *Fagus sylvatica* L., Turkey oak (*Quercus cerris* L.) and holm oak (*Q. ilex* L.), which in turn impacted aboveground productivity (Bussotti et al., 2000). In particular, leaf surface area and foliar N, P and S decreased and leaf mass per area ($g\,m^{-2}$) increased under water stress. Leaf mass per area was the most robust predictor of site productivity under such conditions. In three plantations established on heterogeneous soils in northern France, leaf area and aboveground biomass of six hybrid *Salix* genotypes as well as soil N availability were highest where soil water availability was high (Toillon et al., 2013).

Studies on plant nutrition generally rely on nutrient concentrations, hence denying nutrient interactions (Wilkinson et al., 2000). Nutrient interactions are traditionally described as dual or stoichiometric ratios (Ingestad, 1987; Walworth and Sumner, 1987). Ratios are scale-dependent and generate spurious correlations (Chayes, 1960). Ratios should be averaged using geometric means (Fleming and Wallace, 1986), hence requiring log transformations to compute variance. Because nutrients in a leaf are compositional, they can be modelled using the more robust log ratio transformations of compositional data analysis (Aitchison, 1986; Parent and Dafir, 1992; Souza et al., 2016). To refine our understanding of nutrient cycling and optimize nutrient diagnoses for woody shrubs and trees in the context of global change, there is a need to investigate the relationships between foliar nutrients, atmospheric conditions and biomass production. A large network of *Salix miyabeana* 'SX67' plantations grown as SRC was used to address this question.

We assumed causal relationships between foliar nutrients and atmospheric conditions and in turn, we hypothesized that nutritional factors limiting aboveground biomass yield change across growing seasons. In this respect, we first assessed variations in foliar nutrients and leaf mass over three growing seasons across nine sites in Quebec with various soils and atmospheric conditions. Using different statistical models, we then tested if year-to-year variation in atmospheric conditions (within sites) as well as permanent site characteristics (e.g. parent material depth and soil texture, slope and aspect) could explain the variability in foliar nutrients and leaf mass. Using the centred log ratio transformation, we also developed models that consider nutrient interactions as a mean to come up with the most robust predictions of annual aboveground biomass yields. Finally, we compared the nutritional requirements of highly productive 'SX67' in Quebec to other *Salix* cultivars used for SRC elsewhere.

2. Methods

2.1. Sites

Nine sites of 'SX67' grown as SRC in Quebec (i.e. ABI, BEL, BOI, HTG, LAV, MTL, RXP, SJPJ and STR, Fig. 1) were used for this study.

Field design, previous land use and soil properties are described in detail in Fontana et al. (2016, 2017), however, we provide a brief description here. Using a mechanical type planter, 'SX67' cuttings (i.e. 20–25 cm in length) were inserted in the soil at a depth of 15–20 cm at a

spacing of 30 cm along a single row design. Rows were separated by 1.8 m, giving an approximate density of 18,500 stools ha^{-1}. Row lengths of 'SX67' were over 100 m for nearly all sites (i.e. ABI, BOI, LAV, MTL, RXP, SJPJ and STR). At the HTG site, 'SX67' was planted in 10×12 m as part of a clonal trial with a randomized split-block design. Plowing and cross-disking were carried out before SRC establishment, except at BOI and SJPJ due to the stony nature of the land. Before plowing in the fall, roundup Pro™ (41% glyphosate, the active ingredient (a.i.)) was applied once at a rate of 2–4 L ha^{-1} (0.85–1.7 a.i. ha^{-1}), depending on weed type and abundance. Coppicing was generally performed after the first growing season and harvesting was done between three to five years depending on site. All the SRC were established on mineral soils, except for RXP where soil organic C (C_{org}) concentration is > 60%. Soil particle size distribution varies considerably across sites, with sand content ranging from 19 to 74% and clay content ranging from 4 to 43%. Soil chemistry also varies substantially across sites. Soil pH ranges between 5.1 and 7.5, where BOI and HTG have a higher pH than the others. Except for RXP, which exhibits high soil total N and P concentrations (9.0 mg N kg^{-1} and 0.78 mg P kg^{-1}), all other sites have relatively low soil total N (1.7–3.4 mg N kg^{-1}) and P (0.06–0.17 mg P kg^{-1}) concentrations. The STR, MTL and LAV sites have the lowest C_{org} values (< 7.5%) and exchangeable Ca (< 5.1 $cmol_c\,kg^{-1}$) and Mg (< 0.8 $cmol_c\,kg^{-1}$) concentrations, likely due to their high sand content (> 50%).

2.2. Estimation of annual aboveground biomass yields

At each site, five plots (5×5.4 m, 45 plots in total) were randomly selected for crop establishment. Annual aboveground biomass yields (Mg ha^{-1}) were estimated within all plots using aboveground biomass and basal area increment (mm^2) data (Fontana et al., 2016). Because a few growing seasons are needed for the stools to fully establish and reach their maximum yield potential, productivity was estimated only for growing seasons that had reached their maximum yield potential. This procedure provided a robust comparison between sites, despite their different ages and number of rotations. First growing seasons of subsequent rotations were also excluded from the database because yields were systematically lower than maximum yield potential.

2.3. Foliage sampling, leaf mass and nutrient analysis

Foliage was sampled between the last week of August and the first week of September (i.e. before any night frost) of 2011, 2012 and 2013. The number of sampled sites varied between growing seasons because of the complex logistics of sampling nine sites across a large geographical range in a short period of time. The number of sampled plots and stools also varied between growing seasons and depended upon available resources for sampling and laboratory analysis. In 2011, four contiguous healthy stools were sampled in each of the five plots on seven of the sites, ABI, BOI, LAV, MTL, RXP, SJPJ and STR (140 samples from 35 plots). In 2012, one stool in each of the five plots was sampled on six of the sites, ABI, BOI, LAV, MTL, RXP and HTG (30 samples from 30 plots). In 2013, four contiguous healthy stools were sampled in three of the five plots on eight sites, ABI, BOI, BEL, HTG, LAV, MTL, RXP and SJPJ. In this last case only, we made a composite sample using the four samples collected in each plot (24 samples from 24 plots). For each stool that was sampled in 2011, 2012 and 2013, we collected a minimum of 10 mature and healthy leaves in the upper-third of the canopy (full sunlight) from the stem with the largest basal diameter.

