Nutrients and energy in proleptic branches and leaves of poplar under a short-rotation coppice

Reference:

Vanbeveren Stefan, Gebauer R., Plichta R., Volařík D., Ceulemans Reinhart.- Nutrients and energy in proleptic branches and leaves of poplar under a short-rotation coppice

Biomass and bioenergy - ISSN 0961-9534 - 85(2016), p. 271-277

Full text (Publishers DOI): http://dx.doi.org/doi:10.1016/j.biombioe.2015.12.016

1 Nutrients and energy in proleptic branches and leaves of poplar under a short-rotation coppice

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Abstract

Renewable energy is often generated from biomass, produced in short-rotation coppice (SRC) cultures. These cultures are frequently established on former agricultural land with ample availability of plant nutrients as nitrogen, phosphorous, potassium, calcium and magnesium. Nevertheless, little is known about the annual recycling of these nutrients through the leaves, as well as about the amounts that are removed at harvest. We therefore quantified soil nutrient concentrations, as well as nutrient concentrations and the gross calorific value of the proleptic branches and of the leaves of 12 poplar (*Populus*) genotypes in the second rotation of an operational SRC (with two-year rotations). For the produced leaf biomass, we also quantified the standing energy stock and the nutrient stock of each genotype. After four years the P, K, Ca and Mg soil concentrations had not significantly changed, while the N concentration at 30-60 cm of soil depth had significantly increased. On average, the standing aboveground woody biomass of the 12 genotypes in 2013 was 13.75 Mg ha^{-1} and the total leaf biomass was 3.54 Mg ha^{-1}. This resulted in an average standing energy stock in the leaves of 64.8 GJ ha^{-1}. Nutrient concentrations were lower in the proleptic branches as compared to the leaves, but the proleptic branches and leaf nutrient concentrations significantly varied among the genotypes.

Keywords

Allocation, *Populus*, POPFULL, standing biomass, standing energy stock, standing nutrient stock

1. Introduction

Although coppice forests have existed for a long time in Europe [1], short-rotation coppice (SRC) cultures are not yet widely implemented as a component of European land use [2, 3]. Nevertheless, SRC cultures are of increasing importance in countries with a temperate climate [4] and afforestation on agricultural land is often encouraged through grants or subsidies [5]. Poplar (*Populus* spp.) is one of the most suitable species for SRC cultures because it grows fast, it achieves high yields, and many (disease resistant) selected genotypes are commercially available [6]. SRC poplars planted on converted agricultural lands can benefit from the usually intensive fertilisation that was previously applied. The soil likely contains high amounts of macronutrients, i.e., nitrogen (N), phosphorous (P), potassium (K), calcium (Ca) and magnesium (Mg) [7-9]. However, the nutrient recycling in, and the nutrient losses from, SRC are not yet fully established. This is of great importance if we are to manage long-term SRC plantations sustainably.

SRC cultures are generally coppiced every 2-5 years, with all the aboveground biomass being removed from the site. After each harvest, a multitude of resprouting shoots emerges from every stump (Fig. 1); these gradually undergo self-thinning during the following rotation [10]. As a consequence, and because the relative amount of bark increases with decreasing shoot diameter, the proportion of bark to wood is much higher in SRC than in traditional forestry [11]. As bark contains much higher nutrient concentrations than bole wood [4, 12, 13], this leads to a relatively larger nutrient removal and, consequently, to a higher nutrient requirement for trees grown as SRC [4, 7, 14]. In traditional forestry, managers strive to achieve the lowest amount of bark in the harvested wood, because bark also reduces the combustion quality of the fuel wood [13]. Coppicing of leafless shoots is usually done in winter; this facilitates the mechanised process of coppicing and increases the combustion quality of the woody biomass into the burner. In this way, foliar nutrients are returned to the roots or to the soil [14, 15]. On the other hand, leaves could also be considered

as a source of harvestable energy [16]. In winter, soils are more likely to be frozen, thus minimising soil compaction [17].

