

Plastic Allometry in Coarse Root Biomass of Mature Hybrid Poplar Plantations

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Abstract In this study, we sampled coarse root biomass of three poplar clones in four 13-year-old hybrid poplar (*Populus* spp.) plantations, with the objective of developing an allometric relationship between diameter at breast height (DBH) and coarse root biomass. A second objective was to test significance of site, clone and ×site clone interaction effects on coarse root biomass, using analysis of covariance (ANCOVA), with DBH as a covariate. Across the four sites, the general allometric relationship between DBH and coarse root biomass was highly significant ($R^2=0.78$, $p<0.001$). However, given the high significance of the site effect ($p<0.001$) in the ANCOVA and the differences in data distribution between sites, two allometric relationships were developed based on the fertility class of sites (high and moderate). Environment-specific allometric relationships developed for two site fertility classes had a better fit ($R^2=0.81-0.90$, $p<0.001$). ANCOVA, with DBH as a covariate and site fertility class as a main effect, also showed that both of these variables significantly affected ($p<0.001$) coarse root biomass allocation. Environment-specific equations showed that higher coarse root biomass

was allocated in harsher environments for a given DBH, probably to improve access to growth limiting soil nutrients or to build-up larger storage sites for amino acids and non-structural carbohydrates. Consequently, poplar coarse root biomass growth is both driven by ontogeny (size) and environment, reflecting the plasticity of the root system of mature poplars. Implications of using general vs. environment-specific equations in estimating stand-level root biomass and shoot to root ratios are discussed. Shoot to root ratios calculated using environment-specific equations were more strongly correlated to key environmental variables than ratios calculated using the general equation, with soil NO_3 supply rate being the strongest predictor of the ratio ($R^2=0.90$, $p<0.001$).

Keywords Plasticity · Belowground biomass equation · Site fertility · Large woody roots · Bioenergy · Carbon partitioning and allocation

Introduction

In many parts of the world, poplar (*Populus* spp.) plantations are not only established to meet the growing demand for bioenergy and wood production but also to increase environmental protection [1]. Planted poplars cover approximately 8.6 million ha worldwide, making poplar plantations and agroforestry systems a very important land use at the global scale [1]. Land area under poplar cultivation is also expected to increase in the future because many countries have vast zones of marginal agricultural land that could be converted to bioenergy plantations to satisfy national energy demands [2, 3]. For example, it was estimated that 8 % of the energy demand of Romania could be met with poplar biomass produced on the 1 million ha of recently abandoned arable land [4].

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In the context of global change, afforested poplar plantations for bioenergy are effective to offset carbon (C) emissions because they can contribute to fossil fuel displacement and C storage on former agricultural land [5–8]. Therefore, increasing our knowledge about C cycling and storage in poplar plantations is important to assess the C balance of this expanding type of land use. There is growing evidence that the establishment of short rotation coppices and fast-growing plantations of broadleaved species on agricultural land may not increase soil C stocks on a general basis [9–11], with considerable uncertainties regarding the sustainability of soil organic C enrichment in bioenergy woody crops [12]. However, many of these systems may increase, on the short-term, belowground C storage through root biomass growth [13]. This belowground biomass has a large contribution to the positive C balance achieved by short rotation coppices over multiple rotations [14]. Also, in terms of stability, C stocks in large roots have slow decay rates compared to other forest residues [15].

Important improvements of belowground C estimates in forests and plantations could be made by developing allometric relationships between tree diameter and coarse root biomass of different species across gradients of environmental conditions [16]. This is because large roots generally account for 70 % or more of total root biomass [17]. From an economic perspective, there is also a need for a better quantification of belowground biomass. The growing demand for bioenergy in many parts of the world has stimulated the exploitation of new sources of feedstock, such as stump and coarse root biomass that can be extracted following harvest [18, 19].

Biomass growth and partitioning is a key feature of most bioenergy crop models, with allometry being a common empirical approach to describe the distribution of biomass into different structural components [20, 21]. Yet, the potential effects of environmental conditions on coarse root biomass growth and allometry have received little attention over the years. In poplar plantations, a few studies have developed allometric relationships between diameter at breast height (DBH) and coarse root biomass in different plantation environments [22, 23, 19, 24, 25]. These relationships have also been developed in natural poplar stands [26, 27]. However, all of these field studies reported only a single allometric relationship between DBH and coarse root biomass, with no evidence of coarse root biomass plasticity in relation to environmental factors. This is surprising given that site quality can affect allometric relationships between stem diameter and aboveground compartments in short rotation coppices of willows [28, 29]. In more widely spaced and older poplar plantations, growth environment likely influenced the relationship between DBH and different aboveground woody biomass components [30]. Change of allometry between coarse roots and shoots has also been reported in lodgepole pine (*Pinus contorta*) stands along a stress gradient in forests of the sub-

boreal zone [31]. Furthermore, poplar genotype could influence patterns of biomass allocation to coarse roots since significant genotype effects were observed on the relationships between DBH and different aboveground biomass components of even-aged plantations [32].

Most evidence regarding the plastic response of poplar root systems in field experiments are related to fine root production dynamics [33]. For example, in a recently established poplar plantation for bioenergy, drought conditions in the spring stimulated fine root production, while leading to a decrease in gross primary production [34]. In a field study where environmental conditions had been manipulated, high soil N and elevated atmospheric CO₂ were found to increase fine root production and mortality, with soil N greatly affecting C partitioning between leaves and fine roots [35].

Changes in poplar shoot and root allometry in response to environmental conditions have been mainly reported in greenhouse experiments involving young plant material. As shown by Liu & Dickmann [36], increasing N availability in soil did not affect total root biomass production, but greatly increased shoot biomass of 37-day-old poplars. Similarly, 28 days of exposure to intermediate and luxuriant N concentrations resulted in significant changes in poplar architecture, with stem biomass being positively affected by N treatments, while total root biomass remained unaffected [37]. This short-term plastic response resulted in different allometric relationships between stem and root biomass under the different N treatments, suggesting that poplars can initiate rapid tree architecture changes when N is available, in order to increase C fixation capacity, and eventually favour stem growth over root growth [37]. These allometric trends are consistent with the “optimal partitioning theory,” which suggests that plants invest resources for improving their access to the currently limiting factor [31, 38]. However, is this plastic response of tree architecture to site fertility still perceptible for mature poplar trees growing in contrasted plantation environments? This question is of particular interest given that tree plasticity in response to limited resources may decline with increasing age and/or time of exposure to the limiting resources [39, 40].