Leaves were oven-dried at 40 °C to a constant mass. For each sample, at least ten leaves were weighed and then finely ground using a ball mill (Vibratory Miro Mill Pulverisette 0, Fritsch GmbH, Idar-Oberstein, Germany). Average leaf mass was measured. Carbon and N levels were determined on ground samples using a Vario MicroCube (Elementar, Hanau, Germany) or an EA1108 CHNS-O Analyzer (Thermo Fisons, MA, USA). Ground samples were digested in
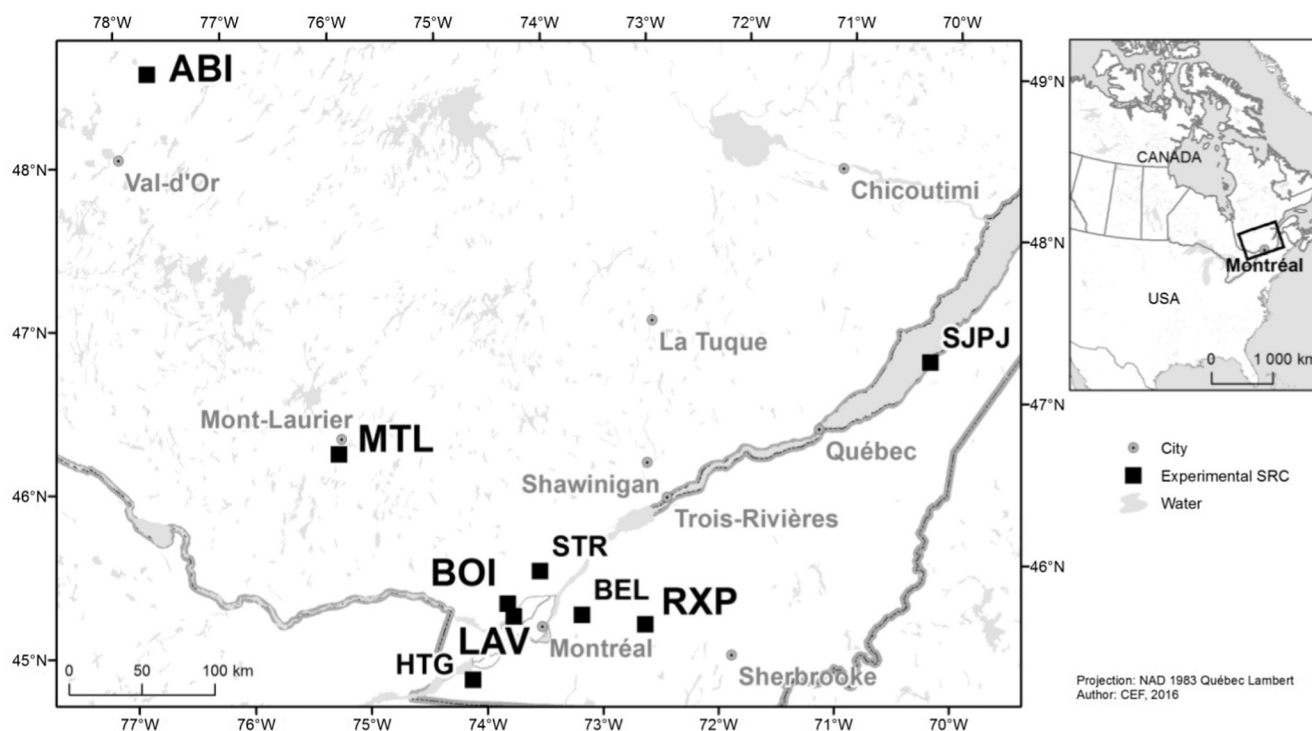
Fig. 1. Location of the nine short rotation willow cultures (SRC) studied in southern Quebec. The five sites for which all three growing seasons (2011, 2012 and 2013) were sampled (temporal data set, $n = 15$) are in the larger font.

concentrated HNO_3. Calcium, K, Mg, Mn, Zn and Fe were quantified from these digests using atomic absorption-emission (model AA-1475, Varian, Palo Alta, CA, USA), whereas P was analyzed colorimetrically (molybdate-based method) by flow injection analysis (QuickChem 8500 series 2 FIA System, Lachat Instruments, Loveland, CO, USA).

2.4. Compositional nutrient diagnosis

To account for interactions among nutrients, we modelled foliar nutrients using centred logarithmic ratios (*clr*) (Parent and Dafir, 1992). Computing clr scores implies that compositional data (i.e., foliar nutrients) interact within a constrained space, e.g., the leaf dry matter. Not all foliar nutrients or elements (e.g., S, Al, Si and trace elements) were measured. A filling value (Fv; Aitchison, 1982) was therefore calculated as follows to provide an estimate of the proportion of unmeasured nutrients or elements:

$$Fv = 100 - (\ C + N + P + K + Ca + Mg + Mn + Fe + Zn) \quad (1)$$

where nutrient levels are expressed in mass percentages. The geometric mean (GM) across proportions of foliar nutrients, including Fv, was computed as follows:

$$GM = (\ C \times N \times P \times K \times Ca \times Mg \times Mn \times Fe \times Zn \times Fv)^{1/10} \quad (2)$$

The clr scores were expressed as follows:

$$clr\ score_{Nutrient} = \ln \frac{\text{Proportion of } Nutrient}{GM} \quad (3)$$

where *Nutrient* refers to the nutrient or element for which the clr score is computed. The clr scores are suitable for visualizing the nutritional balance of foliage with multivariate methods, e.g., Principal Component Analysis (Parent et al., 1994). The clr scores were calculated with the *clr* function in the library *composition* (van den Boogaart et al., 2013) of the R statistical environment (v. 3.01, R Development Core Team, 2012). For the sake of simplicity, foliar levels and clr scores of C, N, P, K, Ca, Mg, Mn, Zn and Fe, together with leaf mass, are hereafter referred to as "leaf traits".

2.5. Atmospheric conditions

The BioSIM model was used to simulate atmospheric conditions for each site and growing season covered in the study (Régnière, 1996; Régnière et al., 2014). Using site elevation, latitude and longitude, BioSIM uses multivariate regressions to extrapolate data from the closest weather stations. BioSIM generates data that are statistically indistinguishable from measured data (Régnière and Bolstad, 1994). Lowest temperatures, means of minimum temperatures (°C), mean temperatures (°C), mean maximum temperatures (°C), maximum temperatures (°C), degree-days (base 5 °C), total solar radiation (MJ m^{-2}), precipitation (mm), mean number of days with precipitation, mean consecutive days with precipitation, highest values of consecutive days with precipitation, mean number of days without precipitation, mean consecutive days without precipitation and highest values of consecutive days without precipitation were modeled using the three closest stations to each site from the beginning of April to the end of August, approximately from bud burst to leaf sampling. Degree-days (base 5 °C) that were averaged over the three growing seasons varied from 1282 to 1866 across sites, with the northernmost site (ABI) having the lowest value and one of the southernmost sites (LAV) having the highest value (Table 1). Coefficients of variation reflecting year-to-year variability within sites were higher for rainfall than for degree-days, whereas coefficients of variation reflecting variability across sites for each growing season were similar between degree-days and rainfall (Table 1). Cumulative rainfall was the lowest during the 2012 growing season, indicating a warm and relatively dry summer. Based on degree-days, the 2012 growing season was warmer than the 2011 and 2013 growing seasons (Table 1).

2.6. Data analysis

The 'SX67' foliage at the nine sites was unevenly sampled 21 times throughout the three growing seasons (7 sites (35 plots) in 2011, 6 sites (30 plots) in 2012, and 8 sites (24 plots) in 2013; $n = 21$, hereafter referred to as the "full data set". The full data set encompasses data

Table 1

Combined average degree-days (base 5 °C) and rainfall for the 2011, 2012 and 2013 growing seasons at each of the nine sites. Average degree-days and rainfall are also reported for each growing season and are calculated with data from all sites. Coefficients of variation are reported in parentheses and indicate the variations within sites across growing seasons (ABI, BEL, BOI, HTG, LAV, MTL, RXP, SJPJ and STR) or within a growing season across sites (2011, 2012, 2013).