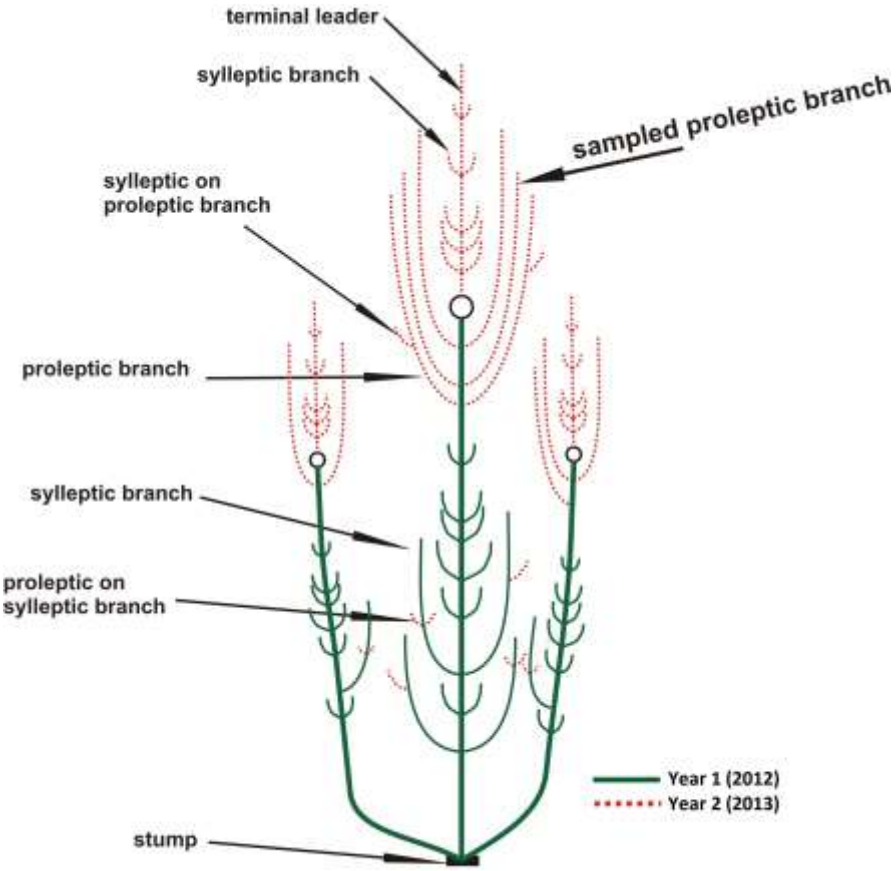


Figure 1. Schematic representation of a two-year old poplar stool in November 2013. Stumps were four years old at the time of sampling (November 2013). Parts below the circles (full lines) present the stem wood formed in 2012 (first year of the second rotation), parts above the circles (dashed lines) present the current-year shoots formed in 2013. The term shoot refers to the combination of the main axis and all proleptic and sylleptic branches (modified after [18]).

The aim of this study was to quantify the amounts of energy and of nutrients in leaves and in the proleptic branches (Fig. 1) in 12 different poplar genotypes of an SRC. We focused on the proleptic branches to assess the average nutrient concentrations in the crown part. The quantification of nutrient fluxes in a managed ecosystem is very important for assessing the fertilisation requirements

66 [4, 14, 19], because fertilisation is the most energy-consuming process in the life cycle of an SRC
67 culture [9, 20]. Reliable data on stand and nutrient dynamics are scarce [5, 21] and they rarely take

Genotype	Parentage	Place of origin	Section	Year of cross/ commercialization	Gender

68 genotypic differences into account [22], although these differences are essential for making correct
69 decisions about fertiliser application [15].

70 ## 2. Materials and Methods

71 ### *2.1 Site description*

72 This study was performed at an operational SRC plantation and fits within the framework of the
73 POPFULL research project [23]. The plantation was established on 18.4 ha located in Lochristi
74 (51°06'44" N, 3°51'02" E; East Flanders, Belgium), from which 14.5 ha were planted with poplar
75 (*Populus*) and willow (*Salix*) cuttings. A detailed site description is given in Broeckx et al. [24]. The
76 study focused on the 12 poplar genotypes planted; these are all commercially available (Table 1).
77 Twenty-five cm long hardwood cuttings were planted at a density of 8000 ha^{-1}, in monoclonal blocks
78 in a double-row planting scheme with alternating inter-row distances of 0.75 and 1.50 m, and 1.10 m
79 between the cuttings in the row. The plantation was established in April 2010 and coppiced for the
80 first time early February 2012 after a two-year rotation [25]. After the second two-year rotation the
81 site was harvested for the second time mid-February 2014. The present study focused on the fourth
82 year (2013) after plantation establishment, i.e. the second year after the first coppice (which took
83 place in early February 2012 [25]). Site preparation, plantation management and coppice conditions
84 have been previously described [26].

85 Table 1: Description of the twelve poplar (*Populus*) genotypes planted in the short-rotation coppice
86 culture. Species or parentage, place of origin/provenance, section, year of the cross and gender of
87 the genotypes have been listed (modified after [24]).