Coarse roots are also multifunctional tree components providing key functions such as transport (nutrients, photosynthate, water), storage (sugars and nutrients) and biomechanical stabilisation, as well as being the framework upon which fine root develop and connect [41–43]. The relative importance of such functions will likely vary with tree development and growth environment. Consequently, as the aboveground components grow taller, wider and heavier, the stabilisation function of coarse roots in fast-growing tree plantations may become of overriding importance in the biomass allocation strategy to roots, potentially obscuring the effect of fertilisation or site fertility on coarse root allometry [41]. Consequently, a plastic response of coarse root biomass will likely depend on the particular requirement for these functions in a particular

environment at a specific time in tree development. Trees are large, modular and long lived, and conflicting and lagged signals travel through the vascular system from different structures over time [44]. This further complicates our understanding of tree C balance and allocation under natural conditions.

In this study, we collected coarse root biomass data of three poplar genotypes in four 13-year-old hybrid poplar plantations located along a gradient of elevation and soil fertility. Two of the plantations have higher site fertility and high aboveground yields, while the two others have moderate site fertility and moderate yields. The first objective of this study was to develop a general allometric relationship between DBH and coarse root biomass for mature poplar plantations. The second objective was to use this allometric relationship to estimate coarse root biomass of the three hybrid poplar clones across the four sites, but also to estimate shoot to root ratio using aboveground biomass data of Truax et al. [32], which were collected in the same year. We also verified the plastic allometry hypothesis [45] for coarse root biomass growth in contrasted plantation environments by testing the significance of the site effect and DBH, as a continuous covariate, on coarse root allocation using analysis of covariance (ANCOVA). The genotype and the site \times genotype interaction effects were also tested.

Materials and Methods

Site Description and Experimental Design

The study sites are located on privately owned abandoned farmland in the Eastern Townships region of southern Québec, Canada. Four different plantation sites (Bedford, Brompton, Melbourne and Ste-Catherine) were chosen along a regional gradient of elevation (climate) and soil characteristics, with higher mean annual temperature and longer growing season being found on lower elevation sites of the region [46].

The Bedford and Brompton sites have a high site fertility and high aboveground woody biomass yields (11.4 and 9.6 t/ha/year after 13 years), while the Melbourne and Ste-Catherine sites have moderate site fertility and moderate yields (5.2 and 6.1 t/ha/year after 13 years) [32] (Table 1). The four study sites are located within a radius of 50 km, with all plantations sites being nearly flat, with slopes always under 5 %. The geology of the study area is complex, but the bedrock is almost completely covered with glacio-fluvial and glacial till deposits [46]. The region is characterised by a continental subhumid moderate climate and mean annual precipitation ranges from 900 to 1,100 mm [46].

In the year of the study (2012), all plantations were in their 13th growing season. Pre-plantation site preparation included ploughing and disking each site in fall 1999. In the spring of 2000, bare-root planting stock with 2-m-long stems were

planted manually with shovels at 30 to 40 cm depth at a spacing of 3 \times 4 m, for a tree density of 833 stems/ha. Planting stock (1–0) was provided by the Berthierville nursery of the Ministère des Ressources naturelles – Forêt (MRNF) of Québec. Competing vegetation was eliminated with glyphosate herbicide application over the entire plantation area in June 2000, and between plantation rows only, in June 2001.

The initial experimental design contained eight plantation sites, with three blocks per site, and nine poplar clones. However, for the purposes of this study, only three clones (with contrasted parentages) and four sites were used. These three unrelated hybrid poplar clones were: *Populus deltoides* \times *nigra* (DxN-3570, also named *P. \times canadensis*), *P. canadensis* \times *maximowiczii* (DNxM-915508) and *P. maximowiczii* \times *balsamifera* (MxB-915311). These clones had been selected for superior disease resistance/tolerance and growth characteristics in MRNF genetic selection trials in southern Québec [47]. A randomized block design was used at each of the four sites, with three blocks (nested in sites) and three plots per block (one plot per hybrid poplar clone), for a total of 36 experimental plots (4 sites \times 3 blocks \times 3 clones, $n=36$). Plots are 12 m wide and 12 m long (144 m²). Each plot initially contained 12 trees from a single clone (3 rows, 4 trees per row). Trees are spaced 3 m apart on the row, and the rows are 4 m apart. At all sites, one guard row of poplar trees was planted around the entire perimeter of the plantation, in order to reduce edge effects that could affect nutrient and water uptake, as well as exposure to open field light and wind conditions.

Soil Characteristics and Nutrient Supply Rates

In each plot, a composite soil sample was collected to a depth of 20 cm. Soil samples were air dried and sieved (2 mm). Soil pH, clay, silt and sand content, percent organic matter, cation exchange capacity (CEC) and base saturation were determined by the Agridirect Inc. soil analysis lab in Longueuil (Québec). Methods used are those recommended by the Conseil des productions végétales du Québec [48]. The determination of soil pH was made using a 1:1 ratio of distilled water to soil. For particle size analyses, the Bouyoucos [49] method was used. Percent organic matter was determined by weight loss after ignition at 550 °C for 4 h. Cation exchange capacity and base saturation were calculated following the recommendations of the Centre de référence en agriculture et agroalimentaire du Québec [50], after Ca, K and Mg extraction with the Mehlich III method [51] and concentration determination using ICP emission spectroscopy [52]. Soil characteristics are presented in Table 1.

