Research paper

Quantifying the effect of nitrogen-induced physiological and structural changes on poplar growth using a carbon-balance model

Lluís Coll[1,3,5], Robert Schneider[2], Frank Berninger[3,4], Susy Domenicano[3] and Christian Messier[3]

[1]Centre Tecnològic Forestal de Catalunya (CTFC), Ctra Sant Llorenç de Morunys km. 2, 25280 Solsona, Spain; [2]Département de biologie, chimie et géographie, Université du Québec à Rimouski, Rimouski, Québec, Canada; [3]Centre d'Étude de la Forêt (CEF), Département des Sciences Biologiques, Université de Québec à Montréal, CP 8888, Montréal H3C3P8, Canada; [4]Present address: Department of Forest Sciences, PO Box 27, 00014 University of Helsinki, Finland; [5]Corresponding author (lluis.coll@ctfc.cat)

We evaluate the importance of changes in photosynthetic capacity, respiration rates, root shoot ratio, pipe model parameters and specific leaf area in the early-growth response of hybrid poplar to nitrogen availability. Juvenile growth simulations for trees with three different levels of leaf nitrogen concentration (N_{leaf}) (low (1.2%), medium (2.4%) and high (3.6%)) were conducted with the carbon-balance model CROBAS. Five-year growth simulations showed the diameter and height of poplar trees to be, respectively, four and three times larger in plants with 2.4% N_{leaf} compared with those with 1.2% N_{leaf}. Increasing N_{leaf} from 2.4 to 3.6% resulted in 34 and 16% higher diameter and height growth of trees. According to the model, changes in the photosynthetic capacity accounted for most of the differences in growth between trees with different levels of N_{leaf}; the other parameters were much less influential. This suggests that in fast-growing early-successional broadleaved species such as poplars, physiological rather than allocational and morphological traits predominate in determining growth, at least under non-limiting light conditions.

Introduction

Nitrogen (N) is the limiting element in the growth of many forests (e.g., Jug et al. 1999, van den Driessche 1999, Brown and van den Driessche 2005 for hybrid poplar). In the particular case of short-rotation crops, such as in hybrid poplar plantations, N fertilization is viewed as a key silvicultural tool to maintain adequate productivity rates in sites presenting nutrient limitations (e.g., boreal forest (DesRochers et al. 2003)). There are several mechanisms by which N may enhance growth. In many cases, the growth improvement has been attributed to the higher capacity of trees to assimilate carbon because N is involved in the regeneration of Rubisco, the primary CO_2-fixing enzyme (Evans 1983, Liu and Dickmann 1993, Coll et al. 2007). The investment of N to photosynthetic components is species specific, being in general higher in deciduous trees

than in conifers (Wullschleger 1993, Reich et al. 1995, 1999). From a physiological standpoint, N fertilization generally implies an increase in the water-use efficiency (which is primarily linked to changes in photosynthesis rates) and respiration rates of plants (Liu and Dickmann 1996, Reich et al. 1998, Harvey and Van den Driessche 1999, Ripullone et al. 2004). However, increasing N availability also induces some structural and morphological changes at the tree level such as decreases in fine root to leaf biomass ratio (Gower et al. 1992, Vanninen and Mäkelä 1999) and leaf foliage to branch basal area ratio (Berninger et al. 2005). At the leaf level, Calfapietra et al. (2005) found a close positive relationship between poplar leaf N content and specific leaf area (SLA), whereas other studies found no or inverse relationships between the two parameters (Heilman and Xie 1994, van den Driessche 1999). Leaf N content and leaf morphological parameters are known to vary at

plant level, depending on their canopy position and developmental stage (Coleman et al. 1998, Casella and Ceulemans 2002, Marron et al. 2002). For example, Al Alfas et al. (2007) found that SLA decreased with increasing canopy height whereas N concentration followed an opposite trend.

The effects of N fertilization on photosynthetic capacity and on allocation changes in trees are well documented (Liu and Dickmann 1992, Heilman and Xie 1994, Ibrahim et al. 1997, Coll et al. 2007, van den Driessche et al. 2008). However, the contribution of structural and morphological N-induced changes on tree growth is much less known. Furthermore, assessing which of the changes (physiological versus structural) is more important in determining tree growth is difficult to achieve empirically since trees will always adjust several attributes simultaneously and collinearity will make statistical inference difficult. Modelling and simulation approaches that incorporate both structure and physiology can therefore be used to independently evaluate the effect of each of these two components on tree growth. Such an approach was used, for example, to identify whether structural or functional processes are more important on sapwood and heartwood dynamics (Sievänen et al. 1997).

In this article, we used CROwn BASe, a carbon-balance model linking tree structural relationships to carbon balance (Mäkelä 1997), to understand how N-induced changes in structural and functional parameters affected tree growth. The first step consisted in determining experimentally how N influences some of the underlying allometric and physiological parameters. The second step consisted in using CROBAS to analyse the influence of N fertilization on tree growth through a sensitivity analysis, where each physiological and morphological parameter was varied according to different N levels. Analyses were restricted to juvenile hybrid poplar trees.

Materials and methods

Site description and plant material

Data were collected in three hybrid poplar (*Populus maximowiczii × balsamifera*, clone nb: 915311) plantations established during the spring of 2003 and 2004 in the province of Québec, Canada. Plantations were set up using 1 m bare-root cuttings spaced 3 m apart. Two sites were located near La Patrie (45°20′N, 71°34′W) in south-eastern Quebec and were established during May 2003 ('LaPatrie1') and 2004 ('LaPatrie2'). These sites were previously used to analyse the competition for N between the poplar trees and the competing vegetation (Coll et al. 2007). The third plantation was located near Montréal (45°25′N, 73°56′W) at McGill University Macdonald Campus ('Macdonald' hereafter). This plantation was established to follow the response of hybrid poplar to different N fertilization treatments (Domenicano et al. 2011). In the present study, we used data from the LaPatrie1 and Macdonald sites for the estimation of tree structural parameters, whereas leaf gas exchange and SLA measurements were conducted in all three sites.