Bakan[1]	T × M	(Washington US x Oregon US) x Japan	Tacamahaca	1975/2005	♂
Brandaris[2]	N	The Netherlands x Italy	Aigeiros	1964/1976	♂
Ellert[2]	D × N	Michigan US x France	Aigeiros	1969/1989	♂
Grimminge[1]	D × (T × D)	(Michigan US x Connecticut US) x (Washington US x (Iowa US x Missouri US))	Aigeiros x (Tacamahaca x Aigeiros)	1976/1999	♂
Hees[2]	D × N	Michigan US x France	Aigeiros	1969/1989	♀
Koster[2]	D × N	Michigan US x The Netherlands	Aigeiros	1966/1988	♂
Muur[1]	D × N	(Iowa US x Illinois US) x (Italy x Belgium)	Aigeiros	1978/1999	♂
Oudenberg[1]	D × N	(Iowa US x Illinois US) x (Italy x Belgium)	Aigeiros	1978/1999	♀
Robusta[3]	D × N	Eastern US x Europe	Aigeiros	1885-1890	♂
Skado[1]	T × M	(Washington US x Oregon US) x Japan	Tacamahaca	1975/2005	♀
Vesten[1]	D × N	(Iowa US x Illinois US) x (Italy x Belgium)	Aigeiros	1978/1999	♀
Wolterson[2]	N	The Netherlands	Aigeiros	1960/1976	♀

D = *Populus deltoides*, M = *Populus maximowiczii*, N = *Populus nigra*, T = *Populus trichocarpa*

[1] Produced by INBO (Geraardsbergen, Belgium)

[2] Produced by Vermeerderingstuinen Nederland (Zeewolde, the Netherlands)

[3] Produced by the nursery Simon-Louis Frères (Metz, France)

88 *2.2 Soil nutrient analyses*

89 To quantify the effect of coppicing on the total nutrient stock of the soil, we collected soil samples
90 before the planting (March 2010) and after the second coppice (March 2014). Samples were taken at
91 random in the middle of a mono-genotypic block of genotype Koster over two soil depths: 0-30 cm
92 and 30-60 cm [27]. A gouge auger set for top soil layers was used (type 04.06, Eijkelkamp Agrisearch
93 Equipment, the Netherlands). In the laboratory, samples were dried at 70 °C until constant dry
94 weight, milled (with an ultra-centrifugal mill ZM200, Retsch, Germany) and sieved at 0.5 mm. From
95 each sample 30 mg was used to determine the total N concentration (NC-2100 element analyser,

Carlo Erba Instruments, Italy) and the rest of the sample was used for the analysis of P, K, Ca and Mg. The latter analyses were performed according to the standard procedures of the Belgian Soil Survey (Leuven, Belgium). There was not enough soil in every sample to allow for all nutrient analyses, thereby limiting the total number of samples (Table 2).

Table 2: Average soil nutrient concentrations (mg kg^{-1}), with standard deviation (±) and number of samples {}, in two years (2010: before the establishment of the plantation; and 2014: after two two-year rotations) and for two soil depths (0-30 and 30-60 cm). Significances between both years are: ** $p < 0.01$; * $0.01 < p < 0.05$; NS $p > 0.05$; NA not applicable.

	Depth	2010			2014			
N	0-30 cm	13.44	(3.3)	{23}	14.71	(4.0)	{84}	NS
	30-60 cm	6.02	(2.0)	{23}	11.37	(4.0)	{59}	**
P	0-30 cm	215.00	(102.1)	{4}	285.00	(50.1)	{8}	NS
	30-60 cm	60.00	(29.4)	{4}			{0}	NA
K	0-30 cm	92.50	(51.2)	{4}	150.63	(26.2)	{8}	NS
	30-60 cm	52.50	(28.8)	{4}			{0}	NA
Ca	0-30 cm	815.00	(167.0)	{4}	785.00	(70.1)	{8}	NS
	30-60 cm	762.50	(213.9)	{4}			{0}	NA
Mg	0-30 cm	135.00	(23.8)	{4}	113.13	(15.1)	{8}	NS
	30-60 cm	107.50	(28.8)	{4}			{0}	NA

To test for differences in N concentrations between both sampling years (2010 and 2014) and between soil depths (0-30 cm and 30-60 cm) we used a generalised mixed effect model with gamma distribution of the errors and a logarithm link function. The mixed effect model (with sampling point as a random effect) was chosen because the different soil depths were sampled at the same point (Table 2). To test for differences in P, K, Ca and Mg concentrations we used repeated measures ANOVAs. The data were logistically transformed to stabilise the variance, because the variance increased with increasing element concentrations. All analyses were performed in R, with extension package lme4 [28]. Differences were qualified as significant when $p < 0.05$.

2.3 Standing aboveground biomass

The aboveground woody biomass (AGWB) of all genotypes was estimated by converting yearly diameter inventories with the allometric relations (per genotype) between shoot diameter and AGWB previously established for this site (described in detail by Broeckx et al. [29]). For this study we used the difference in AGWB between both years (2012 and 2013) as the AGWB increment for 2013.