Nutrient supply rates (availability) in the entire experimental design was determined using Plant Root Simulator (PRSTM-Probes) technology from Western Ag Innovations Inc., Saskatoon, Canada. The PRS-probes consist of an ion exchange membrane encapsulated in a thin plastic probe,

Table 1 Site and soil characteristics (0–20 cm) of the four hybrid poplar plantation sites

Sites	Site fertility	Biomass yield (t/ha/year)	Elevation (m)	Clay–Silt–Sand (%)	pH	Organic matter (%)	CEC (meq/100 g)	Base saturation (%)
Bedford	High	11.4	80	22–22–56	5.64	4.50	13.8	45.2
Brompton	High	9.6	170	24–49–27	5.68	5.00	14.3	47.2
Melbourne	Moderate	5.2	330	14–37–49	5.47	6.81	12.7	26.4
Ste-Catherine	Moderate	6.1	230	13–39–48	5.20	6.23	12.2	13.9
SE	–	–	–	–	0.07	0.22	0.5	2.7
<i>p</i> <	–	–	–	–	0.001	0.001	0.06	0.001

Aboveground woody biomass yield data are from Truax et al. [32]

which is inserted into the ground with little disturbance of soil structure. Nutrient availability predicted with this method is generally significantly correlated with conventional soil extraction methods over a wide range of soil types [53], and which has also been corroborated in poplar riparian agroforestry systems of the study region [54, 55]. In August 2012, four pairs of probes (an anion and a cation probe in each pair) were buried in the A horizon of each plot for a 35-day period. After probes were removed from the soil, they were washed in the field with distilled water, and returned to Western Ag Labs for analysis (NO₃, NH₄, P, K, Ca and Mg). Composite samples were made in each plot by combining the four pairs of probes. Nutrient supply rates at each site are reported as microgram of nutrient per 10 cm² per 35 days (Table 2).

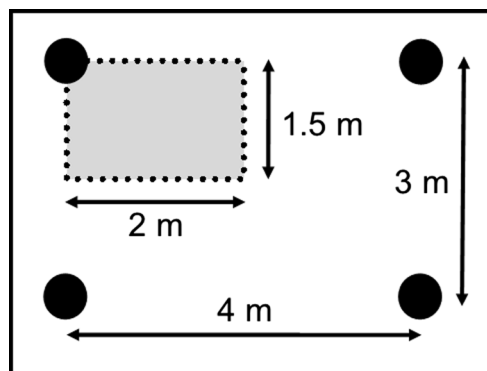
Coarse Root Biomass Sampling

In July 2012, coarse root biomass was sampled in the soil occupied by one representative tree of each plot (*n*=36), in a plot section where there was full stocking. A large rectangular pit was excavated using a small mechanical excavator. The size of the excavated pits was 1.5 m×2 m×0.60 m depth, which corresponds to 25 % of the surface area occupied by a single tree for a plantation density of 833 stems/ha (Fig. 1). This approach was chosen because large monoliths are required for representative coarse root sampling [56]. The position of the quadrant sampled was randomly selected. To

facilitate the work of the excavator operator, the sampling area was delineated with white paint sprayed on the ground. Sampled tree DBH was measured prior to excavation. Once a pit was excavated, the tap root was cleaned and its length, large end and small end diameters were measured in the field with a caliper. All sampled trees had a tap root, which probably reflects the type of plant material that was used to establish the plantations and the planting depth of this material (bare-root plants planted at a 30–40 cm of depth), as planting depth and plant material influence root system architecture in hybrid poplars [57]. Tap root formation have also been observed in a Euramerican clone grown in plantation after 5 years [58]. Tap root volume was calculated using the Smalian formula [59]. Tap root biomass was obtained by multiplying its volume by the mean density of hybrid poplar coarse roots (0.313 g/cm³) [19]. All coarse roots (diameter>2 mm) in excavated pits were hand cut with a saw, removed, cleaned and air dried for 2 months. For each plot, the entire air dried sample of coarse roots was then weighed and a subsample was taken to determine oven dry weight and water content of the air dried samples. This procedure was preferred to the preparation of subsamples in the field on fresh root biomass, which was dirty and required water cleaning prior to subsampling for water content determination. For each sampled tree, total coarse root biomass (oven dry weight) was calculated as follows:

Table 2 Nutrient supply rate (μg/10 cm²/35 days) in soil measured during 35 days at the end of summer 2012 at the four hybrid poplar plantation sites

Sites	NO ₃	NH ₄	P	Ca	K	Mg
Bedford	150.7	4.99	1.43	2389	75.7	249.6
Brompton	35.9	5.58	3.15	1450	62.0	227.1
Melbourne	3.8	5.09	0.70	542	94.0	85.3
Ste-Catherine	3.3	15.46	1.91	281	159.7	197.4
SE	9.4	5.09	0.75	142	17.1	14.8
<i>p</i> <	0.001	NS	NS	0.001	0.01	0.001

**Fig. 1** Sampling design for coarse root biomass. The black circles represent poplars and the grey rectangle is the sampling area. This area is 25 % of the area occupied by each poplar, as defined by the spacing of planted trees

(Biomass collected from pits \times 4)+Taproot biomass=Total coarse root biomass.

Regression Procedures for Allometric Relationships

With coarse root biomass data obtained from the 36 sampled trees, a regression model for coarse root biomass versus DBH was developed, with DBH being the predictor variable (x) and coarse root biomass being the response variable (Y). Common simple models describing allometric relationships in trees were tested, including linear, polynomial, exponential and power functions [60]. Residuals of the different models were plotted and compared to a normal distribution in order to determine the goodness-of-fit according to the Shapiro–Wilk W test, the best omnibus test for testing normality of a distribution for small sample sizes ($n < 50$) [61]. Regression model selection was based on (1) the significance of model parameters, (2) the fit (R^2) of the regression and (3) the goodness of fit (W) or normality in residuals distribution. Therefore, when the fit of two different models with significant parameters was comparable, the model with the highest normality in the distribution of residuals was chosen. For nonlinear models, data were linearized prior to these analyses.

After data exploration and model fitting, one data point was removed from the data set of the Melbourne site (DBH=14.0 cm, coarse root biomass=20.7 kg) because the coarse root biomass measured was disproportionately high for the DBH value. The examination of a residual plot and an outlier boxplot also suggested that this data point was an outlier. This outlier was most likely related to the poor drainage of the soil at this particular location in the plantation, with the bottom of the pit filling up with water during the excavation; a situation that was not representative of the good drainage conditions observed in all of the other plots. As argued by Nikklas [62], outliers in allometric studies may be the result of unusual environmental circumstances, which is reflected by form or function compromises for a given organism within the context of these particular circumstances.