Model description

The CROBAS model (Mäkelä 1997) was used to study the effect of the previously described relationships between N content and the structural and photosynthetic parameters on juvenile growth of 1 m poplar cuttings. CROBAS is a carbon-balance model that relies on functional balance (constant ratio between root and foliage biomass) and pipe model theory (Shinozaki et al. 1964) to simulate stand growth through mean tree growth. The model state variables are mean tree compartment biomasses (stem sapwood, branch sapwood, transport root sapwood, fine root sapwood and foliage) and mean tree dimensions (total height, height to crown base and crown width). These state variables can be obtained either directly from the model inputs (stand density, height, diameter at breast height (dbh) and crown length of the average tree) or from given allometric relationships (cf. Eqs (1–6) in Mäkelä 1997). Net tree growth is obtained by subtracting maintenance respiration (which is assumed to be proportional to both the biomass of each compartment and N concentration) from photosynthesis. Once net tree growth is calculated, maximum specific growth of the foliage is estimated. Foliage shedding is obtained from crown coverage, and is used to predict the actual specific growth rate of the foliage. With foliage increment known, increments of the different state variables can then be derived from allometric relationships. Mean tree growth is calculated continuously using differential equations (cf. Eqs (14–24) in Mäkelä 1997) and is thus derived from foliage biomass increment (cf. Eq. (26) in Mäkelä 1997) using allometric relationships. The model contains a large number of sapwood turnover-related parameters that are not known for poplar and do not influence juvenile growth (since no heartwood is formed). No attempt was made to estimate the values of parameters that cannot be validated without a good knowledge of root standing biomasses. These parameters (notably the parameters d, φ and S (with various sub-indices)) were left at their original Scots pine values. Full details on the model can be found in Mäkelä (1997).

Parameter estimations

Tree structure

At the end of the second growing season, the height, crown base diameter, crown length and width of 28 trees (10 from the LaPatrie1 site and 18 from the Macdonald site) were measured. Then the diameter, shortly after the branch insertion of all the tree branches, was measured using a digital calliper in perpendicular directions.

In order to characterize the relationship between branch cross-sectional area and associated supported leaves

(parameter α_b, Eq. (1)), a sub-sample of six branches per tree was selected randomly and all the leaves were dried and weighed.

The effect of N on branch basal area to foliage biomass was assessed with a linear regression:

$$\alpha_b = \frac{\overline{W}_f}{\overline{A}_b} = \beta_0 + \beta_1 \cdot N_{leaf} + \varepsilon \tag{1}$$

where α_b is the pipe model parameter, $\overline{A}_b$ the mean branch basal area of six sampled branches per tree, $\overline{W}_f$ the mean tree foliage biomass of six sampled branches per tree, N_{leaf} the leaf N concentration, β_0 and β_1 the regression parameters and ε the model error.

The 18 trees from the Macdonald site (mean basal diameter: 7.3 cm; mean height: 4.1 m) were then harvested and the rest of the foliage was also sampled, dried and weighed to obtain the ratio between cross-sectional area at crown base and total foliage weight of the tree (parameter α_s, Eq. (2a)). Finally, the base of each tree was excavated by hand using various digging tools until all the transport roots were visible, and the diameter of each transport root at the stump was then measured with a digital calliper in perpendicular directions. These data were used to estimate the ratio between the cross-sectional area of transport roots and foliage weight (parameter α_t, Eq. (2b)). These parameters were found to be insensitive to leaf N content and were estimated using a linear model:

$$W_f = \alpha_s \cdot A_s + \varepsilon \tag{2a}$$

$$W_f = \alpha_t \cdot A_t + \varepsilon \tag{2b}$$

where W_f is the total tree foliage biomass, A_s the cross-sectional area at crown base, A_t the cross-sectional area of transport roots, and α_s and α_t the estimated model parameters.

Finally, the density and fractal dimensions of the crown were estimated through a linear regression:

$$\ln(W_f) = \beta_0 + z\ln(A_c) + \varepsilon \tag{3}$$

where z is the crown fractal dimension (allometric exponent between vertical projected area and foliage weight), A_c is the vertical projected area of the crown assuming it was elliptical and β_0 is used to calculate the crown density ($\Xi = e^{\beta_0}$).

At the LaPatrie1 site, 36 trees (mean basal diameter: 1.6 cm; mean height: 2.6 m) were harvested at the end of their second growing season (2004) for estimation of the fine root biomass:leaf biomass ratio (parameter α_r, Eq. (4)). The trees were subjected to different weed controls during the two growing seasons (herbicides, mechanical discing and untreated), which led to different levels of foliar N content (Coll et al. 2007). The trees were carefully dug out by hand to prevent breaking the roots and were cool-stored at 5 °C prior to processing in the laboratory. Leaves and fine roots (diameter <2 mm) were then collected and weighed after being oven-dried at 70 °C for 96 h.

As with the branch basal area to foliage biomass ratio, the influence of foliar N content on the functional-balance parameter was established through a linearized exponential function:

$$\ln\alpha_r = \ln\left(\frac{W_r}{W_f}\right) = \beta_0 + \beta_1 \cdot N_{leaf} + \varepsilon \tag{4}$$

where W_r is fine root biomass and W_f is tree foliage biomass.

Tree physiology

The leaf gas exchange of 195 trees from all three sites was measured during August 2004 and 2005 with a portable leaf chamber system (LI-6400; Li-Cor, Lincoln, NE, USA). Measurements were conducted between 10:00 and 14:00 on sunny days. For each tree, steady-state net photosynthetic rates at light saturation (A_{max}) and leaf intercellular CO_2 concentration (C_i) were measured in one mature leaf taken from the upper part of the canopy. For A_{max} and C_i determination, light and CO_2 in the chamber were maintained at 1500 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR) and 360 ppm, respectively, while leaf temperature was set at 25 °C. After the measurements, the leaves were collected and scanned. Leaf area was determined using the Macfolia software package (Régent Instruments, Québec, Canada). From a sub-set of two leaves, we obtained a full leaf photosynthesis curve and fitted a rectangular hyperbola through the data. Once oven-dried, leaf N concentration (N_{leaf}, %) was determined following the Kjeldahl digestion method (Kjeltec Tecator 1030). The same method was used to analyse the foliage N content of the trees used in the structural and biomass assessments. Nitrogen content analysis was carried out in a sub-set of 10 different leaves taken from the upper part of the plant.

The SLA (cm^2 g^{-1}) of each individual leaf was calculated as the dry mass to one-sided leaf area ratio. SLA and A_{max} were related to foliar N content using a linear regression:

$$Y = \beta_0 + \beta_1 \ln\left(N_{leaf}\right) + \varepsilon \tag{5}$$

where Y is either SLA or A_{max}.