The total leaf biomass (kg m^{-2}) produced per genotype in 2013 was obtained by dividing the maximum leaf area index (LAI_{max}) by the specific leaf area (SLA) [29]. The LAI_{max} (m^2 m^{-2}) was assessed by leaf litter collection between the time of LAI_{max} (15 August 2013) and the end of the growing season (6 December 2013) [26]. The genotype-specific SLA (m^2 kg^{-1}) was determined for four stumps per genotype [26]. The resulting total leaf biomass was further divided by the AGWB to obtain the relative amount (in %) of total aboveground dry mass (DM) allocated to the leaves.

2.4 Nutrient and energy analyses

Samples for energy and nutrient analyses were collected from 4 to 8 November 2013. For every genotype, ten proleptic branches (each from a different, randomly selected stump and shoot) were collected from the top of the crown (Table 3, Fig. 1). These branches were sampled as they represented the majority of the current-year biomass, and thus were the most relevant parts for nutrient concentration assessments. The basal diameter of all branches was measured with a digital calliper. Five leaves attached to five proleptic branches, or for leafless proleptic branches five leaves freshly fallen on the ground, were sampled (with a total of 25 leaves per genotype).

Table 3: Diameter (± standard deviation) at the base of the proleptic branches collected. Values are averages of the ten branches that were sampled.

	Ø (mm)
Bakan	11.96 (± 1.38)
Brandaris	8.62 (± 1.28)

Ellert	7.97 (± 0.88)
Grimminge	10.7 (± 0.78)
Hees	11.01 (± 1.21)
Koster	9.52 (± 0.88)
Muur	9.65 (± 1.36)
Oudenberg	10.27 (± 1.24)
Robusta	8.47 (± 1.29)
Skado	12.54 (± 1.14)
Vesten	10.53 (± 0.93)
Wolterson	8.03 (± 0.91)

All samples were oven dried in the laboratory at 70 °C until constant DM. Dry proleptic branches and leaves were separately milled and sieved at 2 mm. At least 6 g DM per sample was used for nutrient analysis at the EKOLA Bruzovice laboratory (Studénka, Czech Republic). The N concentration was measured by the Kjeldahl digestion method, while concentrations of P, K, Ca and Mg were measured by atomic absorption spectrophotometry. Concentrations were analysed twice per genotype, once on a mixture of all sampled leaves and once on a mixture of all sampled proleptic branches.

A correlation matrix was constructed in R [28] to test whether nutrient concentrations in proleptic branches and leaves were correlated. Nutrient concentrations were considered inter-correlated with $r > 0.5$ or < -0.5, and the significance level was set at $p < 0.05$. The total nutrient stocks for leaves were obtained by multiplying the nutrient concentrations with the total leaf DM (see section 2.3 above). The total nutrient stock for AGWB was not calculated because there was no extrapolation factor available from proleptic branches to AGWB. For visualisation purposes, the nutrient concentrations in leaves were subtracted from the nutrient concentrations in the proleptic branches. Differences between concentrations in leaves and proleptic branches were analysed in R [28] with paired t-tests.

To determine the gross calorific value (GCV) all proleptic branches and leaf samples were further dried at 105 °C, cooled to room temperature (21 °C) in a closed box with a desiccator and pelleted with a university-made hand press (Mendel University in Brno, Czech Republic). Pellets of 1.2-1.5 g

157 DM were analysed with an automatic Isoperibol calorimeter (Parr 6400, Parr Instrument Company,
158 USA) in three replicates. The GCV was multiplied by the total leaf biomass (see section 2.3 above) to
159 obtain the standing energy stock. As for the total nutrient stock, the total energy stock could not be
160 calculated for the AGWB. We calculated the coefficient of variance (COV; in %) for each trait as the
161 ratio of its standard deviation to its average. The reported COVs indicate the variation among the
162 genotypic averages; they are relative to the absolute values, though mutually comparable.

163 ## 3. Results

164 The soil N concentration significantly decreased with increasing soil depth ($t = 35.34$, $p < 0.001$) and
165 significantly increased from 2010 to 2014 in the deeper soil layer ($t = 8.20$, $p < 0.001$; Table 2). The soil
166 P, K, Ca and Mg concentrations did not change significantly between 2010 and 2014 in the upper soil
167 layer; this variation could not be investigated for the deeper soil layers due to the lack of sufficient
168 soil mass in the samples (Table 2).