After developing a general allometric relationship between DBH and coarse root biomass using data from the four plantation sites, site, clone and site \times clone interaction effects were tested on the relationship between DBH and coarse root biomass using analysis of covariance (ANCOVA). Data were log (ln) transformed prior to analysis. This ANCOVA tested DBH, as a continuous covariate, and site, clone and site \times clone interaction, as nominal effects on coarse root biomass. The site effect was highly significant ($p < 0.001$), while the clone effect and the site \times clone interaction effect were non-significant ($p = 0.36$ and $p = 0.95$, respectively). After plot examination of DBH to coarse root biomass data distributions at the four study sites, we observed that there was a considerable overlap between data from the Brompton and Bedford sites, but also between the Ste-Catherine and Melbourne sites.

Consequently, the data from the two high fertility sites (Bedford and Brompton) were combined, as were the data from the two moderate fertility sites (Melbourne and Ste-Catherine), creating two distributions, based on the site fertility class of sites (high vs moderate). These site fertility classes were consistent with soil characteristics, local climate in terms of plantation elevation and aboveground woody biomass yield at each site (Tables 1 and 2). Consequently, in this study, the term site fertility is used in its broad sense, as it refers not only to favourable soil conditions, but also to more favourable climatic conditions in terms of elevation or climate, given the temperature dependency of processes important for plant growth, such as N-mineralisation in soil and ion uptake by roots [63]. Important covariation between elevation (climate) and different soil fertility indicators have been reported in poplar plantations of the region [64]. An ANCOVA was then used to test the significance of the site fertility class (high vs moderate), as a main effect, and DBH, as a continuous covariate, on coarse root biomass, using log transformed data. Given that the site fertility class effect and the continuous covariate (DBH) were highly significant ($p < 0.001$) an allometric relationship was developed for each of the two site fertility classes using the procedure aforementioned. Thus, an environment-specific model was developed for each of the two site fertility classes (high and moderate).

Coarse Root Biomass and Shoot to Root Ratio Calculations

Allometric relationships developed were then used to calculate coarse root biomass, from DBH measurements, for each living tree in the entire experimental design (all trees in the 36 sampled plots). The DBH measurements were taken from late October to early November 2012, at the end of the 13th growing season. In each plot, coarse root biomass calculated for each tree was cumulated, and then scaled up to a one hectare area. Mean coarse root biomass per tree data were obtained by dividing total plot coarse root biomass by the number of living trees in the plot. To explore the implications of using the general allometric relationship versus environment-specific allometric relationships developed for the two site fertility classes, we calculated coarse root biomass in the four hybrid poplar plantations using both modelling approaches. The model developed for moderate site fertility was used to calculate coarse root biomass for the Melbourne and Ste-Catherine sites, while the model developed for high site fertility was used in calculations for the Bedford and Brompton sites.

Shoot to root ratios of 13-year-old poplar plantations were calculated at the plot level by dividing total aboveground woody biomass (data from Truax et al. [32]) by total coarse biomass data calculated with general and environment-specific allometric relationships developed in this study. Our

shoot to root ratios did not take into account fine root biomass nor coarse root biomass that would have been found below 60 cm depth, although some coarse roots were observed below this depth in most excavated pits. Therefore, it is likely that we have slightly underestimated coarse root biomass, and similarly slightly overestimated shoot to root ratio.

Statistical Analysis

Soil characteristics, calculated coarse root biomass data at the plot level and shoot to root ratios were analysed using a two-way ANOVA in a fixed factorial design. ANOVA tables were constructed in accordance with Petersen (1985), where degrees of freedom, sum of squares, mean squares and *F* values were computed. When a main effect (site and clone) or the interaction effect (site×clone) was declared statistically significant, the standard error of the mean (SE) was used to evaluate differences between means for three levels of significance (**p*<0.05, ***p*<0.01 and ****p*<0.001). All of the ANOVAs were run with the complete set of data (36 experimental plots). Pairwise correlations were used to identify which of the following environmental factors were significantly correlated with shoot to root ratios: site elevation; soil pH, CEC and base saturation; soil organic matter, clay, silt and sand content, and soil supply rate of NO₃, NH₄, P, Ca, K and Mg. Thereafter, regressions were developed between key environmental variables and shoot to root ratios. All statistical analyses were done using JMP 11 from SAS Institute (Cary, NC).

Results

Site Characteristics and Soil Nutrient Supply Rates

Based on site characteristics and yields, Bedford and Brompton were categorised as high fertility sites for poplar culture in this study (Table 1). Both of these sites are located at low elevation and shared similar soil characteristics in terms of clay content, pH, percent organic matter, CEC and base saturation. The Melbourne and Ste-Catherine site characteristics contrast sharply with those observed at Bedford and Brompton: higher elevation, lower clay content, lower soil pH, higher percent organic matter, lower CEC and lower base saturation (Table 1). Compared to the two moderate fertility sites (Melbourne and Ste-Catherine), much higher NO₃ and Ca supply rates were also observed in late summer 2012, at the two high fertility sites (Bedford and Brompton). At Bedford and Brompton, NO₃ supply rate, respectively, reached 150.7 and 35.9 μg/10 cm²/35 days, while the supply rate of NO₃ only reached 3.8 and 3.3 μg/10 cm²/35 days at the Melbourne and Ste-Catherine sites respectively (Table 2). Meanwhile, Ca supply rate reached 2,389 and 1,450 μg/10 cm²/35 days at Bedford and Brompton, respectively, while it only reached

542 and 281 μg/10 cm²/35 days at Melbourne and Ste-Catherine, respectively (Table 2).

