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

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29 **Keywords:** hybrid poplar, growth, photosynthesis, functional balance hypothesis, pipe
30 model ratios, carbon-balance model

31 **Running head:** Unraveling N-induced changes in poplar growth
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34

35 **Summary**

36

37 We evaluate the importance of changes in the photosynthetic capacity, respiration rates,
38 root shoot ratio, pipe model parameters and specific leaf area in the early-growth
39 response of hybrid poplar to nitrogen availability. Juvenile growth simulations for trees
40 with 3 different levels of leaf nitrogen concentration (N_{leaf}): low (1.2%), medium
41 (2.4%) and high (3.6%) were conducted with the carbon-balance model CROBAS.
42 Five-year growth simulations showed diameter and height of poplar trees to be
43 respectively four and three times larger in plants with 2.4% N_{leaf} compared to those with
44 1.2% N_{leaf} . Increasing N_{leaf} from 2.4 to 3.6% resulted in 34% and 16% higher diameter
45 and height growth trees. According to the model, changes in the photosynthetic capacity
46 accounted for most of the differences in growth between trees with different levels of
47 N_{leaf} , the rest of the parameters were much less influential. This suggests that in fast-
48 growing early-successional broadleaves species such as poplars, physiological rather
49 than allocational and morphological traits predominate in determining growth, at least
50 under non-limiting light conditions.

51

52 **Introduction**

53

54 Nitrogen (N) is the limiting element in the growth of many forests (e.g. Jug et al. 1999,
55 van den Driessche 1999, Brown and van den Driessche 2005 for hybrid poplar). In the
56 particular case of short-rotation crops, such as in hybrid poplar plantations, N
57 fertilisation is viewed as a key silvicultural tool to maintain adequate productivity rates
58 in sites presenting nutrient limitations (e.g. boreal forest (DesRochers et al. 2003)).
59 There are several mechanisms by which nitrogen may enhance growth. In many cases,
60 the growth improvement has been attributed to the higher capacity of trees to assimilate
61 carbon because N is involved in the regeneration of the Rubisco, the primary CO₂-
62 fixing enzyme (Evans 1983, Liu and Dickmann 1993, Coll et al. 2007). The investment
63 of N to photosynthetic components is species-specific being in general higher in
64 deciduous trees compared to conifers (Wullschleger 1993, Reich et al. 1995, 1999).
65 From a physiological standpoint, N fertilisation generally implies an increase in the
66 water-use efficiency (which are primarily linked to changes in photosynthetic rates) and
67 respiration rates of plants (Liu and Dickmann 1996, Reich et al. 1998, Harvey and Van
68 den Driessche 1999, Ripullone et al. 2004). However, increasing N availability also
69 induces some structural and morphological changes at the tree level such as decreases in
70 the fine-root to leaf biomass ratio (Gower et al. 1992, Vanninen and Mäkelä 1999) and
71 leaf foliage to branch basal area ratio (Berninger et al. 2005). At the leaf level,
72 Calfapietra et al. (2005) found a close positive relationship between poplar leaf N
73 content and specific leaf area (SLA), whereas other studies found no or inverse
74 relationships between the two parameters (Heilman and Xie 1994, van den Driessche
75 1999). Leaf N content and leaf morphological parameters are known to vary at plant
76 level depending on their canopy position and developmental stage (Coleman et al. 1998,
77 Casella and Ceulemans 2002, Marron et al. 2002). For example, Al Alfás et al. (2007)

78 found SLA to decrease with increasing canopy height whereas nitrogen concentration
79 followed an opposite trend.

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

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

101 **2. Materials and methods**

102

103 **2.1 Site description and plant material**

104 Data was collected in three hybrid poplar (*P.maximowiczii* x *balsamifera*, clone nb: 915311)
105 plantations established during the spring of 2003 and 2004 in the province of Québec,
106 Canada. Plantations were set up using 1 m bare-root cuttings spaced 3 m apart. Two
107 sites were located near La Patrie (45° 20' N, 71° 34' W) in south-eastern Quebec and
108 were established during May 2003 (*LaPatrie1*) and 2004 (*LaPatrie2*). These sites were
109 previously used to analyse the competition for nitrogen between the poplar trees and the
110 competing vegetation (Coll et al. 2007). The third plantation was located near Montréal
111 (45° 25' N, 73°56' W), at McGill University Macdonald Campus (*Macdonald*,
112 hereafter). This plantation was established to follow the response of hybrid poplar to
113 different nitrogen fertilisation treatments (Domenicano et al. 2006). In the present study,
114 we used data from the *LaPatrie1* and *Macdonald* sites for the estimation of tree
115 structural parameters, whereas leaf gas exchanges and specific leaf area measurements
116 were conducted in all three sites.