Site (soil type)	Degree-days (> 5 °C)	Rainfall (mm)
ABI (clay/agriculture)	1282 (6%)	414 (8%)
BEL (loamy/agriculture)	1801 (6%)	525 (20%)
BOI (loam/hardwood forest)	1787 (7%)	481 (19%)
HTG (silty clay loam/agriculture	1804 (5%)	502 (23%)
LAV (sandy loam/agriculture)	1866 (7%)	453 (22%)
MTL (loamy sand/mixed forest)	1556 (7%)	436 (21%)
RXP (organic/agriculture)	1748 (6%)	559 (26%)
SJPJ (loam/forage)	1424 (8%)	511 (15%)
STR (sandy loam/agriculture)	1751 (6%)	532 (10%)
2011	1681 (13%)	566 (13%)
2012	1766 (12%)	398 (11%)
2013	1559 (12%)	496 (10%)

Sites included in the temporal data set ($n = 15$) are indicated in bold.

that can be used to test for both spatial and temporal variations. The data set from the 2011 sampling season was the only one large enough to develop robust models across plots ($n = 35$, hereafter referred to as the "spatial data set"). For a balanced comparison of leaf traits between growing seasons, only data from the five sites for which all three growing seasons had been sampled were used, ABI, BOI, LAV, MTL and RXP ($n = 15$, hereafter referred to as the "temporal data set"). The most productive site in the temporal data set is RXP at 20.6 Mg ha^{-1} yr^{-1} (Table 2). The RXP site is also singular compared to the other sites given it is the only one characterized by an organic soil. The temporal data set therefore does not contain the data from the most productive sites and the range of aboveground biomass yields of mineral sites (i.e. 7.7–14.5 Mg ha^{-1} yr^{-1}) is much smaller than those covered by the full data set (i.e. 7.7–28 Mg ha^{-1} yr^{-1}) (Table 2), which means the temporal data set is not as statistically conducive as the full data set to model 'SX67' aboveground biomass productivity. Also, the temporal and spatial data sets were attributed these names for the sake of simplicity and to highlight their main characteristics. For example, the temporal data set can be used to test for spatial variation, not just the spatial data set. The use of a data set is therefore not limited to its name, nor does the name of a data set mean it is the only data set of this nature.

All statistics presented below were performed with the R statistical environment. The analyses were listed and linked to the relevant data

Table 3

Overview of the data sets and R functions and packages used for each statistical analysis.

Analyses	Data set	R function, package and reference (if relevant)
Coefficients of variation	Temporal	*cv, raster* (Hijmans and Van Etten, 2014)
Linear discriminant analyses	Temporal	*betadisper, vegan* (Oksanen et al., 2015), *lda, MASS* (Venables and Ripley, 2013), *predict, vegan*
Mixed models	Temporal	*nlme, nlme* (Pinheiro et al., 2014)
Forward selection	Full, Spatial, Temporal	*forward.sel, packfor* (https://r-forge.r-project.org/R/?group_id=195)
Linear regressions	Full, Temporal	*lme*
Variance partitioning	Full, Spatial, Temporal	*contr.helmert, STATS* (Team, 2013), *vapart, vegan, rda, vegan, anova, vegan*
Multivariate regression trees	Full, Spatial	*mvpart, mvpart* (De'ath, 2006)

set and R functions and packages in Table 3. Coefficients of variation (CV) of leaf traits were computed across growing seasons (i.e., 2011, 2012 and 2013) and sites using the temporal data set. We then tested if foliar levels of a specific nutrient and leaf mass could be explained by year-to-year atmospheric conditions. Mixed models were run with site as a random effect to take into account permanent site characteristics, and atmospheric variables as fixed effects. This was tested for all variables generated from BioSIM. To test for permanent site characteristics *vs* year-to-year atmospheric effects on foliar nutrients, we performed, again with the temporal data set, linear discriminant analyses using the clr scores for: (1) each growing season with site as the grouping factor and (2) each site with growing season as the grouping factor. Prior to analysis, multivariate homogeneity of variances within groups was tested. A posteriori classification was also performed. Site effect in this study therefore generally refers to permanent site characteristics only, excluding atmospheric conditions.

Linear regression models relating leaf traits to annual aboveground biomass yields were run across sites for each growing season individually using both the temporal and full data sets, which allowed to test if the outcomes were similar with the full *vs* truncated ranges of 'SX67' aboveground biomass productivity. The clr scores and leaf mass were the predictors, whereas the response variable was annual aboveground yields. The variance of annual aboveground biomass yields was partitioned (Peres-Neto et al., 2006) with site and clr scores (and leaf mass) as explanatory variables using the temporal and spatial data sets. The site effect was modelled concomitantly with the explanatory variables because these data sets did not respect the condition of

Table 2

Average foliar nutrient levels of N, P, K, Ca, Mg and Mn, leaf mass (LM), and mean annual aboveground biomass yield for the 2011, 2012 and 2013 growing seasons combined. Coefficients of variation (CV) across growing seasons are reported in parentheses.

Sites	Concentrations of foliar nutrients									LM	Yield
	C	N	P	K	Ca	Mg	Mn	Fe	Zn	mg leaf^{-1}	t ha^{-1} y^{-1}
	mg g^{-1}						µg g^{-1}				
ABI	45.8 (4%)	17.9 (8%)	1.6 (20%)	12.0 (25%)	17.0 (25%)	4.0 (19%)	1.77 (16%)	1.08 (109%)	1.30 (24%)	68 (2%)	10.1 (7%)
BEL	46.4	25.1	1.8	10.4	24.2	4.6	0.28	0.67	0.72	244	28.0
BOI	45.9 (4%)	19.2 (28%)	1.4 (30%)	12.0 (28%)	19.0 (23%)	4.2 (17%)	0.46 (12%)	0.48 (22%)	0.78 (14%)	129 (3%)	14.5 (16%)
HTG[b]	44.8 (6%)	20.5 (17%)	1.6 (5%)	8.1 (11%)	20.4 (26%)	4.5 (6%)	0.29 (4%)	0.33 (22%)	0.86 (3%)	163 (6%)	21.9 (34%)
LAV	45.3 (4%)	17.0 (24%)	2.3 (20%)	22.6 (5%)	17.1 (37%)	1.2 (12%)	2.12 (18%)	0.65 (40%)	0.80 (14%)	91 (3%)	13.6 (12%)
MTL	45.6 (3%)	16.7 (5%)	1.6 (45%)	9.3 (10%)	16.6 (7%)	1.9 (15%)	2.28 (7%)	0.44 (19%)	2.73 (72%)	65 (1%)	7.7 (26%)
RXP	43.8 (2%)	24.5 (12%)	1.6 (8%)	5.5 (64%)	36.9 (1%)	3.7 (27%)	2.32 (23%)	0.45 (14%)	3.59 (114%)	122 (3%)	20.6 (12%)
SJPJ[a]	45.8 (2%)	28.5 (25%)	2.2 (65%)	13.6 (15%)	24.1 (45%)	1.9 (18%)	1.52 (14%)	0.50 (46%)	1.23 (7%)	139 (11%)	23.8 (9%)
STR	44.7	17.8	1.4	19.6	24.4	1.9	1.56	0.33	1.02	72	9.9

No coefficient of variation is available for the BEL and STR sites because only one measurement was performed at each site.

Sites included in the temporal data set ($n = 15$) are indicated in bold.

[a] 2011 and 2013 only were used for calculation at SJPJ because stems were one-year-old in 2012.

[b] 2012 and 2013 only were available for calculation at HTG.

independence. A Helmert contrast (Legendre and Legendre, 2012) was performed to represent the site effect. The variance of the modelled response variable was then partitioned into three parts: (1) the effect that was explained only by selected variables, (2) the effect that was explained by selected variables and site, and (3) the effect that was explained only by site. When this was possible, the significance of the partitions was determined by permutation tests (999 permutations) with partial redundancy analysis (Davies and Tso, (1982). Didactic explanations are provided in Legendre and Legendre (2012). We finally partitioned the variance of annual aboveground biomass yields with site and foliage using the full data set to compare the percentages that were explained by foliar nutrients (i.e. clr scores) *vs* leaf mass. No Helmert contrast was performed because the numbers of annual measurements carried out at each site were unbalanced. The condition of independence was not met, but previous analyses suggested that the site effect was controlled by leaf traits (see Results section). Prior to these analyses, forward selection of explanatory variables had been performed.