Allometric Relationships for Coarse Root Biomass

The selected general model describing the relationship between DBH (in centimetres) and coarse root biomass (in kilogrammes per tree) of hybrid poplars across the four plantation sites was in the form of a power function ($Y = \beta x^\alpha$; Table 3), with parameter β being the allometric constant and parameter α the scaling exponent [62]. Power functions have been widely used to describe allometric relationship between tree diameter and biomass components for a wide range of tree species and taxa [65, 66]. This model and the estimated parameters were all highly significant (*p*<0.001) and the model had a reasonably good fit ($R^2=0.78$; Fig. 2, Table 3). Allometric relationships developed with the same variables, but for the two site fertility classes, were also highly significant, as was the case for their estimated parameters (Table 3). However, the fit of these environment-specific models, both in the form of power functions, was higher ($R^2=0.81-0.90$) than the fit of the general model (Table 3). These relationships suggest that for a given DBH, a higher coarse root biomass was allocated by 13-year-old hybrid poplars on moderate fertility sites, compared to what was observed on high fertility sites (Fig. 3). This trend in root biomass allocation pattern also increased as hybrid poplar DBH increased, a consequence of the larger scaling exponent for the relationship developed with data from moderate soil fertility sites. The ANCOVA testing the significance of the site fertility class (high vs moderate), as a main effect, and DBH, as a continuous covariate, on coarse root biomass (using log transformed data) showed that the site fertility class effect was highly significant (*p*<0.001), as was the case for DBH. However, the clone (genotype) and site×clone interaction effects were non-significant (see “Materials and methods” section for additional details). Moreover, the positive linear relationships between mean aboveground woody biomass per tree and mean coarse root biomass per tree, calculated at the plot level, showed that coarse root biomass increases linearly with increasing aboveground biomass, with the rate of increase (slope) being higher on moderate soil fertility sites, compared to what was observed on high soil fertility sites (Fig. 4).

Coarse Root Biomass and Shoot to Root Ratios

A significant site×clone interaction was observed on both coarse root biomass and shoot to root ratio estimates (Table 4), a trend reflecting observations made on aboveground woody biomass [32]. Based on data calculated with environment-specific allometric relationships, this interaction suggests that a small variation in coarse root biomass is observed for *P. maximowiczii* hybrids across the four sites, while

Table 3 Allometric relationships between diameter at breast height (DBH, in centimetres), as the predictor variable (x), and coarse root biomass (in kilogrammes per tree), as the response variable (Y)

Model name	Trees sampled (n)	DBH range (cm)	Model	R^2	F ratio	W	$p < W$
General	35	10.2–37.6	$Y=0.1083 x^{1.6506}$	0.78	114	0.97	0.38
Moderate site fertility	17	10.2–27	$Y=0.0238 x^{2.2246}$	0.90	136	0.91	0.10
High site fertility	18	20.1–37.6	$Y=0.0344 x^{1.9608}$	0.81	67	0.95	0.49

The general model combines data from the four sites, the moderate site fertility model combines data from the Melbourne and Ste-Catherine sites, while the high site fertility model combines data from the Bedford and Brompton sites. All models and model parameters are significant at $p < 0.001$. For each model, goodness of fit expressed by the Shapiro–Wilk statistic (W) is presented with its associated p value

more than a threefold variation in coarse root biomass was observed for the D×N hybrid across sites. Coarse root biomass ranged from 12.4 to 18.5 t/ha at Bedford, 12.4 to 13.2 t/ha at Brompton, 5.2 to 18.1 t/ha at Melbourne and 10.4 to 16.1 at Ste-Catherine, depending on the clone (Table 4). However, if the general model had been used to calculate coarse root biomass of the same poplar plantations, coarse root biomass would have been overestimated by up to 18 % on the high fertility sites, and underestimated by up to 25 % on the moderate fertility sites (Table 4). Likewise, the estimated shoot to root ratio was also influenced by the modelling approach used to calculate coarse root biomass. Using the models developed for the two fertility classes, instead of the general model, resulted in a larger variation in the shoot to root ratio between the high and moderate fertility sites, with high fertility sites having higher shoot to root ratios than moderate fertility sites (Table 4).

Relationship Between Shoot to Root Ratio and Environmental Variables

Strong and highly significant relationships ($p < 0.001$) were observed between several proxies of soil fertility and shoot to root ratios calculated using coarse root biomass equations developed for the two soil fertility classes, with R^2 ranging

between 0.78 and 0.90, depending on the variable (Fig. 5). These relationships suggest that the shoot to root ratio in poplar plantations is positively linked to soil NO_3 supply rate, Ca supply rate, clay content and base saturation, but negatively linked to percent soil organic matter. Weaker positive relationships were also observed between soil pH and the shoot to root ratio ($R^2 = 0.56, p < 0.01$), and between soil CEC and the shoot to root ratio ($R^2 = 0.34, p < 0.05$; data not shown). Additionally, a strong negative relationship was observed between elevation, a proxy of growing season length in the region [46], and the shoot to root ratio of hybrid poplar plantations ($R^2 = 0.76, p < 0.001$; Fig. 5). Significant relationships were equally observed between environmental variables and the shoot to root ratio calculated using the general allometric relationship for coarse root biomass (Fig. 5). However, the rate at which environmental variables modulated this shoot to root ratio was lower, as was also the fit (R^2) of these relationships.

Discussion

This study provides evidence that site fertility or quality influences the trajectory, or shape, of the allometric relationship between DBH and coarse root biomass of mature hybrid

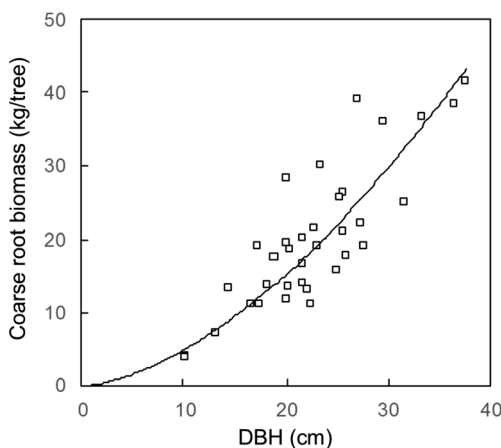


Fig. 2 General allometric relationship between diameter at breast height (DBH; in centimetres) and coarse root biomass (in kilogrammes per tree) in 13-year-old hybrid poplar plantations

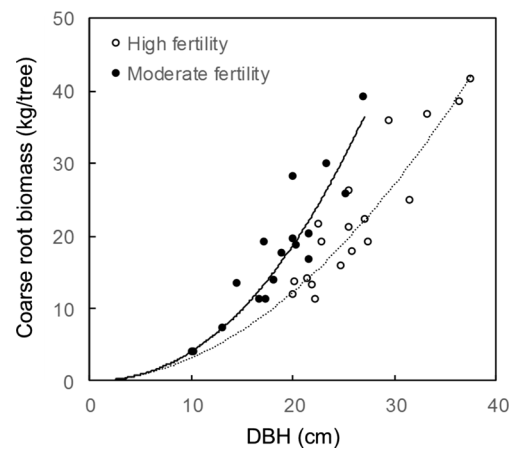


Fig. 3 Environment-specific allometric relationships between diameter at breast height (DBH; in centimetres) and coarse root biomass (in kilogrammes per tree) for two classes of soil fertility (high and moderate) in 13-year-old hybrid poplar plantations