Annual photosynthesis was calculated assuming that the response of photosynthesis to light can be represented by a rectangular hyperbola. Since we lacked information on the development of leaf photosynthetic capacity over the season, we assumed that photosynthesis has maximum capacity and started when leaves had attained half of their maximal size (June 10) and terminated on 1 September (when many leaves were rapidly turning yellow) (based on the data of L. Coll unpublished). The maximal photosynthesis for an entirely exposed leaf was calculated using hourly irradiance data from

a nearby weather station (Plattsburgh, NY, USA, data coming from the National Solar Radiation Data Base, National Renewable Energy Laboratory 2007). We assumed that there is a conversion factor of 2 (μmol s^{-1} W^{-1}) between irradiance (W m^{-2}) and photosynthetic active photon flux density (μmol m^{-2} s^{-1}), which is within the range of the values given by Hu et al. (2007) and which we considered realistic given the humid summer climate in Montréal. Photosynthesis was assumed to reach half of its capacity at a PAR value of 451 μmol m^{-2} s^{-1} (estimated from field measurements). Our analysis of environmental data indicated that neither soil water deficit nor vapour pressure deficit were important limitations to photosynthesis. To calculate the parameter P_0, which is the annual photosynthetic production of a thick (leaf area saturated) canopy, we assumed that light in a canopy decreases according to the Lambert–Beer law. We used a light extinction coefficient of 0.15 (lower than those reported in previous studies for poplar (e.g., Ceulemans et al. 1996) because our analysis was limited to an early phase of stand development) that was corrected for the openness of the canopy (with a final canopy cover between 0.26 and 0.3).

For the simulations we separated the effects of a gravimetric increase in photosynthetic capacity (g C g^{-1} leaf) from a change in SLA by making the maximum photosynthetic production (P_0) dependent on the photosynthetic capacity (A_{max}) and the decrease of P_0 with shading dependent on the changes in SLA.

Model simulations

Of all the model parameters determined from measurements in the field, four were functions of leaf N content: foliage biomass ratio to branch basal area (α_b, Eq. (1)), fine root to foliage biomass ratio (α_r, Eq. (4)), SLA (Eq. (5)) and maximum rate of canopy photosynthesis per unit leaf area (A_{max}, Eq. (5)) (Table 1). In addition, the specific respiration rates (Resp) of active tissues and xylem tissues were assumed to be proportional to the leaf N concentration according to Ryan (1995). Yearly respiration was modelled as 0.13 g DM/g DM × N concentration (%) for active and inactive parts of the tree alike excluding growth respiration. The other parameters used in

the simulations can be found in Appendix 1. The simulations were set up with three different levels of foliar N: low (1.2% N_{leaf}), medium (2.4% N_{leaf}) and high (3.6% N_{leaf}). The simulations were then run as follows: a first set of simulations was carried out (i) with all the N-dependent parameters set to the N_{leaf} level and (ii) with all parameters set at 2.4% (baseline) but only one N-dependent parameter changed to the next (3.6%) or previous (1.2%) level (e.g., N_{leaf} set at 2.4% for all the parameters, except for α_b where N_{leaf} was set at 1.2%). The effects of each N-dependent parameter on 5-year model tree growth output were then compared to identify which parameter had the most effect.

Results

Parameter estimates

For the N-independent parameters, strong allometric relationships were observed (Table 1), with the proportion of explained variance (R^2) ranging between 0.7 and 0.9. The estimates indicate that there was more foliage biomass per stem cross-sectional area than per transport root cross-sectional area ($\alpha_s > \alpha_t$). Moreover, the crown surface area density of the hybrid poplar was 0.0171 kg m^{-z}, with z being the fractal dimension calculated as 2.03.

Branch cross-sectional area (α_b), maximum rate of canopy photosynthesis per unit leaf area (A_{max}), fine root to foliage biomass ratio (α_r) and SLA were significantly correlated with N leaf content (Table 1, Figure 1). More specifically, both structural parameters (α_b, α_r) decreased with increasing foliage N content. In other words, branch basal area was proportional to N concentration for a given level of foliage biomass, whereas the fine root biomass was proportional to foliar N concentration for the same foliage biomass. Conversely, photosynthesis and SLA were both proportional to foliar N content. Moreover, SLA showed high variability, with values ranging between 70 and 120 cm^2 g^{-1}.

Effect of N content on tree growth using CROBAS

Five-year simulations of poplar growth and development show that tree growth significantly increases with foliar N

Table 1. Parameter estimates (standard errors in parentheses) and fit statistics for Eqs (1–5) (all parameters are highly significant, i.e., $P < 0.0001$).

| Equation Parameter (code, mean, SE)	Nitrogen invariant				Nitrogen dependent							
	Equation (2a)	Equation (2b)	Equation (3)		Equation (1)		Equation (4)		Equation (5) (SLA)		Equation (5) (P_0)	
	α_s	α_t	β_0	z	β_0	β_1	β_0	β_1	β_0	β_1	β_0	β_1
	322.01 (13.39)	187.44 (6.92)	−4.07 (0.67)	2.04 (0.32)	283.53 (14.93)	−29.34 (5.35)	−0.71 (0.31)	−0.72 (0.18)	91.05 (0.99)	14.06 (1.81)	11.18 (0.24)	12.56 (0.43)
R^2	0.97	0.97	0.72		0.55		0.31		0.24		0.84	
RMSE	0.25	0.22	0.19		24.26		0.50		9.11		2.06	