169 On average 13.75 ± 3.75 Mg ha^{-1} of AGWB and 3.54 ± 0.43 Mg ha^{-1} of leaf biomass were produced by
170 the twelve genotypes in 2013, i.e. the second year of the second rotation (Table 4). A large COV value
171 (27%) was observed among genotypes for AGWB, while the genotypic variation in leaf biomass was
172 lower (COV of 12%). In 2013, the AGWB ranged from 8.52 Mg ha^{-1} (Brandaris) to 21.93 Mg ha^{-1}
173 (Skado), and the total leaf biomass ranged from 2.65 Mg ha^{-1} (Brandaris) to 4.96 Mg ha^{-1} (Bakan).
174 Genotype Hees allocated the smallest amount of total aboveground biomass to the leaves (19%),
175 while the largest amount of total aboveground biomass was allocated to the leaves by genotype
176 Robusta (37%). In general, the more productive genotypes allocated a lower proportion of
177 aboveground biomass to the leaves. The least productive genotypes (≤ 10 Mg ha^{-1} of AGWB; i.e.,
178 genotypes Brandaris, Muur and Robusta) allocated the highest proportion of aboveground biomass
179 to leaf biomass (≥ 30%). The only exception to this trend was genotype Bakan (*Populus trichocarpa* x

180 *P. maximowiczii*), which combined a high AGWB (18 Mg ha^{-1}) with a high proportion of leaf biomass
181 (27%).

182 Table 4: Aboveground woody biomass (AGWB) and leaf standing biomass, gross calorific value of the
183 proleptic branches (PB) and of the leaves, and standing energy stock of the leaves for the 12 poplar
184 genotypes in the short-rotation coppice in November 2013, for the second year of the second
185 rotation. St.dev. = standard deviation, COV = coefficient of variance.

186

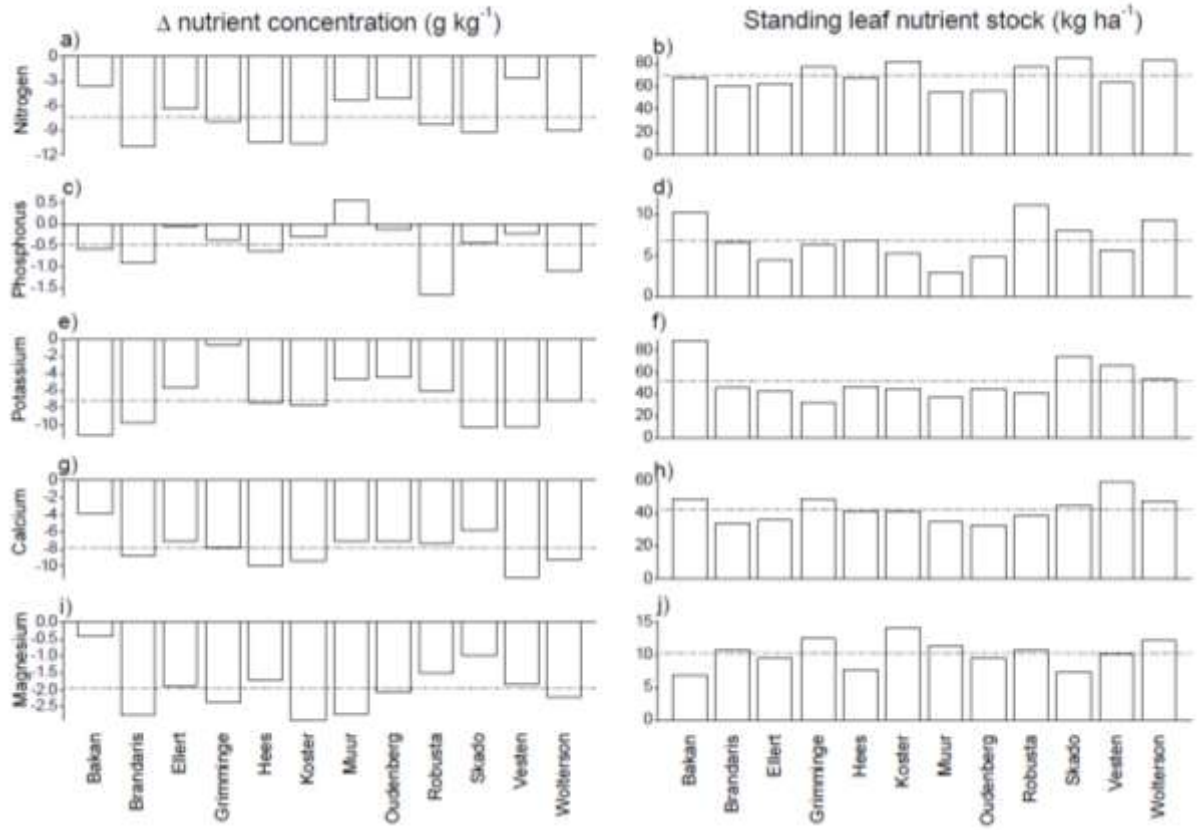
	Standing biomass (Mg ha^{-1} y^{-1})		Gross calorific value (MJ kg^{-1})		Standing energy stock (GJ ha^{-1})
	AGWB	Leaves	PB	Leaves	Leaves
Bakan	18.08	4.96	18.40	18.53	91.90
Brandaris	8.52	2.65	18.87	18.69	49.44
Ellert	12.14	3.12	18.80	18.13	56.64
Grimminge	13.09	3.85	18.73	18.48	71.14
Hees	16.30	3.11	18.30	17.94	55.79
Koster	12.26	3.49	18.89	18.26	63.77
Muur	10.26	3.09	18.53	17.68	54.63
Oudenberg	14.56	3.00	18.51	18.03	54.07
Robusta	9.95	3.70	17.84	18.09	66.84
Skado	21.93	4.35	18.61	18.77	81.75
Vesten	12.86	3.65	18.11	17.72	64.72
Wolterson	15.05	3.62	17.77	18.45	66.72
Average	13.75	3.54	18.36	18.16	64.38
St.dev.	3.75	0.43	0.39	0.37	8.91
COV (%)	27	12	2	2	14