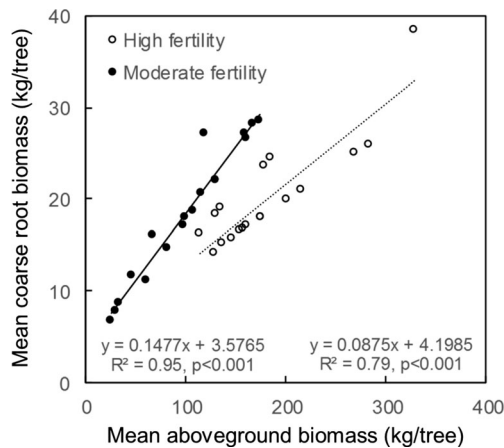


Fig. 4 Linear relationships between calculated mean aboveground woody biomass and mean coarse root biomass at the plot level for two classes of soil fertility (high and moderate) in 13-year-old hybrid poplar plantations. Mean aboveground biomass data are from Truax et al. [32]. For each relationship, $n=18$

poplar trees grown on abandoned fields (Fig. 3). This interpretation is supported by the ANCOVA results showing that site fertility class, as a main effect, and DBH, as a continuous covariate, were both highly significant ($p < 0.001$) in predicting coarse root biomass. In other words, coarse root biomass allocation in 13-year-old poplars is plastic, being both tree size and environment dependent. While the general allometric relationship between DBH and coarse root biomass was highly significant, with a relatively good fit ($R^2=0.78$, $p < 0.001$; Fig. 2, Table 3), both allometric relationships

developed for the two site fertility classes (moderate and high), using the same data set, had a better fit ($R^2=0.90$ and 0.81 , $p < 0.001$; Fig. 3, Table 3). Consequently, environment-specific equations describe more accurately the relationship between tree diameter growth and coarse root biomass growth in mature poplar plantations.

Our results support the “plastic allometry” hypothesis [45], but also the “optimal partitioning theory,” which suggests that plants invest resources or allocate C to improve their access to the limiting factor [38]. A similar pattern of plastic allometry was equally found for shoot/root allometry in lodgepole pine stands along a fertility gradient [31]. In our specific case, exponentially higher root biomass was allocated for a given tree DBH in more nutrient poor environments, also located at higher elevation (Melbourne and Ste-Catherine sites; Tables 1 and 2, Fig. 3). The different slopes of the relationships between estimated mean aboveground biomass and mean coarse root biomass per tree also support the evidence of a flexible allometry (change in tree architecture) that optimises biomass allocation along a site fertility gradient (Fig. 4).

These results corroborate previous glasshouse experiments showing that a favourable N soil environment triggers changes in hybrid poplar tree architecture, which favours aboveground structures over the root system to increase C fixation capacity [37, 36]. Evidence of plastic allocation patterns in response to resource availability have also been shown for seedlings of different tree species, including *Betula pendula* [67], *Fagus sylvatica* and, to a much lower extent, *Picea abies* [39]. Similar observations have been reported for herbaceous

Table 4 Site×clone interaction for aboveground woody biomass, coarse root biomass and the shoot to root ratio in 13-year-old hybrid poplar plantations

Sites	Clones	Aboveground biomass (t/ha)	Coarse root biomass (t/ha)		Variation (%)	Shoot/root ratio	
			General	Plastic		General	Plastic
Bedford	MxB-915311	117	14.6	12.4	+18	8.0	9.4
	DNxM-915508	186	19.5	17.4	+12	9.5	10.6
	DxN-3570	146	20.0	18.5	+8	7.3	7.9
Brompton	MxB-915311	117	14.7	12.4	+18	7.9	9.4
	DNxM-915508	119	14.1	12.1	+17	8.4	9.8
	DxN-3570	94	15.4	13.2	+16	6.1	7.1
Melbourne	MxB-915311	106	13.5	18.1	-25	7.7	5.8
	DNxM-915508	85	11.0	14.3	-23	7.6	5.9
	DxN-3570	22	4.5	5.2	-13	4.6	4.1
Ste-Catherine	MxB-915311	71	10.5	12.6	-17	6.6	5.6
	DNxM-915508	95	12.5	16.1	-23	7.5	5.9
	DxN-3570	44	8.6	10.4	-17	4.6	4.1
	SE	14	1.6	2.2		0.4	0.2
	$p <$	0.05	0.05	0.05		0.01	0.05

Coarse root biomass and the shoot to root ratio were calculated using a general allometric relationship, but also using the environment-specific relationships (plastic allometry) developed for the two site fertility classes. Data for aboveground woody biomass were taken from Truax et al. [32]