RMSE, root mean square error.
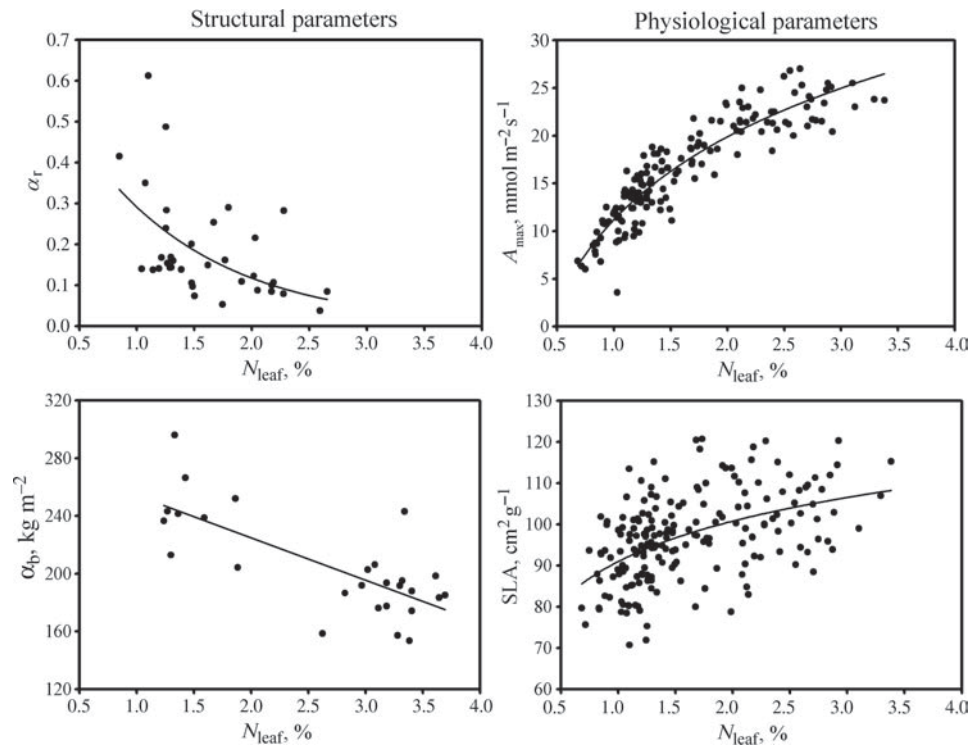
Figure 1. Effect of foliar N concentration on structural (α_b, foliage biomass to branch basal area ratio; α_r, fine root biomass to foliage biomass ratio) and physiological parameters (A_{max}, maximum steady-state net photosynthetic rates at light saturation; SLA, specific leaf area).
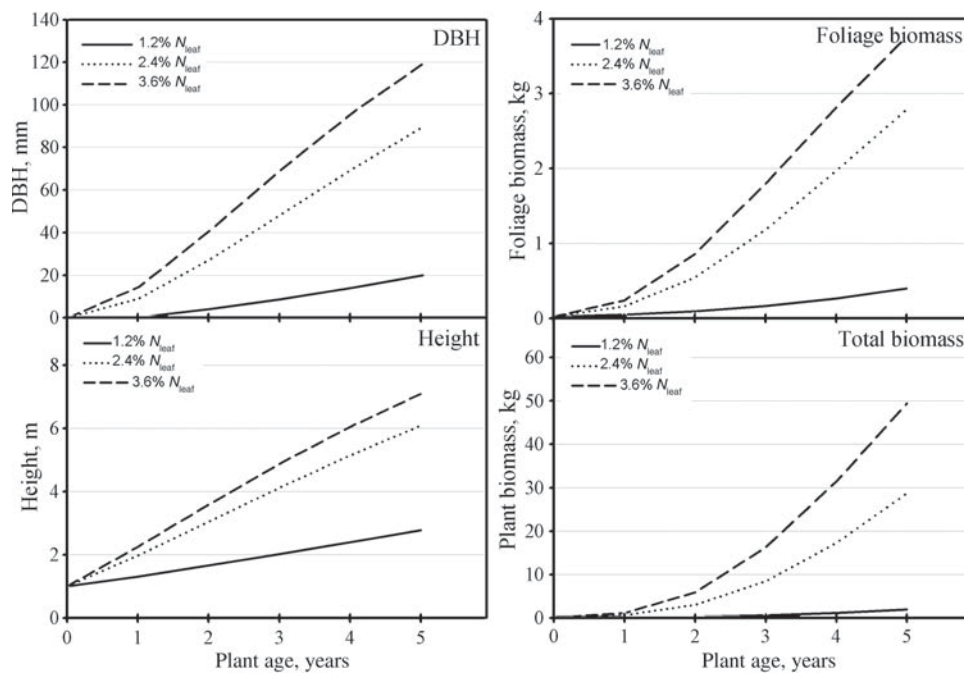

Figure 2. CROBAS predictions for juvenile hybrid poplar growth.

concentration (Figure 2). After 5 years, trees with 3.6% N_{leaf} were 34% larger in diameter (11.9 versus 8.9 cm) and 16% taller than trees with 2.4% N_{leaf} (7.1 versus 6.1 m). More importantly, the diameter and height differences between the 1.2% N_{leaf} and the 2.4% N_{leaf} trees were much greater than

those between the 2.4% N_{leaf} and the 3.6% N_{leaf} trees. Model simulations showed that after 5 years of growth, plants with 2.4% N_{leaf} have a diameter and height 4.5–3 times larger than those with 1.2% N_{leaf}. Foliage and total plant biomass followed the same pattern (Figure 2). The leaf to total plant
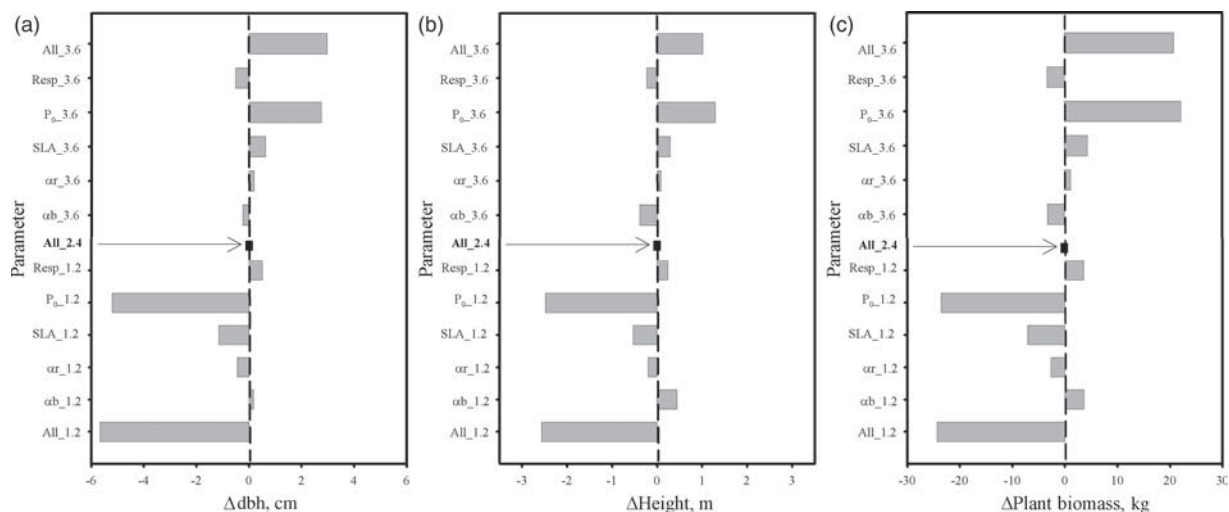
Figure 3. Individual effects of N-dependent parameter changes in different tree variables: (a) diameter at breast height, (b) total height and (c) total tree biomass. The bars show the increment or decrease of the variables when each individual parameter (y-axis) was entered in the model with its value corresponding to the next N_{leaf} level (>3.6% or <1.2%), while maintaining the rest of the parameters to the baseline level (2.4%). Parameter abbreviations are as in text.