193

194

195 All nutrient concentrations were significantly higher in leaves as compared to the proleptic branches
196 (Fig. 2). The P concentration in genotype Muur was the only exception (Fig. 2c). The p-values for the
197 difference in N, K, Ca and Mg concentration were < 0.001 and the p-value for the difference in the P
198 concentration was 0.012. The Ca concentration in the proleptic branches and the P concentration in
199 the leaves were the most variable among the 12 genotypes (Annex 1). On the other hand, the
200 proleptic branches P and the leaf N concentrations were the least variable nutrients within the

201 studied genotypes. The leaf N concentration was significantly and positively correlated with the leaf
202 Mg concentration (r = 0.66, p = 0.021), and significantly and negatively correlated with the proleptic
203 branches Ca concentration (r = -0.78, p = 0.003; Fig. 3). There were no other significant correlations
204 among nutrient concentrations. The COV for proleptic branches and for leaf nutrient concentrations
205 between genotypes varied from 8 to 30%.



206

207 Figure 2. Difference in nutrient concentrations between proleptic branches and leaves (a, c, e, g and
208 i; g kg^{-1}); and the standing leaf nutrient stocks (b, d, f, h and j; kg ha^{-1}) for 12 poplar genotypes
209 collected in November 2013 (i.e. after two rotations of two years each). Dashed lines represent the
210 average value for all 12 genotypes.