Finally, multivariate regression trees (MRT, De'ath (2002)) were also built to test if leaf traits could explain variations in annual aboveground biomass yields. The MRT were constructed using foliar nutrient levels alone, despite spurious correlations between nutrients, because MRT do not require that data be independent. The MRT were specifically built to assess whether successive thresholds (previously cross validated) of foliar nutrient levels (i.e., for comparison with literature values) and clr scores (i.e., for comparison with computed linear relationships) could explain the variation in annual aboveground biomass yields. Leaf mass was also tested in the MRT. These analyses were performed on both, the temporal and full data sets. Some didactic explanations and examples are described in Legendre and Legendre (2012) and Borcard et al. (2011).

3. Results

3.1. Variation in leaf traits and relationships with permanent site characteristics and atmospheric conditions

Foliar macronutrient levels decreased in the following order: N and Ca were roughly similar (except at RXP where foliar Ca level was dramatically high, likely favoured by the rich organic soil), followed by K and Mg, and then P (Table 2). Foliar micronutrient levels such as Mn or Zn were in the same order of magnitude, whereas Fe was lower. Variation in foliar nutrient levels across sites was greatest for Zn, followed by K and Mg, then Fe, Mn, Ca, P and N, and finally C (Table 4). Across growing seasons, variation in foliar nutrient levels was generally lower than across sites, except for C, N and P for which it was comparable. Variation in clr scores is not shown because they include negative values (logarithmic transformations). Also, the clr scores are of orders of magnitude that are not comparable between nutrients, but they have trends similar to foliar nutrient levels (results not shown). Variation in leaf mass across growing seasons (22.9%) and sites (31.1%) were in a range comparable to those of foliar nutrient levels across
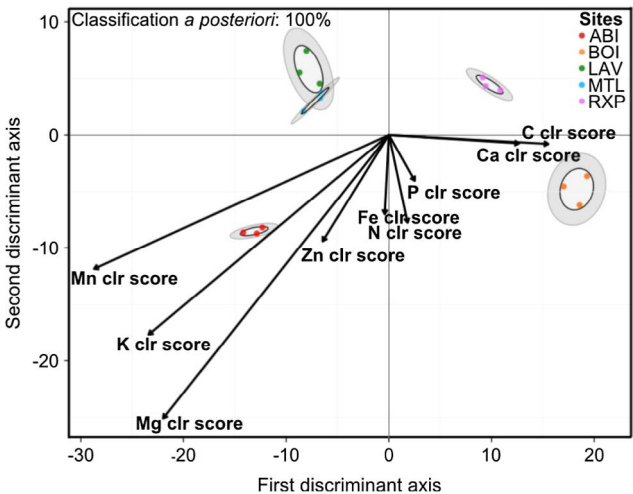

Fig. 2. Linear discriminant analysis of the clr scores of C, N, P, K, Ca, Mg, Mn, Fe and Zn specific to each site (temporal data set, $n = 15$). The ellipse surrounds 95% of the theoretical inner group dispersion.

growing seasons (13.4–31.6%) and across sites (16.7–68.6%).

The classification functions perfectly (100%) predicted group membership of the clr scores relative to the original group assignment when site was used as a grouping factor (Fig. 2). In contrast, classification functions failed to predict group membership of the clr scores when growing season was used as a grouping factor.

When considering site effect as a random factor in mixed models, average air temperature, consecutive days with precipitation, radiation, total precipitation, and degree-days (base 5 °C) explained 94%, 81%, 93%, 92%, 90%, and 82% of the variation in foliar C, N, Ca, K and Mg levels and leaf mass, respectively (Table 5).

3.2. Relationships between leaf traits and annual aboveground biomass yields

Many of the clr scores of Ca and N for the 2011, 2012 and 2013 growing seasons were linearly related to the respective annual aboveground biomass yields (Table 6). The clr scores of Ca were related to annual aboveground biomass yields for each growing season, whereas the clr scores of N were not related to the 2012 aboveground biomass yields. The presence and strength of a relationship depended on the data set used. Leaf mass was only significantly related to the 2012 and 2013 aboveground biomass yields (Table 6).

All of the variation in annual aboveground biomass yields that was

Table 4
Percentage of variation in foliar levels of C, N, Ca, Mg, K, P, Fe, Mn and Zn and leaf mass (LM) between growing seasons, and coefficients of variation (CV) across sites and growing seasons.

	C	N	P	Ca	Mg	K	Fe	Mn	Zn	LM
	%									%
CV across sites	1.9	16.7	20	41.0	44.9	51.7	44.2	43.4	68.6	31.1
CV across growing seasons	3.2	14.3	18.1	13.4	17.3	17.5	31.6	10.2	16.9	22.9

Growing season averages are calculated from the temporal data set (n = 15).

Table 5
Results of mixed models (R^2) performed across sites and growing seasons (*i.e.*, 2011, 2012 and 2013) with foliar nutrient levels (*i.e.*, N, Ca, K, Mg, P, Mn, Fe, Zn), atmospheric variables and site as response variable, fixed and random factors, respectively. Positive (+) and negative (−) relationships are indicated in parentheses.

Foliar nutrient	Weather variables	Mix. mod. R^2
C	Air temperature	0.94[***] (−)
N	Consecutive days with precipitation	0.81[**] (+)
Ca	Radiation	0.93[*] (−)
K	Radiation	0.92[*] (−)
Mg	Precipitation	0.90[*] (+)
P	NS	NS
Mn	NS	NS
Fe	NS	NS
Zn	NS	NS

Linear models are significant at [*]$p \le 0.05$, [**]$p \le 0.01$ and [***]$p \le 0.001$; NS, not significant ($p > 0.05$).

Models were developed using the temporal data set ($n = 15$).

Table 6
Linear regression results (adjusted R^2) of annual aboveground biomass yields *vs* clr scores and leaf mass (LM) performed across sites for the 2011, 2012 and 2013 growing seasons individually. Positive (+) and negative (−) relationships are indicated in parentheses.

Growing seasons	n	CND	LM
2011	7	Ca 0.75** (+)	NS
		N 0.74* (+)	
	5	Ca 0.84* (+)	NS
2012	6	Ca 0.80** (+)	0.70* (+)
	5	Ca 0.75* (+)	NS
2013	8	N 0.69** (+)	0.85*** (+)
		Ca 0.42* (+)	
	5	NS	NS

Linear models are significant at $^*p \leq 0.05$ and $^{**}p \leq 0.01$. Models are built using either the yearly data of the temporal data set ($n = 5$ each year) or full data set ($n = 7$ in 2011, $n = 6$ in 2012 and $n = 8$ in 2013).

Table 7
Variance partitioning of annual aboveground biomass yields between selected leaf traits (clr scores of nutrients or leaf mass [LM]) and site effect. Positive (+) and negative (−) relationships are indicated in parentheses. The column denoted Sel. var. ₵ Site indicates the adjusted R^2 of the selected leaf traits, which does not overlap the site effect. The column denoted Sel. var. ∩ Site indicates the adjusted R^2 of the variance explained by selected variables and site effect. The column denoted Site ₵ Sel. var indicates the adjusted R^2 of site effect, which does not overlap selected variables. The column denoted $R^2_{\text{Sel. var}}$ indicates the R^2 of the effect of selected variables as a whole. The models presented in the shaded area are similarly constructed, although they test the effect of LM instead of site effect. These models also did not meet the condition of independence.