biomass ratio is predicted to decrease with plant size for all N_{leaf} levels. The changes in different model outputs after a 5-year growth period between different foliar N levels are presented in Figure 3. According to model predictions, changes in the photosynthetic capacity of the tree due to increased N concentrations in the leaf account for most differences between the different levels of N_{leaf}. N-induced changes in SLA also had a positive influence on yield, but to a much lesser extent. Both structural parameters had very little impact on tree growth, where N-induced changes in α_r had a slightly positive effect on growth, and in α_b a slightly negative impact on growth. However, these effects and the increase in respiration rates with N concentration are negligible when compared with the positive effect of N-induced changes in A_{max}.

Discussion

As expected, the N status of poplar trees strongly affected several physiological and structural parameters. These changes were not restricted to the root:shoot ratio, the only parameter used by Mäkelä (1997) to modify model behaviour for different site conditions, but also to parameters that we would not have expected to change. It is noteworthy that Mäkelä (1997) designed CROBAS for Scots pine, where the response of photosynthetic capacity to N is not very strong (Vapaavuori et al. 1995).

We obtained close correlations between the crown base cross-sectional area of trees and foliage mass, branch and root area, showing that the pipe model theory (Shinozaki et al. 1964) is a good approximation of tree structure for our data. Tight allometric relationships between the aerial and belowground compartments of trees are common in the scientific literature (Brown et al. 1989, Salas et al. 2004, Coll et al. 2008, Schneider et al. 2008). We found that foliage biomass supported by a branch of a given area decreased with the mean N_{leaf} of the plant. Very little research has been conducted on the effect of site quality on these allometric relationships. However, Berninger et al. (2005) reported a similar trend in *Pinus sylvestris* trees. This may reflect a compensatory effect of plants in response to the increase in carbon in their foliage, which they experience under non-limiting nutrient conditions (Schäfer et al. 2002). Our results indicate that changes occur in the leaf water relations because stomatal conductance (data not shown) and SLA increase with increasing N concentration. These observed changes in tree structure could reflect an acclimation of plants to the higher water demand of the foliage. Our results agreed with the functional-balance hypothesis that claims dependence of root activity (mainly nutrient and water uptake) on leaf activity (mainly carbon assimilation) (Brouwer 1962). The ratio between fine roots and leaf biomass of poplar plants increased in response to low foliage N concentration, as has been reported in past studies for other species (Keyes and Grier 1981, Beets and Whitehead 1996, Vanninen and Mäkelä 1999). However, this response could be driven by the accelerated development of trees promoted by N availability since this ratio has been found to decrease ontogenically in poplar trees (Coleman et al. 2004, Coyle and Coleman 2005, Coll et al. 2007). At the leaf level, poplar trees presented a positive correlation between N_{leaf} and both SLA and A_{max}. These relationships hold for many species (Wright et al. 2004) and have been reported in previous studies with different *Populus* species and clones (Curtis et al. 2000, Calfapietra et al. 2005, Coll et al. 2007).

We used both empirical data and the CROBAS model to simulate the first 5-year growth of hybrid poplar plants with different leaf N status. The model was used as a carbon and allocation bookkeeping tool. Our data were all derived using young plants and we did not use many parameters that might be of importance in the long run (e.g., processes like sapwood turnover). Since the simulated stands refer to even-aged plantations, the model assumption of horizontal homogeneity ought to hold (Mäkelä 1997).

Simulated plant height increased linearly over the first years, whereas diameter growth followed an exponential trend. During the first year, small increments in diameter are probably associated with the fact that roots are not yet well developed (Coll et al. 2004, Deckmyn et al. 2004). Juvenile growth simulations of trees with different N_{leaf} values diverged considerably. Those differences were particularly noticeable between trees with 1.2% and those with 2.4% N_{leaf} confirming the rapid reaction of poplars to fertilization, particularly to N (Liu and Dickmann 1992, Heilman and Xie 1994). The simulated tree growth reaction with increasing N status from 2.4 to 3.6 mg g^{-1} was moderate and may respond to the existing logarithmic relationship between N_{leaf} and the maximum carbon assimilation capacity (A_{max}) of leaves (Evans 1983, Coll et al. 2007). Increases in respiration decreased somewhat the total growth of trees, but changes in photosynthesis dominated the growth response. Simulated 5-year diameter and height growth of poplar clones were within the range of those presented for comparable studies (Stettler et al. 1988, Zhang et al. 2003, van den Driessche et al. 2008). The model slightly over- and underestimated diameter and height growth for, respectively, medium and high leaf N levels (data not shown). However, adequate validation of the model from hybrid poplar fertilization trials was not possible since completely independent data were not available (and trees in our sites did not all present the same N_{leaf} values as the ones used in our simulations). In addition, comparisons of simulated results and available data from the three sites used in this paper would not give enough insight into validity of a mean stand model such as CROBAS.

The CROBAS simulations suggested that the positive relationship between N_{leaf} and A_{max} is the main factor explaining tree growth and biomass increases with N fertilization, whereas allocation and structural parameters played a much smaller role. Fast-growing early-successional species such as poplars are known to present high photosynthetic rates and to rapidly respond to resource availability changes (Bazzaz 1979). These species are able to incorporate N more efficiently in compounds involved in photosynthesis (i.e., leaves) compared with slow-growing ones, and are then able to rapidly increase their biomass (Poorter 1989). The response of photosynthetic capacity to increase in N concentrations confirms earlier results (Evans 1989). There is evidence that the slope of this regression is much lower for evergreen conifers than for broadleaves

(Reich et al. 1995). For example, Ripullone et al. (2004) found the increment of carbon assimilation rate with N to be threefold higher in poplar than in Douglas fir. The other N-dependent parameters had only relatively small effects on simulated growth. The smaller effects of SLA on growth were due to the fact that photosynthesis was defined on a per ground area and per leaf mass basis. Therefore, changes in SLA affected only the shading inside the canopy. Since poplar stands have typically low leaf area indices (Gielen et al. 2001), the effects of mutual shading on canopy photosynthesis are probably limited. The fact that CROBAS calculates photosynthesis on a leaf mass basis can lead to an underestimation of the effect of SLA on the growth response of plants to N. The use of individual functional–structural plant models that explicitly take into account the spatial distribution of leaves (see Godin and Sinoquet 2005, Delagrange et al. 2006) would probably be more appropriate to accurately analyse the above-mentioned dependencies.