211

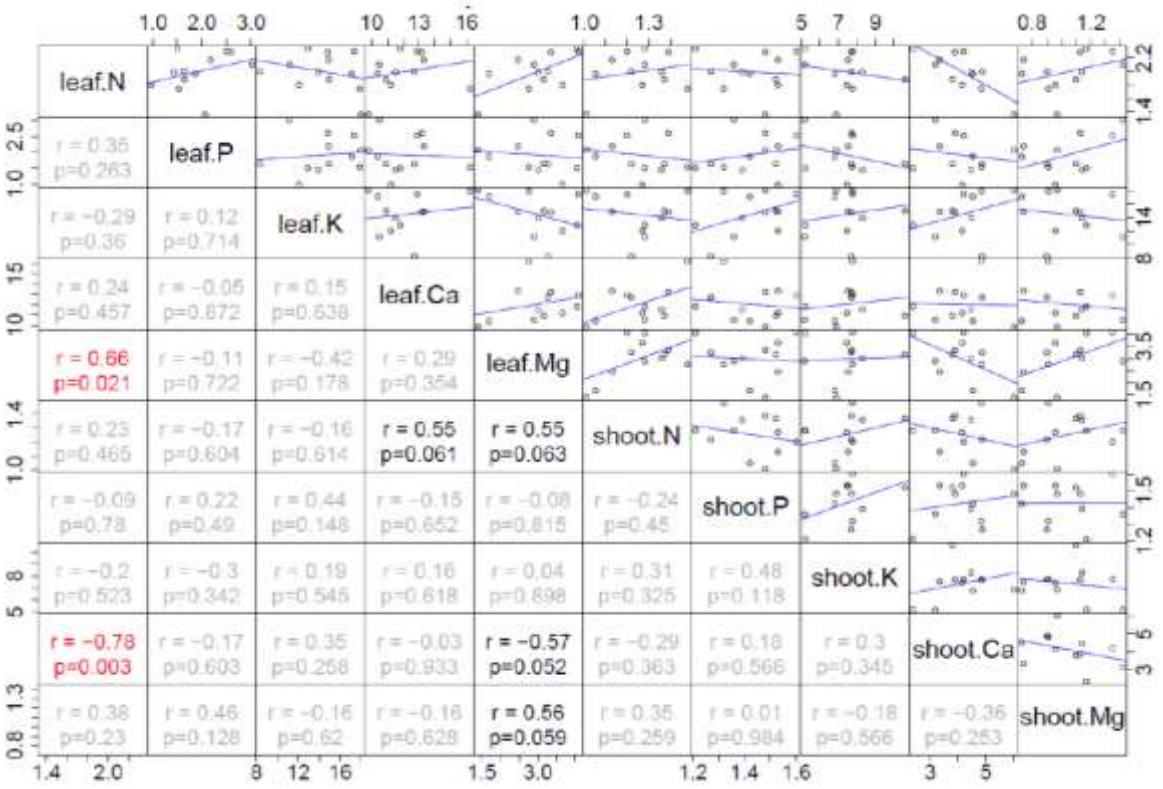


Figure 3. Correlation matrix among nutrient concentrations (g kg^{-1}) of proleptic branches (shoot.X) and leaves (leaf.X) of 12 poplar genotypes. The r-value (Pearson‘s correlation coefficient) ranged from -1 (negative correlation) to +1 (positive correlation). The p-value represents the significance of the Pearson’s correlation coefficient (r-value). Grey boxes: r < 0.5, black boxes: 0.5 < r < 0.6, red boxes: r > 0.6. The values on the X- and Y-axes represent the range confining the specific nutrient concentration.

The GCV showed very little variation among genotypes, and between proleptic branches and leaves; COV values were close to zero (Table 4). The average GCV for proleptic branches was 18.36 MJ kg^{-1} and ranged from 17.77 (Wolterson) to 18.89 MJ kg^{-1} (Koster). For leaves, the GCV ranged from 17.68 (Muur) to 18.77 MJ kg^{-1} (Skado) and was on average 18.16 MJ kg^{-1}. Therefore, the variation in standing energy stock (on average 64.38 GJ ha^{-1}) was mainly determined by, and followed the same trends as, the variation in standing leaf biomass.

4. Discussion

The significantly increased soil N concentration over the first four years might be explained by the high atmospheric deposition (> 30 kg N ha^{-1} yr^{-1}) in Flanders [30], in combination with the slower growth during the first (establishment) rotation [29]. From a soil nutrient point of view the culture of SRC leads to less nutrient leakage as compared to conventional agricultural crops [31, 32] because of the perennial character of the SRC. This can be explained by the increased mineralisation (due to tillage and land preparation) and the reduced input of organic matter (due to weed control) during the establishment of the SRC culture [33], as well as by the nutrient uptake by the SRC culture.

The high N concentration in the soil and the previously intensively fertilised agricultural land use explained the high productivity, which is amongst the highest values reported under our climate conditions for managed SRC cultures [34]. Although poplar has lower nutrient concentrations when compared to other biomass fuels (e.g., switchgrass [35]) its wood has higher nutrient concentrations than willow (*Salix* spp.) [13]. Selecting genotypes with low nutrient concentrations in the woody biomass therefore not only benefits the sustainability of the soil nutritional status [13, 22], but also enhances the feedstock quality. This enhanced feedstock quality decreases the fouling and corrosion processes on furnace walls and increases the ash quality because of lower P, K, Ca and Mg concentrations [36].

The nutrient concentrations of the 12 genotypes corresponded well with values reported for poplar in the literature. For the proleptic branches of this study the N, P and K concentrations were similar to other values for shoots (N: 2.15-10.00; P: 0.28-1.49; K: 1.56-5.19 g kg^{-1}) [7, 13], the Ca concentration conformed to wood values (1.96-6.30 g kg^{-1}) [12, 21], and the Mg concentration resembled bark values (0.68-1.48 g kg^{-1}) [12, 13, 21]. The proleptic branch and leaf nutrient concentrations were closer to the highest reported values in literature, which may reflect the high initial soil nutrient concentrations at our site [13]. We confirmed for poplar that nutrient

concentrations in leaves were significantly higher than those in branches and in shoots in general [5, 14, 21, 37, 38]. Nevertheless, care should be taken when comparing plant nutrient concentrations to literature values. Firstly, different studies separated trees into different compartments: we compared leaves with proleptic branches of two-year-old shoots, while other studies examined nutrient concentrations of stems versus bark [13] or stems versus branches [22, 39]. Secondly, it is not always clear how trees are compartmentalised, whether top sections (the terminal leaders) are included in the stems or in the branches. Thirdly, the height at which shoot samples are collected is important [15, 36], as is the age of the sampled trees [40] and the season of sampling [41]. Fourthly, the poplar genotypes used in various studies all have different nutrient use efficiencies [13, 22] and few studies have performed genotypic comparisons [4, 15, 19].

Although a balanced nutrient accumulation is essential for plant growth [42], only two correlations between nutrient concentrations within leaves, and between leaves and proleptic branches were found. The reason could be the translocation of nutrients from leaves to lower shoots and roots before leaf fall [41]. Due to the different mobility of different nutrients, these relationships might be different in functional leaves. It is important to note that the lowest and the highest nutrient concentrations were found for different genotypes, making it important to match genotype to soil composition (Annex 1). Nevertheless, care should be taken with generalizations: the nutrient uptake and biomass increment of different genotypes could be different on different soil types with different nutrient concentrations and ratios among nutrients.