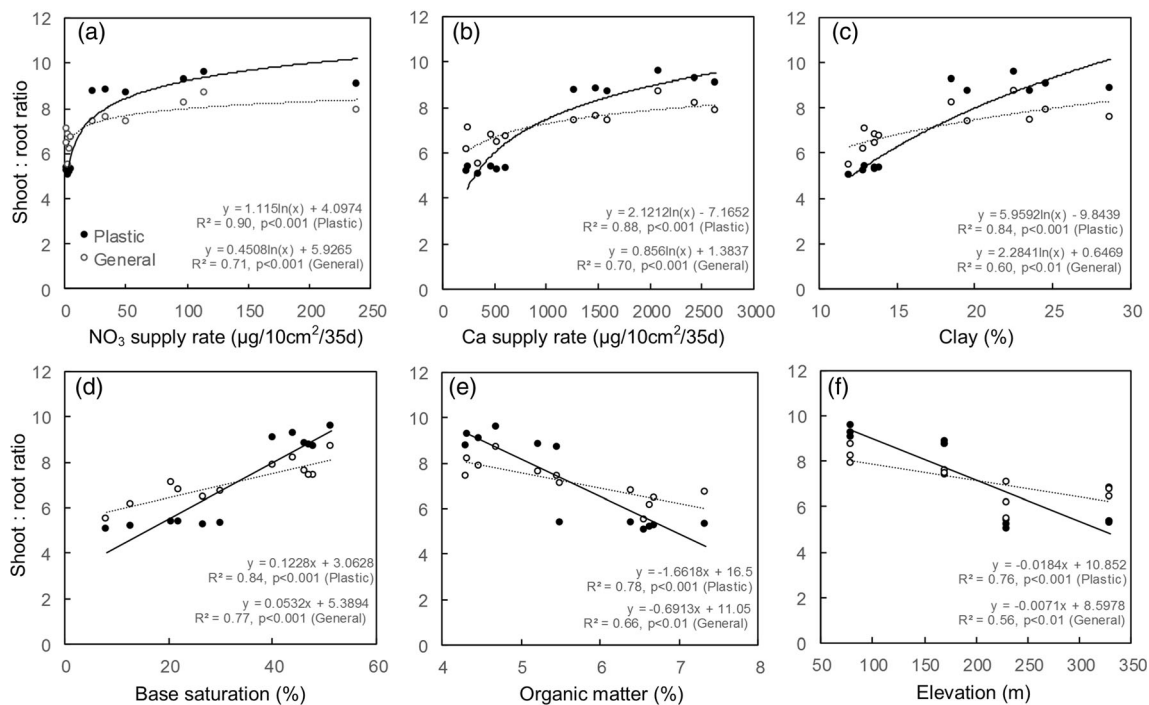


Fig. 5 Shoot to root ratio in hybrid poplar plantations as a function of **a** soil NO₃ supply rate, **b** soil Ca supply rate, **c** soil clay content, **d** soil base saturation, **e** soil organic matter content and **f** site elevation. Shoot to root ratios were calculated using the general allometric relationship, but also

using the environment-specific relationships (plastic allometry) developed for the two soil fertility classes (See Table 4). Data were averaged at the block level for each relationship ($n=12$)

plants [68, 69] and for different tree species growing in forest environments [31, 70, 71]. In willow bioenergy crops, site fertility also causes changes in the relationship between stem diameter and aboveground biomass growth [28, 29]. Aboveground allometry was also likely affected by environmental conditions for a T×M hybrid growing in different locations of southern Scandinavia [30].

Being pioneer riparian species, the parental species of studied hybrid poplars (*Aigeiros* and *Tacamahaca* sections) often colonise nutrient poor mineral substrates such as sand or gravel bars along streams, but also sand dunes and beaches [72]. In these low fertility and well-drained soil habitats, newly established seedlings often have to grow under the additional stress of a low or rapidly declining water table [73]. The rapid development of root systems for resource acquisition, at the expense of shoot growth, is therefore critical to ensure seedling survival when resource availability is low or rapidly declining [74]. This adaptive strategy in response to riparian habitat features could explain the plasticity in root biomass allocation observed in this study. In many cases, tree ability to respond to limited resources by plasticity in allocation often declines with tree size and/or time of the exposure to the environmental stress [40, 39]. However, this study provides evidence that a prolonged exposure (13 years) to different levels of soil fertility results in different allocation patterns to coarse root biomass (Tables 1 and 2, Figs. 3 and 4). Differences in elevation between moderate and high fertility

sites could have also contributed to the plastic allometry pattern observed. Lower elevation sites benefit from a warmer climate in the region [46], and therefore higher soil temperature conditions, which may reduce the need to invest C in the root system because higher root ion uptake rates are generally observed at higher soil temperature [63].

To a certain extent, the interpretation that higher coarse root biomass allocation on lower fertility sites occurs to allow a higher nutrient uptake capacity is debatable. It is widely assumed that nutrient uptake is restricted to the narrow region of young fine roots located just behind the root tip [75]. Yet, recent evidence suggests that the majority of N uptake occurs in older woody roots of both coniferous and broadleaved seedlings [76]. Nitrogen uptake rate in older woody roots was found to be lower than in young fine roots, but the much higher total surface area of these woody roots provides the higher total N uptake [76]. Small woody roots also had important P and K uptake rates in 12-year-old slash pines growing under field conditions [77]. Additionally, despite the water uptake rate per surface area decline with woody root size, significant water uptake has been measured in spruce, beech and oak for woody roots of 4–5 cm in diameter [78]. Consequently, we cannot completely discard the idea that larger woody roots of poplars can contribute to nutrient uptake, although rates of nutrient or water uptake by coarse roots might be very low. The large surface area of coarse roots could be a determinant factor in nutrient absorption, especially on

low fertility sites. Still, clear demonstration of the nutrient uptake capacity of larger woody roots of different tree species remains to be shown under field conditions.

On the other hand, the plastic allocation to coarse biomass observed in this study (Figs. 3 and 4) may be more linked to the storage function rather than the nutrient uptake function of coarse roots. As trees become more mature, internal remobilisation of stored C and N may become proportionally more important than uptake to fulfill nutritional requirements, because mature trees have larger storage pools and often slower uptake rates [79]. It is well-known that poplar coarse root biomass is an important storage site for non-structural carbohydrates, but also for amino acids in the form of bark storage proteins [43, 44]. On lower fertility sites, it may be advantageous for poplars to allocate more belowground biomass to build a larger coarse root system for storage purposes. Stored carbohydrates and amino acids in roots could then be used locally, and in timely fashion, to sustain a higher level of fine root growth, symbiotic associations with fungi [80, 81] and root exudation [82, 83]. These three processes have an increasing importance for nutrient capture as site fertility decreases [84–86]. This interpretation is consistent with the observations of Kobe et al. [87] made in seedlings of seven temperate tree species. These authors showed that total root mass, as a proportion of whole-plant mass, was higher in low vs. high soil N environment, with changes in root mass being mostly influenced by the increased storage of total non-structural carbohydrates. The build-up of a larger pool of non-structural carbohydrates in roots could provide flexibility to temporal resource variations in soil environments [87], with such resource variations being typical of riparian habitats where parental species of the studied hybrid poplars naturally grow [74, 72]. During periods when nutrients become scarce, non-structural carbohydrates stored in roots could be used to increase access to soil nutrients by providing an energy source for mycorrhizae and organic matter decomposers in the rhizosphere [87]. This energy source could then be used for the rapid production of fine roots and to support metabolic costs of nutrient uptake, as nutrients become more available [87]. In short, though our results are in accordance with the optimal partition theory, we cannot firmly conclude to which extent the plastic allocation to coarse root biomass is related to the nutrient uptake and/or the storage functions.