Year	n	Selected variables	Sel. var. ₵ Site	Sel. var. ∩ Site	Site ₵ Sel. var.	$R^2_{\text{Sel. var.}}$
2011	35	Ca (+)	0.05	0.59	0.00	0.73**
		N (+)				
		Mn (−)				
2011 2012 2013	15	Ca (+)	0.00	0.66	0.19**	0.91**
		LM (+)				

Year	n	Sel. var.	Sel. var. ₵ LM	Sel. var. ∩ LM	LM ₵ Sel. var.	$R^2_{\text{Sel. var.}}$
2011 2012 2013	21	N (+)	0.14*	0.42	0.20**	0.80**
		Ca (+)				

Linear models are significant at $^*p \leq 0.05$ and $^{**}p \leq 0.01$. Simple R^2 are presented instead of adjusted R^2 in order to compare model results with those in Fig. 4. Models are built using either the spatial data set ($n = 35$), full data set ($n = 21$), or temporal data set ($n = 15$).

explained by the site effect was concomitantly explained by clr scores selected from the spatial data set (adjusted $R^2 = 0.59$, Table 7). The clr scores explained an additional 5%. Consequently, the clr scores of Ca, N and Mn explained 64% of the variance (i.e. sum of adjusted R^2: $0.59 + 0.05$) in annual aboveground biomass yields (Table 7). Across sites and growing seasons, leaf mass and the clr scores of Ca explained 66% of the variation in annual aboveground biomass yields and, therefore, did not completely overlap the site effect (Table 5). The combination of the clr scores of N and Ca explained 56% (i.e. sum of adjusted R^2: $0.14 + 0.42$) of the variance in annual aboveground biomass yields across sites. Furthermore, 42% of this variance was also controlled by leaf mass. This latter variable explained another 20% of the variance in annual aboveground biomass yields across sites that clr scores could not explain (Table 7).

The MRT that were developed with foliar nutrient levels and the clr scores as explanatory variables yielded two distinct cross-plot structures when the spatial data set was used (Fig. 3a, b). The MRT developed from the clr scores had a slightly higher R^2 than that developed from foliar nutrient levels. However, the same nutrients were selected in matching order in both MRT, i.e. Ca, followed by N and finally P. Using

the spatial data set, leaf mass was not detected as a significant variable. However, when the full data set was used for the analysis of the variance in annual aboveground biomass yields (Fig. 3c, d), foliar nutrient levels and the clr scores of N explained 73% and 81%, respectively, whereas leaf mass explained 54% with one detected threshold (0.13 g leaf^{-1}, not shown).

4. Discussion

4.1. Variation in leaf traits and relationships with permanent site characteristics and atmospheric conditions

Two trends emerged in regard to the variations in foliar nutrients across sites and growing seasons. Firstly, variations in foliar Ca, Mg, K, Mn and Zn levels were smaller across growing seasons than across sites (Table 4), suggesting a larger impact of soil properties compared to atmospheric conditions. Ericsson (1981a) suggested a mechanism of diffusion for Ca and Mg uptake by *Salix* grown hydroponically. Bauer et al. (1997) also found foliage of European beech (*F. sylvatica*) collected from Italy to Norway to be a relatively robust mirror of soil Ca, Mg and K levels. Similarly, using the same temporal data set as in this study on 'SX67', Fontana (2016) showed positive relationships between soil exchangeable and foliar Ca, Mg, K, Mn and Zn levels. However, despite stronger variations across sites, the year-to-year variations in foliar Ca, Mg and K levels were on average 15% (Table 4) and were significantly explained by atmospheric conditions (Table 5). The negative relationship that was found between foliar Ca levels and total radiation is in agreement with Kobe (1996) who suggested that foliar Ca levels improved light use efficiency and tolerance to low light availability in American beech (*Fagus grandifolia* 'Ehrh'), white ash (*Fraxinus americana* L.), and sugar maple (*Acer saccharum* 'Marsh'). However, as a whole, how atmospheric conditions influence foliar demand of Ca, Mg or K by trees has not yet been clearly explained.

Secondly, variations in leaf mass and foliar C, N, P and Fe levels across growing seasons were quite comparable to those across sites, suggesting that soil properties and atmospheric conditions affected these foliar traits at similar levels (Table 4). Leaf size is generally positively related to rainfall (Marcysiak, 2012; McLean et al., 2014). Because rainfall is a limiting factor for 'SX67' growth within and across sites (Fontana et al., 2017), leaf transpiration, which is related to leaf surface and thus to leaf mass, may be critical in explaining the negative relationship between leaf mass and degree days (Table 5). Growth and biomass allocation of *Salix matsudana* cuttings were sensitive to small variations in air temperature (i.e. 0.5–1.0 °C), which modified photosynthetic rates and leaf turnover (He and Dong, 2003). Foliar C levels were poorly correlated with leaf mass across sites and growing seasons ($r = 0.29$), whereas this relationship was stronger using mixed models (with site as a random factor, $p = 0.06$ and $R^2 = 0.76$, results not shown), suggesting a linear relationship specific to permanent characteristics of each site. Interestingly, while variation in foliar C levels was very low across sites and growing seasons, it was the only element for which the variation across growing seasons was higher than that across sites (Table 4). This suggests that leaf C investment is mainly driven by atmospheric conditions and more specifically by air temperature (Table 5). For *Populus deltoides* × *Populus nigra* clones, foliar C was positively correlated with the increment rate (d^{-1}) of the total number of leaves and leaf age (Monclus et al., 2005).

It is well known that *Salix* foliar N levels are influenced by both soil N content and water status (Bowman and Conant, 1994; Christersson, 1986; Ens et al., 2013). The positive relationship between foliar N levels of 'SX67' and consecutive days with precipitation (Table 5) corroborates these previous findings. Despite large year-to-year variations in foliar P levels, we were unable to detect a relationship with either atmospheric conditions or soil P levels (Fontana, 2016). Due to high P requirements of many plant species and its low mobility in soils (Hinsinger et al., 2011), P uptake is dramatically influenced by root
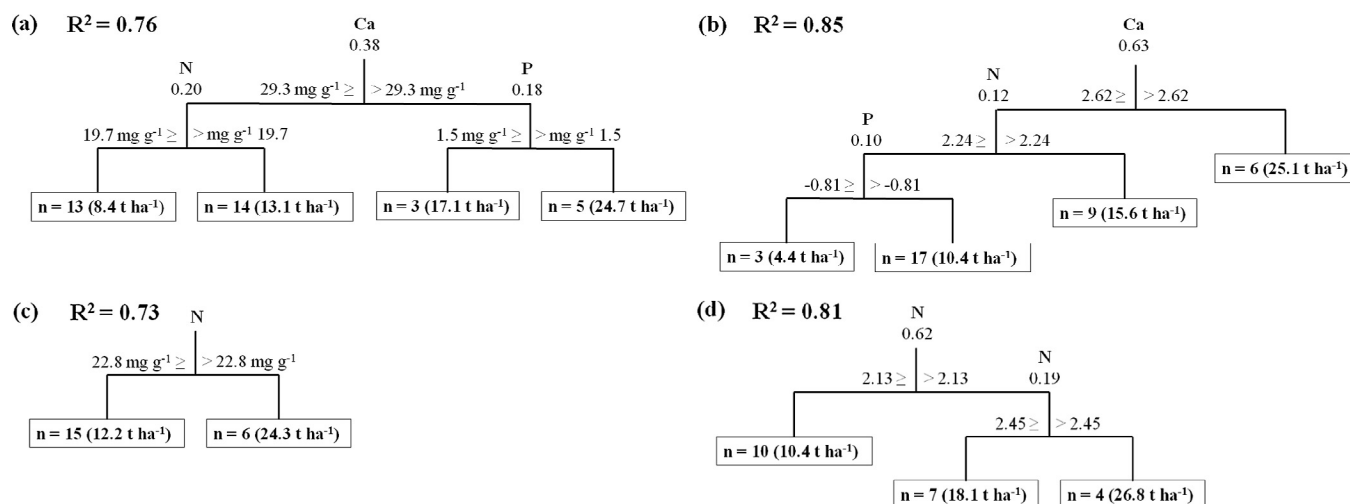
(a)   R² = 0.76