When SRC is planted for phytoremediation applications, leaves may be removed before or during harvest with the aim of extracting as many pollutants as possible [43-45]. From an energy point of view, this would mean that on average 64.4 GJ ha^{-1} could be extracted as leaves from the field in our experiment (Table 3). This would, however, inherently increase the nutrient extraction rates with on average 69.8 (N), 6.8 (P), 51.6 (K), 42.4 (Ca) and 10.2 (Mg) kg ha^{-1} y^{-1} (Annex 1). To get an idea of the

amount of nutrients removed with the AGWB at each harvest, concentrations in the different woody parts of the shoot should be quantified at the time of harvest.

In conclusion, our results showed that N fertilisation was not needed in our managed SRC culture, when only woody biomass is removed with coppicing. This observation can be explained by the fact that the site was previously intensively fertilised as agricultural land and had high atmospheric N deposition. The results are based on the second year of the second SRC rotation only. Long-term monitoring of changes in soil nutrient concentrations remains necessary for multiple rotations of SRC.

5. Acknowledgements

This research has received funding from the European Research Council under the European Commission's Seventh Framework Programme (FP7/2007-2013) as ERC grant agreement n° 233366 (POPFULL). Further funding to the Flemish research team was provided by the Flemish government through the Hercules Foundation as Infrastructure contract ZW09-06 and by the Methusalem Programme. Funding to the Czech research team was provided by the European Social Fund and by the Czech Republic as project 'Indicators of tree vitality' (Reg. N° CZ.1.07/2.3.00/20.0265). We gratefully acknowledge Laura S. Broeckx, Melanie S. Verlinden and Gonzalo Berhongaray for help with data collection, as well as Kristof Mouton for logistic support at the field site and John Gash for language editing. This contribution fits within COST Actions FP1301 'EuroCoppice' and FP1106 'STReESS' of the EC's Seventh Framework Programme.

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Annex 1 – Nutrient concentrations and standing nutrient stocks for proleptic branches and leaves of 12 poplar genotypes.

		Bakan	Brandaris	Ellert	Grimminge	Hees	Koster	Muur	Oudenberg	Robusta	Skado	Vesten	Wolterson	Average (± stdev)
Nutrient concentration (g kg^{-1})														
N	Branches	10.10	12.00	13.60	12.20	11.30	12.80	12.70	13.70	12.80	10.50	14.80	13.90	12.53 (± 1.40)
	Leaves	13.60	23.00	19.90	20.00	21.70	23.40	18.00	18.80	21.00	19.60	17.40	22.90	19.94 (± 2.80)
P	Branches	1.48	1.60	1.39	1.27	1.53	1.21	1.53	1.52	1.36	1.42	1.32	1.48	1.43 (± 0.12)
	Leaves	2.06	2.51	1.44	1.64	2.18	1.51	0.97	1.65	3.02	1.86	1.54	2.60	1.92 (± 0.58)
K	Branches	6.89	7.75	8.29	7.70	7.51	5.22	7.45	10.60	5.15	6.79	7.74	7.72	7.40 (± 1.41)
	Leaves	18.00	17.40	13.90	8.35	14.90	12.90	12.10	15.00	11.20	17.10	17.90	14.80	14.46 (± 2.97)
Ca	Branches	6.01	4.21	4.47	4.88	3.35	2.39	4.16	3.81	3.18	4.54	4.85	3.89	4.15 (± 0.93)
	Leaves	9.83	12.90	11.50	12.70	13.30	11.80	11.20	10.90	10.50	10.40	16.20	13.20	12.04 (± 1.75)
Mg	Branches	0.97	1.35	1.14	0.90	0.74	1.17	0.96	1.10	1.42	0.73	0.91	1.13	1.04 (± 0.22)
	Leaves	1.40	4.09	3.02	3.27	2.47	4.06	3.66	3.17	2.91	1.70	2.77	3.35	2.99 (± 0.83)
Standing nutrient stock (kg ha^{-1})														
N	Leaves	67.44	60.84	62.17	77.00	67.48	81.73	55.60	56.37	77.60	85.36	63.57	82.79	69.83 (± 10.60)
P	Leaves	10.22	6.64	4.50	6.31	6.78	5.27	3.00	4.95	11.16	8.10	5.63	9.40	6.83 (± 2.45)
K	Leaves	89.26	46.02	43.42	32.15	46.33	45.05	37.38	44.98	41.39	74.47	65.40	53.51	51.61 (± 16.60)
Ca	Leaves	48.75	34.12	35.93	48.89	41.36	41.21	34.60	32.68	38.80	45.29	59.19	47.72	42.38 (± 7.87)
Mg	Leaves	6.94	10.82	9.43	12.59	7.68	14.18	11.31	9.51	10.75	7.40	10.12	12.11	10.24 (± 2.19)