Increasing the foliage to root mass ratio with N_{leaf} slightly increased tree growth, but its effect was small compared with the effect associated with A_{max}.

As a summary, the results of the model predicted that physiological traits rather than allocational and morphological traits predominate in determining poplar plant growth. This agrees with the findings of Poorter (1999), who found net assimilation rate to be the main factor explaining growth differences among a number of tree species under high–light conditions. In addition, simulations indicated that the contribution of the different parameters modulated by N_{leaf} on plant growth was additive. In other words, the differences between the simulations with one N level and another are approximated by the sum of the effects of each N-varying parameter taken individually. There seems to be very little interaction between each parameter. This additivity is an interesting emerging property of model simulations, since mechanisms for interactive effects are built into CROBAS. For example, photosynthetic production depends on foliage biomass, photosynthetic capacity and SLA. Foliage biomass, on the other hand, is determined to a large extent by allocation to new foliage, which depends on plant size, pipe model parameters and allocation to fine roots. If this additivity is confirmed in further studies, it would facilitate our understanding of the effects of fertilization since more simple models could be used.

This study constitutes a first attempt to analyse independently the role played by different morphological and physiological parameters modulated by N_{leaf} on hybrid poplar growth. The model gives us the opportunity to understand the relative importance of the different acclimation of plant functioning and structure to N. Furthermore, the relationships that underlie the model (i.e., the pipe model and functional balance) are solid and seem to be consistent across treatments. Hence, the model acts more as a 'simple carbon-tracking tool'. We suggested that

physiological responses to N fertilization are much more important in affecting poplar tree growth than structural changes when light is not limiting. The effects of parameter changes are additive, showing that simple models might be used to estimate short-term effects of changes in plant nutrition.

Acknowledgments

Funding

References

Al Alfas, N., N. Marron and R. Ceulemans. 2007. Variability in *Populus* leaf anatomy and morphology in relation to canopy position, biomass production, and varietal taxon. Ann. For. Sci. 64:521–532.

Bazzaz, F.A. 1979. Physiological ecology of plant succession. Annu. Rev. Ecol. Syst. 10:351–371.

Beets, P.N. and D. Whitehead. 1996. Carbon partitioning in *Pinus radiata* stands in relation to foliage nitrogen status. Tree Physiol. 16:131–138.

Berninger, F., L. Coll, P. Vanninen, A. Mäkelä, S. Palmroth and E. Nikinmaa. 2005. Effects of tree size and position on pipe model ratios in Scots pine. Can. J. For. Res. 35:1294–1304.

Brouwer, R. 1962. Nutritive influences on the distribution of dry matter in the plant. Neth. J. Agric. Sci. 10:399–408.

Brown, K.R. and R. van den Driessche. 2005. Effects of nitrogen and phosphorus fertilisation on the growth and nutrition of hybrid poplars on Vancouver Island. New For. 29:89–104.

Brown, S., A.J.R. Gillespie and A.E. Lugo. 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. For. Sci. 35:881–902.

Calfapietra, C., I. Tulva, E. Eensalu, M. Perez, P. De Angelis, G. Scarascia-Mugnozza and O. Kull. 2005. Canopy profiles of photosynthetic parameters under elevated CO_2 and N fertilisation in a poplar plantation. Environ. Pollut. 137:525–535.

Casella, E. and R. Ceulemans. 2002. Spatial distribution of leaf morphology and physiological characteristics in relation to local radiation regime within the canopies of 3-year-old *Populus* clones in coppice culture. Tree Physiol. 22:1277–1288.

Ceulemans, R., A.J.S. McDonald and J.S. Pereira. 1996. A comparison among eucalypt, poplar and willow characteristics with particular reference to a coppice, growth-modelling approach. Biomass Bioenergy 11:215–231.

Coleman, M.D., R.E. Dickson and J.G. Isebrands. 1998. Growth and physiology of aspen supplied with different fertilizer addition rates. Physiol. Plant. 103:513–526.

Coleman, M., A.L. Friend and C.C. Kern. 2004. Carbon allocation and nitrogen acquisition in a developing *Populus deltoides* plantation. Tree Physiol. 24:1347–1357.

Coll, L., P. Balandier and C. Picon-Cochard. 2004. Morphological and physiological response of beech (*Fagus sylvatica*) seedlings to grass-induced belowground competition. Tree Physiol. 24:45–54.

Coll, L., C. Messier, S. Delagrange and F. Berninger. 2007. Growth, allocation and leaf gas exchanges of hybrid poplar plants in their establishment phase on previously forested sites: effect of different vegetation management techniques. Ann. For. Sci. 64:275–285.

Coll, L., C. Potvin, C. Messier and S. Delagrange. 2008. Root architecture and allocation patterns of eight native tropical species with different successional status used in open-grown mixed plantations in Panama. Trees 22:585–596.

Coyle, D.R. and M.D. Coleman. 2005. Forest production responses to irrigation and fertilisation are not explained by shifts in allocation. For. Ecol. Manage, 208:137–152.

Curtis, P.S., C.S. Vogel, X. Wang, K.S. Pregitzer, D.R. Zak, J. Lussenhop, M. Kubiske and J.A. Teeri. 2000. Gas exchange, leaf nitrogen, and growth efficiency of *Populus tremuloides* in a CO_2-enriched atmosphere. Ecol. Appl. 10:3–17.

Deckmyn, G., I. Laureysens, J. Garcia, B. Muys and R. Ceulemans. 2004. Poplar growth and yield in short rotation coppice: model simulations using the process model SECRETS. Biomass Bioenergy 26:221–227.

Delagrange, S., P. Montpied, E. Dreyer, C. Messier and H. Sinoquet. 2006. Does shade improve light interception efficiency? A comparison among seedlings from shade-tolerant and -intolerant temperate deciduous tree species. New Phytol. 172:293–304.