Ca
0.38

N
0.20   29.3 mg g⁻¹ ≥ | > 29.3 mg g⁻¹   P
0.18

19.7 mg g⁻¹ ≥ | > mg g⁻¹ 19.7   1.5 mg g⁻¹ ≥ | > mg g⁻¹ 1.5

n = 13 (8.4 t ha⁻¹) | n = 14 (13.1 t ha⁻¹) | n = 3 (17.1 t ha⁻¹) | n = 5 (24.7 t ha⁻¹)

(b)   R² = 0.85

Ca
0.63

N
0.12   2.62 ≥ | > 2.62

P
0.10   2.24 ≥ | > 2.24   n = 6 (25.1 t ha⁻¹)

−0.81 ≥ | > −0.81   n = 9 (15.6 t ha⁻¹)

n = 3 (4.4 t ha⁻¹) | n = 17 (10.4 t ha⁻¹)

(c)   R² = 0.73   N

22.8 mg g⁻¹ ≥ | > 22.8 mg g⁻¹

n = 15 (12.2 t ha⁻¹) | n = 6 (24.3 t ha⁻¹)

(d)   R² = 0.81   N
0.62

2.13 ≥ | > 2.13   N
0.19

n = 10 (10.4 t ha⁻¹)   2.45 ≥ | > 2.45

n = 7 (18.1 t ha⁻¹) | n = 4 (26.8 t ha⁻¹)

Fig. 3. Variance of annual aboveground biomass yields that was explained by leaf traits through multivariate regression trees (MRT) using foliar nutrient levels (a) and the clr scores (b) (spatial data set, $n = 35$), as well as foliar nutrient levels (c) and the clr scores (d) from the 2011, 2012 and 2013 growing seasons (full data set, $n = 21$). The R^2 (i.e., 1 – residual error) and threshold values are presented for each node of the MRTs. For each cluster, the mean annual aboveground biomass yield is reported in parentheses.

prospection and mycorrhizae, particularly when P availability is low (Thingstrup et al., 1998), and thus by climatic conditions. When mineral P availability does not meet plant requirements, organic P is mobilized through alkaline phosphatase which is affected by the soil microclimate (Krämer and Green, 2000). The microbial P also forms a pool of potentially available P (Tang et al., 2014). This is an explanation as to why the relationships between soil and foliar P levels have generally not been straightforward (Ling and Silberbush, 2002; Bowman et al., 2003; Ens et al., 2013). Results focused on foliar Fe levels of *Salix* are scarce. However, our observations of foliar Fe levels of 'SX67' (i.e. ranging from 11.2 to 19.7 mg kg⁻¹) are in agreement with large variations observed for *Salix schwerinii* x *viminalis* (var. 'Björn') grown hydroponically with various concentrations of Fe in solution (Larsen and Trapp, 2006).

Even if this study was not designed to test mechanisms linking atmospheric conditions and leaf traits, mixed model results (Table 5) suggest that some atmospheric variables (i.e. those showing significant relationships) influence leaf traits similarly within each site. For atmospheric variables that did not yield significant relationships, they probably affected leaf traits differently at each site due to site-specific interactions between soil properties and atmospheric conditions and/or to different limiting factors across sites. As a whole, atmospheric conditions could not discriminate foliar nutrients independently of permanent site characteristics, whereas foliar nutrients were successfully discriminated by permanent site characteristics, independently of the growing seasons. The two trends previously discussed (Table 4) are reflected through the length of vectors in Fig. 2, especially for clr scores of Mg, K and Mn *vs* N and P.

4.2. Relationships between leaf traits and annual aboveground biomass yields

Because foliar nutrient levels changed across growing seasons, nutrients related to annual aboveground biomass yields also differed from year-to-year. Significant and positive relationships were found between 'SX67' yields and clr scores of Ca and N, but the strength of the relationships decreased from 2012 > 2011 > 2013 for Ca and 2013 > 2011 > 2012 for N (Table 6). The 2013 growing season was the most productive for most sites (Fontana et al., 2016), despite that it was an average rainfall year and that accumulated degree-days were lower compared to the 2011 and 2012 growing seasons (Table 1). Conversely, the 2012 growing season was the least productive for most of the sites (Fontana et al., 2016) due to lower water availability

(Fontana et al., 2017, Table 1). Since transpiration is the main driver of nutrient uptake, the filling value (Fv) in Eq. (1) was higher for the 2012 growing season (not shown), highlighting a lower nutrient uptake.

Foliar N levels peak at the beginning of the growing season and then decrease gradually until leaf senescence, whereas foliar Ca levels increase continuously (Chapin et al., 1980). These patterns were observed at the BOI site where foliar N and Ca levels were exceptionally measured for samples collected on May 14, June 4, July 29, September 5, and October 8 and 22 of 2013, with respective N levels of 31.1, 27.7, 22.9, 23.2, 23.1 and 17.6 mg g⁻¹ and Ca levels of 8.8, 15.1, 18.1, 22.3, 24.5 and 26.9 mg g⁻¹ (unpublished data). Variation in atmospheric conditions influence phenological stages and the dynamics of nutrient uptake (Nord and Lynch (2009)). These authors suggested that nutrient uptake (e.g. Ca) tend to increase when the transpiration period is prolonged (e.g. during moist growing seasons in southern Québec). Interestingly, radiation, which is related to foliar Ca levels (Table 5), was used to model tree transpiration, for instance *Prunus dulcis* and *Malus pumila* (Espadafor et al., 2015; Thorpe, 1978). It is therefore suspected that clr scores of Ca were strongly related to aboveground biomass productivity in 2012 partly because foliar Ca levels reflected the seasonal transpiration within sites. Because water availability is a function of the permanent site characteristics specific to each of the studied sites (e.g. soil depth, texture, porosity and drainage (Fontana et al., 2017)), it likely modulated the magnitude of photosynthetic limitations (concomitantly with leaf mass) and nutrient uptake differently at each site. Additionally, soil Ca availability can increase with soil moisture (Oliveira et al., 2010) and is positively correlated to soil organic matter, texture, pH and CEC (Havlin et al., 2005). Therefore, the relationships between clr scores of Ca and annual aboveground biomass yields of 'SX67' (Tables 6 and 7) were likely favoured by the gradients in soil pH (5.15–7.51) and exchangeable Ca (1.3–63.4 cmol꜀ kg⁻¹) encompassed by the nine sites (Fontana et al., 2017). This suggest that foliar Ca is a reliable indicator of 'SX67' growth, but it is not necessarily a limiting factor *per se* because foliar Ca levels can be higher than the physiological need, as in the case of *Salix dasyclados* (Von Fircks et al., 2001). However, because Ca is an essential macronutrient, serious plant stress can be observed if plant requirement is not fulfilled (Bangerth, 1979) and it is clear from this study on 'SX67' that lower uptake of Ca can directly limit aboveground productivity. For example, foliar Ca is involved in physiological mechanisms to deal with water stress (Hawkesford et al., 2012). Foliar Ca was related to growth for many species. Positive linear relationships between basal area increment and foliar Ca levels of red oak (*Quercus rubra* L.) and eastern white pine

(*Pinus strobus* L.) were demonstrated for five sites (northern New York to western Maine) that were characterized by sandy acidic soils (Hallett and Hornbeck, 1997). It is also well known that the growth of sugar maple on acidic soils is limited by the availability of Ca (St. Clair et al., 2008) and liming has both beneficial outcomes on foliar Ca levels and growth rates (Horsley et al., 2000; Juice et al., 2006).