117 2.2 Model description

118 The CROBAS model (Mäkelä 1997) was used to study the effect of the previously
119 described relationships between nitrogen content and the structural and photosynthetic
120 parameters on juvenile growth of 1 m poplar cuttings. CROBAS is a carbon-balance
121 model relying on functional balance (constant ratio between root and foliage biomass)
122 and the pipe model theory (Shinozaki et al. 1964) to simulate stand growth through
123 mean tree growth. The model state variables are mean tree compartment biomasses
124 (stem sapwood, branch sapwood, transport root sapwood, fine root sapwood, foliage)
125 and mean tree dimensions (total height, height to crown base, crown width). These state
126 variables can be obtained either directly from the model inputs (stand density, height,
127 diameter at breast height (dbh) and crown length of the average tree) or from given
128 allometric relationships (c.f. Eqs. 1-6 in Mäkelä 1997). Net tree growth is obtained by

129 subtracting maintenance respiration (which is assumed to be both proportional to the
130 biomass of each compartment and the nitrogen concentration) from the photosynthesis.
131 Once net tree growth is calculated, maximum specific growth of the foliage is
132 estimated. Foliage shedding is obtained from crown coverage, and is used to predict the
133 actual specific growth rate of the foliage. With foliage increment known, the increments
134 of the different state variables can then be derived from the allometric relationships.
135 Mean tree growth is calculated continuously using differential equations (c.f. Eqs. 14-24
136 in Mäkelä 1997) and is thus derived from foliage biomass increment (c.f. Eqs. 26 in
137 Mäkelä 1997) using allometric relationships. The model contains a large number of
138 sapwood turnover related parameters that are not known for poplar and do not influence
139 juvenile growth (since no heartwood is formed). No attempt was done to estimate the
140 values of parameters that cannot be validated without a good knowledge of root
141 standing biomasses. These parameters (notably the parameters named d , φ and S (with
142 various sub-indices)) were left at their original Scots pine values. Full details on the
143 model can be found in Mäkelä (1997).

144 2.3 Parameter estimations

145 *Tree structure*

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

150 In order to characterize the relationship between branch cross-sectional area and
151 associated supported leaves (parameter α_b , Eq. 1), a sub-sample of six branches per tree
152 was selected randomly and all the leaves were dried and weighed.

153 The effect of nitrogen on the branch basal area to foliage biomass was assessed with a
154 linear regression:

155 [1]
$$\alpha_b = \frac{\overline{W}_f}{\overline{A}_b} = \beta_0 + \beta_1 \cdot N_{leaf} + \varepsilon$$

156 Where α_b is the pipe model parameter, \overline{A}_b mean branch basal area of six sampled
157 branches per tree, \overline{W}_f mean tree foliage biomass of six sampled branches per tree and
158 N_{leaf} leaf nitrogen concentration, β_0 and β_1 regression parameters and ε the model error.
159

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

170 [2a]
$$W_f = \alpha_s \cdot A_s + \varepsilon$$

171 [2b]
$$W_f = \alpha_t \cdot A_t + \varepsilon$$

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

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

177 [3]
$$\ln(W_f) = \beta_0 + z \cdot \ln(Ac) + \varepsilon$$

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

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

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

192 [4]
$$\ln \alpha_r = \ln \left(\frac{W_r}{W_f} \right) = \beta_0 + \beta_1 \cdot N_{leaf} + \varepsilon$$

193 Where W_r is the fine root biomass and W_f the tree foliage biomass.

194 *Tree physiology*

195 Leaf gas exchange of 195 trees from all three sites was measured during August 2004
196 and 2005 with a portable leaf chamber system (LI-6400, Li-Cor, Lincoln, NE, USA).
197 Measurements were conducted between 10:00 and 14:00 on sunny days. For each tree,
198 steady-state net photosynthetic rates at light saturation (A_{max}) and leaf intercellular CO₂

199 concentration (C_i) were measured in one mature leaf taken from the upper part of the
200 canopy. For A_{\max} and C_i determination, light and CO_2 in the chamber were maintained
201 at $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR and 360 ppm respectively, while leaf temperature was set at
202 25°C . After the measurements, the leaves were collected and scanned. Leaf area was
203 determined using the Macfolia software package (Régent instruments, Québec,
204 Canada). From a subset of two leaves we obtained a full leaf photosynthesis curve and
205 fit a rectangular hyperbola through the data. Once oven-dried, leaf N concentration
206 (N_{leaf} , %) was determined following the Kjeldahl digestion method (Kjeltec Tecator
207 1030). The same method was used to analyse the foliage N content of the trees used in
208 the structural and biomass assessments. Nitrogen content analysis was carried out in a
209 sub-set of 10 different leaves taken from the upper part of the plant.