DesRochers, A., R. van den Driessche and B.R. Thomas. 2003. Nitrogen fertilization of trembling aspen seedlings grown on soils of different pH. Can. J. For. Res. 33:552–560.

Domenicano, S., L. Coll, C. Messier and F. Berninger. 2011. Nitrogen forms affect root structure and water uptake in the hybrid poplar. New For. doi:10.1007/s11056-011-9256-x.

Evans, J.R. 1983. Nitrogen and photosynthesis in the flag leaf of wheat (*Triticum aestivum*). Plant Physiol. 72:297–302.

Evans, J.R. 1989. Photosynthesis and nitrogen relationship in leaves of C3 plants. Oecologia 78:9–19.

Gielen, B., C. Calfapietra, M. Sabatti and R. Ceulemans. 2001. Leaf area dynamics in a closed poplar plantation under free-air carbon dioxide enrichment. Tree Physiol. 21:1244–1255.

Godin, C. and H. Sinoquet. 2005. Functional–structural plant modelling. New Phytol. 166:717–722.

Gower, S.T., K.A. Vogt and C.C. Grier. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: influence of water and nutrient availability. Ecol. Monogr. 62:43–65.

Harvey, H.P. and R. van den Driessche. 1999. Nitrogen and potassium effects on xylem cavitation and water-use efficiency in poplars. Tree Physiol. 19:943–950.

Heilman, P.E. and F.G. Xie. 1994. Effects of nitrogen fertilization on leaf area, light interception, and productivity of short-rotation *Populus trichocarpa* × *Populus deltoides* hybrids. Can. J. For. Res. 24:166–173.

Hu, B., Y. Wang and G. Liu. 2007. Spatiotemporal characteristics of photosynthetically active radiation in China. J. Geophys. Res. 112:D14106.

Ibrahim, L., M.F. Proe and A.D. Cameron. 1997. Main effects of nitrogen supply and drought stress upon whole-plant carbon allocation in poplar. Can. J. For. Res. 27:1413–1419.

Jug, A., C. Hofmann-Schielle, F. Makeschin and K.E. Rehfuess. 1999. Short-rotation plantations of balsam poplars, aspen and willows on former arable land in the Federal Republic of Germany. II. Nutritional status and bioelement export by harvested shoot axes. For. Ecol. Manage. 131:67–83.

Keyes, M.R. and C.C. Grier. 1981. Above- and belowground net production in 40-year-old Douglas fir stands on low and high productivity sites. Can. J. For. Res. 11:599–605.

Liu, Z. and D.I. Dickmann. 1992. Responses of two hybrid *Populus* clones to flooding, drought, and nitrogen availability. I. Morphology and growth. Can. J. Bot. 70:2265–2270.

Liu, Z. and D.I. Dickmann. 1993. Responses of two hybrid *Populus* clones to flooding, drought, and nitrogen availability. II. Gas exchange and water relations. Can. J. Bot. 71:927–938.

Liu, Z. and D.I. Dickmann. 1996. Effects of water and nitrogen interactions on net photosynthesis, stomatal conductance, and water-use efficiency in two hybrid poplar clones. Physiol. Plant. 97:507–512.

Mäkelä, A. 1997. A carbon balance model of growth and self-pruning in trees based on structural relationships. For. Sci. 43:7–24.

Marron, N., E. Dreyer, E. Boudouresque, D. Delay, J.-M. Petit, F.M. Delmotte and F. Brignolas. 2002. Physiological traits of two *Populus × euramericana* clones, Luisa Avanzo and Dorskamp, during a water stress and re-watering cycle. Tree Physiol. 22:849–858.

Nadelhoffer, K.J., J.D. Aber and J.M. Melillo. 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. Ecology 66:1377–1390.

National Renewable Energy Laboratory. 2007. National Solar Radiation Database 1991–2005 Update: User's Manual Technical Report NREL/TP-581–41364. 374 p.

Oker-Blom, P. 1986. Photosynthetic radiation regime and canopy structure in modeled forest stands. Acta For. Fenn. 197: 44 p.

Penning de Vries, F. W. T. 1974. Substrate utilization and respiration in relation to growth and maintenance in higher plants. Neth. J. Agric. Sci. 22:40–44.

Pliura, A., S.Y. Zhang, J. Mackay and J. Bousquet. 2007. Genotypic variation in wood density and growth traits of poplar hybrids at four clonal trials. For. Ecol. Manage. 238:92–106.

Poorter, H. 1989. Interspecific variation in relative growth rate: on ecological causes and physiological consequences. *In* Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants. Eds. H. Lambers, M.L. Cambridge, H. Konings and T.L. Pons. SPB Academic Publishing, The Hague, pp 45–68.

Poorter, L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. Funct. Ecol. 13:396–410.

Pregitzer, K.S., D.R. Zak, P.S. Curtis, M.E. Kubiske, J.A. Teeri and C.S. Vogel. 1995. Atmospheric CO_2, soil nitrogen and turnover of fine roots. New Phytol. 129:579–585.

Reich, P.B., B.D. Kloeppel, D.S. Ellsworth and M.B. Walters. 1995. Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. Oecologia 104:24–30.

Reich, P.B., M.B. Walters, M.G. Tjoelker, D. Vanderklein and C. Buschena. 1998. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. Funct. Ecol. 12:395–405.

Reich, P.B., D.S. Ellsworth, M.B. Walters, J.M. Vose, C. Gresham, J.C. Volin and W.D. Bowman. 1999. Generality of leaf trait relationships: a test across six biomes. Ecology 80:1955–1969.

Ripullone, F., M. Lauteri, G. Grassi, M. Amato and M. Borghetti. 2004. Variation in nitrogen supply changes water-use efficiency of *Pseudotsuga menziesii* and *Populus × euroamericana*; a comparison of three approaches to determine water-use efficiency. Tree Physiol. 24:671–679.

Ryan, M.G. 1995. Foliar maintenance respiration of subalpine and boreal trees and shrubs as a function of leaf nitrogen-content. Plant, Cell Environ. 18:565–572.

Salas, E., H. Ozier-Lafontaine and P. Nygren. 2004. A fractal root model applied for estimating the root biomass and architecture in two tropical legume tree species. Ann. For. Sci. 61:337–345.