The limiting effect of N on aboveground yield of 'SX67' is less ambiguous than for Ca and was observed for *Salix* in many studies (Ens et al., 2013, Ericsson, 1981b, Labrecque et al. 1998). However, foliar N can also be adversely affected by drought (Vizcayno-Soto and Côté, 2004) and can enhance drought resistance (Weih et al., 2011). Foliar N of 'SX67' was higher during the wetter growing seasons (Table 5) likely in part because growing seasons with atmospheric conditions that extended phenological stages meant that foliar N decreased more slowly during the season. Compared to 2012, it is suspected that aboveground productivity of 'SX67' in 2013 was only slightly limited by water and that Ca requirements were fulfilled, which would mean that the limiting effect of N was preponderant in 2013.

The annual aboveground biomass yield models that were developed from the spatial data set take into account the variability within plots. They had lower adjusted R^2 compared to those developed from the full data set (Tables 6 and 7). The model developed from the spatial data set showed that: (1) site effect was completely controlled by the selected leaf traits, (2) variability in annual aboveground biomass yields within sites was not well explained, indicating that this was likely influenced by nutritional factors specific to each site and different from those governing the variability in annual aboveground biomass yield across sites, and (3) the clr scores of Ca and N were positively related to annual aboveground biomass yields, whereas the clr scores of Mn were negatively related to annual aboveground biomass yields in 2011. Manganese bioavailability varies depending on soil acidity and redox conditions – it increases with acidity (Sanders, 1983; Martinez and Motto, 2000) and reducing (anoxic) conditions (Gotoh and Patrick, 1972; Sanders, 1983). *Salix* can survive with relatively high foliar Mn levels (Yang et al., 2015), whereas toxicity symptoms with reduced growth mostly appear in poorly drained conditions (Kovalchik, 1992). A negative effect of Mn on aboveground biomass yields was reported for hybrid poplar in central Alberta (Pinno et al., 2010) and sugar maple growing on acidic soils in southern Quebec (Houle et al., 2007). Foliar Mn levels were relatively homogeneous across the growing seasons (CV = 10%, Table 4). The negative effect of Mn on growth only appeared when analyzing the spatial data set, which included seven sites. The inclusion of the clr scores of Mn only explained an additional 7% of the variance in annual aboveground biomass yields (results not shown in Table 7). This result suggests that the negative effect of Mn on annual aboveground biomass yields of 'SX67' was masked, at a larger spatial scale, by the most important limiting factors.

Across sites and growing seasons, leaf mass was the most robust predictor of annual aboveground biomass yields (Table 7). This result suggests a proportional investment of C between wood and foliage by 'SX67'. Relationships between aboveground biomass yields and leaf size (or leaf elongation) have been frequently reported for *Salix* within and across species (Bowman and Conant, 1994; Weih et al. 2011, 2006; Weih and Nordh, 2005). In our study on 'SX67', leaf mass overlapped most of the effects of foliar nutrients on annual aboveground biomass yields and explained an additional 29% of the variance in annual aboveground biomass yields (Table 7). In contrast, foliar nutrients were better predictors of annual aboveground biomass yields than leaf mass for individual years (Fig. 3, Tables 6 and 5). We are unaware of other studies comparing leaf mass and foliar nutrients as predictors of tree productivity.

4.3. Model performance in predicting annual aboveground biomass yields

Although a leaf mass threshold was identified using MRT (results not shown), linear models were more robust in predicting annual

aboveground biomass yields (Tables 6 and 7) probably because leaf mass integrates the factors governing growth, so no threshold effect is expected (e.g. a critical value highlighting a boundary between sufficiency and deficiency). Therefore, the detected leaf mass threshold more likely highlighted a discontinuity within the scattered plot (i.e. the relationship between leaf mass and annual aboveground biomass yields) rather than a critical threshold *per se*. Conversely, for foliar nutrients, the MRT were more suitable than linear models in explaining annual aboveground biomass yields and detecting plot-scale variations within individual growing seasons (spatial data set) or landscape-scale variations across growing seasons (full data set), regardless of whether the same number or fewer explanatory variables were used (Fig. 3, Table 7). In particular, it was possible to isolate the three least productive plots (MTL2, MTL3 and MTL4, results not shown). Furthermore, this approach produced a cluster of the three sites with the greatest annual aboveground biomass yields for a given growing season, BEL, HTG and SJPJ in 2013 (results not shown). Therefore, the MRT dealt with specific nutritional constraints that were associated with each growing season or site as opposed to the linear relationships, which lumped together all plots and sites for the three growing seasons without further differentiation (Table 7). The few studies that have used regression trees to model tree growth from foliar nutrients have all reinforced the idea that binary recursive partitioning using CHAID (CHi-square Automated Interaction Detection; Kass, 1980) or conditional inference-based decision trees (e.g., ctree, Hothorn et al., 2006) are highly relevant and efficient approaches (Afif-Khouri et al., 2011; Álvarez-Álvarez et al., 2011; Ouimet et al., 2013a).

Major foliar nutrients (N and Ca) that exhibited a linear relationship with annual aboveground biomass yields of 'SX67' when analyzing the spatial data set (i.e., plot-scale) also appeared in the MRT, whereas only foliar N thresholds were detected by the MRT when analyzing the full data set (i.e., landscape-scale and across growing seasons). This result is in agreement with those of Afif-Khouri et al., (2011) and Álvarez-Álvarez et al., (2011) who compared linear models and regression trees to highlight the factors (leaf traits, soil and atmospheric conditions) limiting the growth of maritime pine (*P. pinaster* 'Ait') and sweet chestnut (*Castanea sativa* 'Mill') in Spain. They found a correspondence between the two methods with regard to selected variables. In both studies, the linear relationships between growth and foliar P levels were significant; however, the regression trees detected foliar P level only in the study of Álvarez-Álvarez et al., (2011). Ouimet et al., (2013b) diagnosed P deficiency for sugar maple in southern Quebec when using conditional regression trees only. Similarly, in our study on 'SX67', foliar levels and the clr scores of P were significant variables in the MRT when analyzing the spatial data set (Fig. 3), but they were not linearly related to 'SX67' productivity (Tables 6 and 7). This result suggests a critical P threshold under and above which annual aboveground biomass yields would be hindered or unaffected, respectively. In addition, interactions with other nutrients probably influence the magnitude of this threshold.