One outlier was removed from the data set of the Melbourne site (moderate fertility) because the coarse root biomass measured was disproportionally high for the DBH value (DBH=14.0 cm, coarse root biomass=20.7 kg). Compared to the other plots of the Melbourne plantation, the plot where the outlier was observed had the lowest NO₃ supply rate (1 µg/10 cm²/35 days), the lowest Ca supply rate (377 µg/10 cm²/35 days) and the lowest pH value (5.2). These low soil richness indicators and the presence of grey birch and willow seedlings in the plot understory were likely

linked due to the poorer drainage conditions that were observed during root sampling of this outlier tree (J. Fortier, personal observation). Lower pH, lower N mineralisation rate and soil decalcification/acidification are often observed in wetter soils [88]. Still, this outlier is in agreement with the idea that poplars allocate a higher proportion of biomass to coarse roots in low fertility environments. Consequently, much higher allocation to coarse root biomass than what is reported in this study may occur if hybrid poplars are grown on very low quality sites (ex: in acidic soils of clear-cut forest sites of the boreal shield ecoregion of Canada).

In this study, we have only sampled coarse root biomass located at a limited distance from the tree base, where most root biomass may be expected to provide a stability or anchorage function. This stability function may be especially important when plantation soil had been cultivated for site preparation prior to tree establishment, as was the case in this study. However, if the stability function of coarse root biomass would have been of overriding importance in the studied mature hybrid poplar trees, biomass allocation to coarse roots would have only been dependant of aboveground biomass allocation or DBH, regardless of site quality. Thus, our results contrast with those of Resh et al. [41] suggesting that only aboveground parameters of mature *Eucalyptus* need to be used to predict coarse root biomass, irrespective of fertilisation treatments or site quality. This result could be reflecting the high requirements for biomechanical stability in large *Eucalyptus* trees, or an indication of the non-plastic response of *Eucalyptus* coarse root biomass to nutritional environment.

Our results also challenge the notion that allometry of biomass allocation in plants is rarely affected by environmental features, with plant form or biomass allocation being generally the same at a given size independently of soil nutrient availability in the local environment [89, 90, 62]. Many studies have reported relationships between shoot to root ratio and environmental factors, but these relationships were often the sole consequence of allometric growth or apparent plasticity [91, 45]. This is because shoot to root ratios generally increase as plant size increases, and plants are generally smaller and more “rooty” in harsher environments, but larger and more “shooty” in more favourable environments [45, 89, 92, 93]. As shown in Fig. 5, significant relationships were observed between environmental variables and shoot to root ratios calculated using the general allometric relationship for coarse root biomass (Fig. 2), but these were the consequence of allometric growth, not plasticity. However, when the shoot to root ratio was calculated using the environment-specific allometric relationships (Fig. 3), environmental factors had a more pronounced influence on the size of the shoot to root ratio because this ratio integrates both ontogeny and environmental effects (Fig. 5). Likewise, using the environment-specific relationships for coarse root biomass also yields much wider

variations in the shoot to root ratio across plantation sites, compared to shoot to root ratios calculated using the general allometric relationship (Table 4).

In a meta-analysis on the root biomass of upland forests, Cairn *et al.* [17] found no relationship between shoot to root ratio and selected key environmental variables. In this study, shoot to root ratios of mature poplar plantations were strongly and positively correlated to several key indicators of soil fertility (Ca supply rate, clay content and base saturation; Fig. 5), with soil NO₃ availability being the best predictor of the ratio ($R^2=0.90$, $p<0.001$; Fig. 5). This provides additional evidence that N availability in soils is a key factor driving biomass partitioning towards aboveground structures to increase or maintain C fixation capacity in hybrid poplars. Strong negative correlations between soil organic matter or elevation and shoot to root ratio were also observed (Fig. 5). This trend potentially reflects the co-variation between local climate and soil fertility (Tables 1 and 2) [64], with colder sites (higher elevation) generally being characterised by slower litter decomposition [94] and N mineralisation rates, higher soil organic matter content [95] and lower soil pH (Table 1), which could have favoured biomass allocation to roots.

Biomass estimates calculated with the environment-specific relationships also suggest little variation of coarse root biomass in 13-year-old poplar plantations. With the exception of clone DxN-3570 that produced very low aboveground and coarse root biomass at the Melbourne site, coarse root biomass estimates had a similar range on moderate fertility sites (10.4–18.1 t/ha) and high fertility sites (12.1–18.5 t/ha), despite aboveground woody biomass production showing much wider variations (Table 4). Greenhouse experiments also suggest that similar root biomass was observed between hybrid poplars growing under low and high N availability, with higher shoot biomass being observed when N was more available [37, 36]. Our results are consistent with the analysis of Vicca *et al.* [85] who observed no differences in root biomass production between temperate forests growing on high and low fertility sites, despite aboveground wood production being three times higher in forests located on high soil fertility sites.

Finally, the results presented in this study have important implications for bioenergy crop models and C stock estimations because both rely on allometric equations developed for the different tree biomass compartments [16, 20, 21]. Being the largest biomass C pool after stems and branches, poplar coarse root biomass needs to be more accurately quantified [96]. Until now, only general allometric relationships had been developed for poplar coarse root biomass [24, 26, 22, 23, 19, 27, 25], with no consideration for the potential effect of plantation environment on allometric trajectory. In this study, using the general allometric relationship developed across the four sites (Fig. 2, Table 3), instead of the environment-specific relationships, would have resulted in a coarse root

biomass overestimation of 8 to 18 % on the high fertility sites (Bedford and Brompton), and an underestimation of 17 to 25 % on the moderate fertility sites (Melbourne and Ste-Catherine; Table 4). Increasing the accuracy of coarse root biomass estimates is also important for a better understanding of C cycling in the soils. Large roots have particularly slow decay rates, and they can contribute to the belowground biomass C pool over a century after harvest [97], while having a short-term positive effect on soil organic C stocks once incorporated into the soil [98]. Lastly, more accurate coarse root biomass estimates are also needed, as coarse root biomass may eventually represent a valuable bioenergy feedstock in some countries [19].

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Conflicts of Interest The authors declare that they have no conflict of interest.

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