Schäfer, K.V.R., R. Oren, L. Chun-Ta and G.G. Katul. 2002. Hydrologic balance in an intact temperate forest ecosystem under ambient and elevated atmospheric CO2 concentration. Glob. Change Biol. 8:895–911.

Schneider, R., F. Berninger, C.H. Ung, P.Y. Bernier, D.E. Swift and S.Y. Zhang. 2008. Calibrating jack pine allometric relationships with simultaneous regressions. Can. J. For. Res. 38:2566–2578.

Shinozaki, K., K. Yoda, K. Hozumi and T. Kira. 1964. A quantitative analysis of plant form: the pipe model theory. I. Basic analyses. Jpn. J. Ecol. 14:97–105.

Sievänen, R., E. Nikinmaa and J. Perttunen. 1997. Evaluation of importance of sapwood senescence on tree growth using the model LIGNUM. Silva Fenn. 31:329–340.

Stettler, R.F., R.C. Fenn, P.E. Heilman and B.J. Stanton. 1988. *Populus trichocarpa × Populus deltoides* hybrids for short rotation culture: variation patterns and 4-year field performance. Can. J. For. Res. 18:745–753.

Tuskan, G.A. and M.E. Walsh. 2001. Short-rotation woody crop systems, atmospheric carbon dioxide and carbon management: a US case study. Forest. Chron. 77:259–264.

van den Driessche, R. 1999. First-year growth response of four *Populus trichocarpa × Populus deltoides* clones to fertilizer placement and level. Can. J. For. Res. 29:554–562.

van den Driessche, R., B.R. Thomas and D.P. Kamelchuk. 2008. Effects of N, NP, and NPKS fertilizers applied to four-year old hybrid poplar plantations. New For. 35:221–233.

Vanninen, P. and A. Mäkelä. 1999. Fine root biomass of Scots pine stands differing in age and soil fertility in southern Finland. Tree Physiol. 19:823–830.

Vapaavuori, E.M., A.H. Vuorinen, P.J. Aphalo and H. Smolander. 1995. Relationship between net photosynthesis and nitrogen in Scots pine: seasonal variation in seedlings and shoots. Plant Soil 168–169:263–270.

Wright, I.J., P.B. Reich, M. Westoby, *et al.* 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Wullschleger, S.D. 1993. Biochemical limitations to carbon assimilation in C3 plants—a retrospective analysis of the A/Ci curves from 109 species. J. Exp. Bot. 44:907–920.

Yoder, B.J., M.G. Ryan, R.H. Waring, A.W. Schoettle and M.R. Kaufmann. 1994. Evidence of reduced photosynthetic rate in old trees. For. Sci. 40:513 -527.

Zhang, S.Y., Q. Yin, G. Chauret and A. Koubaa. 2003. Selection for both growth and wood properties in hybrid poplar clones. For. Sci. 49:901–908.

Appendix 1. Parameter values used for poplar simulations using the CROBAS model

Parameter	Description	Source	Value	Units
φ_s	Form factor of sapwood below crown	As implied by the pipe model (Mäkelä 1997)	1	
φ_c	Form factor of sapwood in stem within crown	As suggested by Mäkelä (1997) for conical form	0.75	
φ_b	Form factor of sapwood in branches	As guessed by Mäkelä (1997)	0.75	

Continued

Appendix 1 Continued

Parameter	Description	Source	Value	Units
φ_t	Form factor of sapwood in transport roots	As suggested by Mäkelä (1997) for absence of heartwood in coarse roots	1	
c_b	Ratio of crown radius to crown length	From data used in this study	0.28	
C_t	Ratio of transport root length to stem length	As suggested by Mäkelä (1997)	1	
ρ_s	Wood density of stem	Pliura et al. (2007)	300	kg m^{-3}
ρ_b	Wood density of branches	Pliura et al. (2007)	300	kg m^{-3}
ρ_t	Wood density of transport roots	Pliura et al. (2007)	300	kg m^{-3}
Y	Carbon-use efficiency	C% DW = 0.45 (Tuskan and Walch 2001) + 0.15 (Penning de Vries 1974)	0.60	kg C kg^{-1} DW^{-1}
S_f	Specific senescence rate of foliage	Poplar is a deciduous tree	1	year^{-1}
S_r	Specific senescence rate of fine roots	Estimated from Nadelhoffer et al. (1985) and Pregitzer et al. (1995)	1	year^{-1}
d_{s0}	Specific sapwood area turnover rate per unit relative pruning for stem	By definition as presented in Mäkelä (1997)	1	
d_{b0}	Specific sapwood area turnover rate per unit relative pruning for branches	By definition as presented in Mäkelä (1997)	1	
d_{t0}	Specific sapwood area turnover rate per unit relative pruning for transport roots	By definition as presented in Mäkelä (1997)	1	
d_{s1}	Specific sapwood area turnover rate in case of no pruning for stem	As guessed by Mäkelä (1997)	0.01	year^{-1}
d_{b1}	Specific sapwood area turnover rate in case of no pruning for branches	As guessed by Mäkelä (1997)	0.01	year^{-1}
d_{t1}	Specific sapwood area turnover rate in case of no pruning for transport roots	As guessed by Mäkelä (1997)	0.01	year^{-1}
ψ_s	Form factor of senescent sapwood in stem below crown	As implied by the pipe model (Mäkelä 1997)	1	
ψ_c	Form factor of senescent sapwood in stem inside crown	As guessed by Mäkelä (1997)	0.5	
ψ_b	Form factor of senescent sapwood in branches	As guessed by Mäkelä (1997)	0.9	
ψ_t	Form factor of senescent sapwood in transport roots	As suggested by Mäkelä (1997) for absence of heartwood in coarse roots	0	
a_σ	Decrease in photosynthesis per unit crown length	Yoder et al. (1994)	0.02	m^{-1}
K	Extinction coefficient	Oker-Blom (1986)	0.18	
Q	Degree of control by crown coverage of self-pruning	As suggested by Mäkelä (1997) and confirmed through trial and error	1	
P	Degree of control by crown coverage of mortality	As suggested by Mäkelä (1997) and confirmed through trial and error	5	
α_q	Parameter related to self-pruning	As suggested by Mäkelä (1997) and confirmed through trial and error	0.5	
m_0	Specific mortality rate independent of density	As suggested by Mäkelä (1997) and confirmed through trial and error	0.001	year^{-1}
m_1	Density-dependent mortality parameter	As suggested by Mäkelä (1997) and confirmed through trial and error	0.01	year^{-1}