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

213 [5]
$$Y = \beta_0 + \beta_1 \ln(N_{\text{leaf}}) + \varepsilon$$

214 Where Y is either SLA or A_{\max} .

215 Annual photosynthesis was calculated assuming that the response of photosynthesis to
216 light can be represented by a rectangular hyperbola. Since we lacked information on the
217 development of leaf photosynthetic capacity over the season, we assumed that
218 photosynthesis has maximum capacity and started when leaves had half of their
219 maximal size (June 10) and terminated on September 1 (when many leaves were rapidly
220 turning yellow) (based on the data of Coll et al., unpublished). The maximal
221 photosynthesis for an entirely exposed leaf was calculated using hourly irradiance data
222 from a nearby weather station (Plattsburgh, NY, USA, data coming from the National
223 Solar Radiation Data Base, National Renewable Energy Laboratory 2007). We assumed

224 that there is a conversion factor of 2 ($\mu\text{mol s}^{-1} \text{W}^{-1}$) between irradiance in (W m^{-2}) and
225 photosynthetic active photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$) which is in the range of the
226 values given by Hu et al. (2007) and which we considered realistic given the humid
227 summer climate in Montréal. Photosynthesis was assumed to reach half of its capacity
228 at a PAR value $451 \mu\text{mol m}^{-2} \text{s}^{-1}$ (estimated from field measurements). Our analysis of
229 environmental data indicated that neither soil water deficit nor vapour pressure deficit
230 were important limitations to photosynthesis. To calculate the parameter P_0 , which is
231 the annual photosynthetic production of a thick (leaf area saturated) canopy, we
232 assumed that light in a canopy decreases according to the Lamberts-Beer law. We used
233 a light extinction coefficient of 0.15 (lower than those reported in previous studies for
234 poplar (e.g. Ceulemans et al. 1996) because our analysis was limited to an early phase
235 of stand development) that was corrected for the openness of the canopy (with a final
236 canopy cover between 0.26 and 0.3).

237 For the simulations we separated the effects of a gravimetical increase in
238 photosynthetic capacity ($\text{g C g}^{-1} \text{Leaf}$) from a change in specific leaf area by making the
239 maximum photosynthetic production (P_0) dependent on the photosynthetic capacity
240 (A_{max}) and the decrease of P_0 with shading dependent on the changes in SLA.

241

242 2.4 Model simulations

243 Of all the model parameters determined from measurements in the field four were
244 functions of leaf nitrogen content: foliage biomass ratio to branch basal area (α_b , Eq. 1),
245 fine root to foliage biomass ratio (α_r , Eq. 4), specific leaf area (SLA, Eq. 5) and
246 maximum rate of canopy photosynthesis per unit of leaf area (A_{max} , Eq. 5) (Table 1). In
247 addition, the specific respiration rates ($Resp$) of active tissues and xylem tissues were
248 assumed to be proportional to the leaf nitrogen-concentration according to Ryan (1995).

249 The yearly respiration was modelled as $0.13 \text{ g DM} / \text{g DM} \times \text{N-concentration (\%)}$ for
250 active and inactive parts of the tree alike excluding growth respiration. The other
251 parameters used in the simulations can be found in Appendix 1. The simulations were
252 setup with three different levels of foliar nitrogen: low ($1.2 \% N_{leaf}$), medium (2.4%
253 N_{leaf}) and high ($3.6 \% N_{leaf}$). The simulations were then run as follows: (i) a first set of
254 simulations were carried out with all of the N-dependent parameters set to the N_{leaf} level
255 and (ii) with all parameters set at 2.4% (baseline) but only one N-dependent parameter
256 changed to the next (3.6%) or previous (1.2%) level (e.g. N_{leaf} set at 2.4% for all of the
257 parameters, except for α_b where N_{leaf} was set at 1.2%). The effects of each N-dependent
258 parameter on 5-year model tree growth outputs were then compared to identify which
259 parameter had the most effect.