Centered log ratio (clr) transformation, which considers the nutritional structure of foliage, is a suitable approach to understanding plant nutrition, especially when combined with multivariate analysis (Parent et al., 1994). This was verified through using this same statistical approach with foliar nutrient levels alone and failing to find site-specific foliar nutritional signatures (results not shown). Log ratio transformation provides variables that are linearly independent (Aitchison, 1986) and allows the detection of nutrient interactions (García-Hernández et al., 2004; Raghupathi et al., 2002). For instance, in southwestern Quebec, the clr scores of hybrid poplar indicated that lower aboveground biomass yields were related to a global nutritional imbalance (Lteif et al., 2008). Our results for 'SX67' emphasize the need to look at foliar nutrition as a whole instead of considering nutrients individually (Parent and Dafir, 1992).
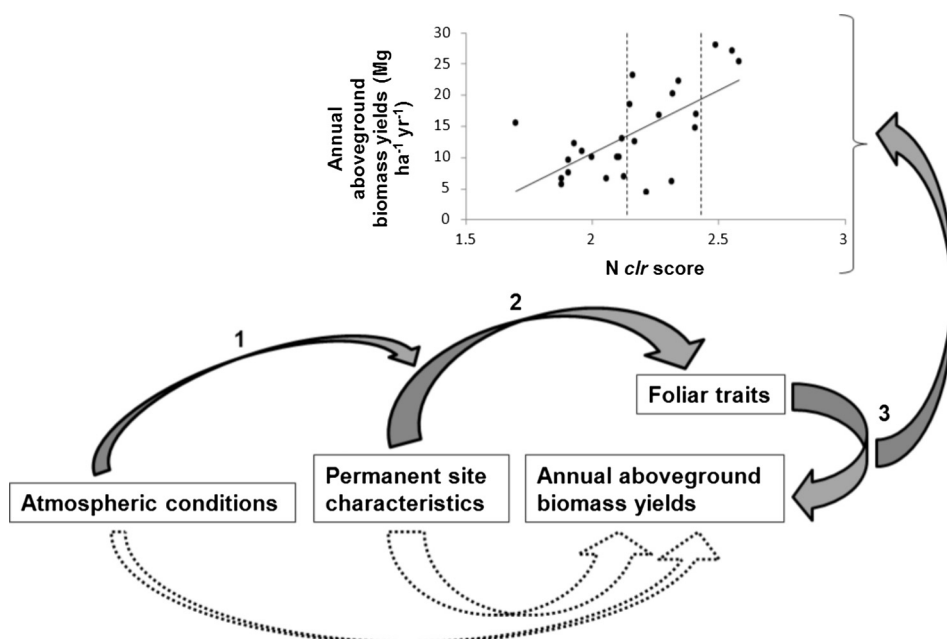
Fig. 4. Schematic representation of interactions between factors controlling annual aboveground biomass yields of *Salix miyabeana* SX67 SRC in Quebec. The width of the dashed line/arrow indicates the relative strength of the relationship. Atmospheric conditions influence foliar traits with respect to permanent site characteristics (1); foliar traits are predominantly influenced by permanent site characteristics (2); foliar traits are significantly related to annual aboveground biomass yields (3) which are better explained by thresholds of foliar nutrients than by linear regressions (4). These results are highly consistent with the study of Fontana et al. (2017) (i.e. performed at the same sites as the present study) in which soil physical and chemical properties mainly influenced annual aboveground biomass productivity (5) compared to atmospheric conditions (6).

4.4. Nutritional requirements of 'SX67'

Using MRT, a threshold of 22.8 mg N g^{-1} was identified for foliar N of 'SX67', beyond which no annual yield lower than 20 Mg ha^{-1} y^{-1} was observed (Fig. 3c). The optimal threshold suggested by Kopinga and Van den Burg (1995) for *Salix viminalis* (< 20 mg N g^{-1} means a deficiency, 23–30 mg N g^{-1} is normal and > 30 mg N g^{-1} is optimal for a leaf collected between early August and mid-September) was higher than the threshold set for 'SX67' in our study. The threshold for 'SX67' is also lower than foliar N levels of *Salix viminalis* and *Salix discolor* after sludge application (Labrecque et al., 1998), but this comparison has to be nuanced given the leaves were collected at the end of July and foliar N levels likely decreased until the end of August and early September, which corresponds to the sampling period in this study. However, the foliar N threshold of 'SX67' was within the range of values that have been previously reported for other *Salix* cultivars (Viherä-Aarnio and Saarsalmi, 1994; Ens et al., 2013) for the same sampling period as in this study. Furthermore, annual aboveground biomass yields of 'SX67' measured at some of the studied sites (BEL, HTG and SJPJ) were among the highest values reported for *Salix* cultivars grown in southern Quebec (Labrecque and Teodorescu, 2005; Guidi Nissim et al., 2013) or in similar temperate climates, for example, Poland (Szczukowski et al., 2002). These findings suggest that 'SX67' uses N very efficiently compared to other *Salix* cultivars, which is perfectly in line with the findings of Quaye et al. (2015) for 'SX64'.

The plots with foliar P and Ca levels of 'SX67' above 1.5 mg g^{-1} and 29.3 mg g^{-1}, respectively, were also the most productive (Fig. 3a). Kopinga and Van den Burg (1995) reported that foliar P levels above 2.1 mg g^{-1} were optimal for *Salix viminalis*. Again, results for 'SX67' suggest a more efficient use of P than *Salix viminalis*. However, Quaye et al. (2015) observed that foliar P levels are higher for 'SX64' than for *Salix discolor* 'Muhl' and *S. viminalis* (Labrecque et al., 1998) and concluded that 'SX64' does not use P very efficiently. Moreover, foliar Ca levels for 'SX67', 17 to 37 mg g^{-1}, were dramatically greater than the range of 7 to 19 mg g^{-1} reported for other *Salix* cultivars growing on different soil types (Viherä-Aarnio and Saarsalmi, 1994; Labrecque et al., 1998; Simon et al., 2013), suggesting a high Ca requirement for 'SX67'. This response is especially striking considering that fast-growing species of *Salix* or *Populus* are already known for maintaining large reserves of Ca in their foliage (Ericsson, 1981a; Camiré and Brazeau, 1998). In particular, foliar Ca is known to increase physical protection

against diseases (Franceschi, 2001) and water shortages (Hawkesford et al., 2012). Foliar Ca levels of 'SX67' may provide some insight as to why *Salix viminalis* is more sensitive to insect infestation and drought compared to 'SX67' in southern Quebec (Labrecque and Teodorescu, 2005).

5. Conclusion

In the present study, we investigated the effects of permanent site characteristics and atmospheric conditions on the foliar nutrition of *Salix miyabeana* 'SX67'. Despite variations in atmospheric conditions across growing seasons, specific foliar nutrient levels were largely determined by permanent characteristics specific to each site (Fig. 4). Foliar C, N and P and leaf mass varied as greatly across years as across sites. Leaf mass was the most robust foliar trait to estimate annual aboveground biomass yields. During moist conditions (assuming no severe water stress), foliar N was likely the most important nutrient limiting annual aboveground biomass yields of 'SX67', whereas foliar Ca was a reliable indicator of growth. When low water availability conditions limited aboveground productivity, foliar Ca levels were more strongly related to growth compared to N, likely because low Ca accumulation in leaves reflected, in part, periods of lower water availability. Manganese also exerted a negative effect on 'SX67' annual aboveground biomass yields. The synergy between the effects of permanent site characteristics and atmospheric conditions was reflected in the relationship between 'SX67' leaf traits and annual aboveground biomass yields (Fig. 4). Linear models encompassing several growing seasons were the most robust to accurately forecast annual aboveground biomass yields using leaf mass as an explanatory variable, suggesting a proportional allocation between foliage and aboveground wood. Whereas, non-linear models using foliar nutrient thresholds were more robust than linear models for explaining the variance of annual aboveground biomass yields. Non-linear models were able to: (1) deal with the variation across sites and growing seasons, and (2) identify thresholds delimiting sufficiency from deficiency. Rather, these thresholds suggested high N and P use efficiencies of 'SX67' as well as a large Ca demand for leaves.

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