260 **3. Results**

261 3.1 Parameter estimates

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

268 The branch cross-sectional area (α_b), the maximum rate of canopy photosynthesis per
269 unit of leaf area (A_{max}), the fine root to foliage biomass ratio (α_r) and the specific leaf
270 area (SLA) were significantly correlated with the nitrogen leaf content (Table 1, Figure
271 1). More specifically, both structural parameters (α_b , α_r) decreased with increasing
272 foliage nitrogen content. In other words, branch basal area was proportional to nitrogen
273 concentration for a given level foliage biomass, whereas the fine root biomass was

274 proportional to foliar nitrogen concentration for the same foliage biomass. Inversely,
275 photosynthesis and specific leaf area were both proportional to foliar nitrogen content.
276 Moreover, SLA showed high variability, with values ranging between 70 and 120 cm²
277 g⁻¹.

278 3.2 Effect of N content on tree growth using CROBAS

279 Five-year simulations of poplar growth and development show that tree growth
280 significantly increases with foliar nitrogen concentration (Figure 2). After five years,
281 trees with 3.6% N_{leaf} were 34% larger in diameter (11.9 cm versus 8.9 cm), and 16%
282 taller than trees with 2.4% N_{leaf} (7.1 m versus 6.1 m). More importantly, the diameter
283 and height differences between the 1.2% N_{leaf} and the 2.4% N_{leaf} trees were much
284 greater than those between the 2.4% N_{leaf} and the 3.6% N_{leaf} . Model simulations showed
285 that after 5 years of growth plants with 2.4% N_{leaf} have a diameter and height, 4.5 to 3
286 times larger than the ones with 1.2% N_{leaf} . Foliage and total plant biomass followed the
287 same pattern (Figure 2). The leaf to total plant biomass ratio is predicted to decrease
288 with plant size for all N_{leaf} levels. The changes in different model outputs after a 5-year
289 growth period between different foliar nitrogen levels are presented in Figure 3.

290 According to the model predictions, changes in the photosynthetic capacity of the tree
291 due to increase nitrogen concentrations in the leaf account for the most differences
292 between the different levels of N_{leaf} . N-induced changes in specific leaf area also had a
293 positive influence on yield, but to a much lesser extent. Both structural parameters had
294 very little impact on tree growth, where N-induced changes in α_r had a slightly positive
295 effect on growth, and α_b a slightly negative impact on growth. However, these effects
296 and the increase of respiration rates with nitrogen concentration are negligible when
297 compared to the positive effect of N-induced changes in A_{max} .

298
299

300 **4. Discussion**

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

307 We obtained close correlations between the crown base cross-sectional area of trees and
308 foliage mass, branch and root area showing that the pipe model theory (Shinozaki et al.
309 1964) is a good approximation of tree structure in our data. Tight allometric
310 relationships between the aerial and belowground compartments of trees are common in
311 the scientific literature (Brown et al. 1989, Salas et al. 2004, Schneider et al. 2008, Coll
312 et al. 2008). We found that foliage biomass supported by a branch of a given area to
313 decrease with the mean N_{leaf} of the plant. Very little research has been done on the effect
314 of site quality on these allometric relationships. However, Berninger et al. (2005)
315 reported a similar trend in *Pinus sylvestris* trees. This may reflect a compensatory effect
316 of plants in response to the increase of carbon in their foliage which they experience
317 under non-limiting nutrient conditions (Schäfer et al. 2002). Our results indicate that
318 changes occur in the leaf water relations since stomatal conductance (data not shown)
319 and specific leaf area increase with increasing nitrogen concentration. These observed
320 changes in the tree structure could reflect to an acclimation of plants to the higher water
321 demand of the foliage. Our results agreed with the functional balance hypothesis that
322 claims dependence of root activity (mainly nutrient and water uptake) on leaf activity
323 (mainly carbon assimilation) (Brouwer 1962). The ratio between fine roots and leaf
324 biomass of poplar plants increased in response to low foliage nitrogen concentration as

325 has been reported in past studies for other species (Keyes and Grier 1981, Beets and
326 Whitehead 1996, Vanninen and Mäkelä 1999). However, this response could be driven
327 by the accelerated development of trees promoted by nitrogen availability since this
328 ratio has been found to decrease ontogenically in poplar trees (Coleman et al. 2004,
329 Coyle and Coleman 2005, Coll et al. 2007). At the leaf level, poplar trees presented a
330 positive correlation between N_{leaf} and both SLA and A_{max} . These relationships hold for
331 many species (Wright et al. 2004) and have been reported in previous studies with
332 different *Populus* species and clones (Curtis et al. 2000, Calfapietra et al. 2005, Coll et
333 al. 2007).

334 We used both empirical data and the model CROBAS to simulate the first five-year
335 growth of hybrid poplar plants with different leaf N status. The model was used as a
336 carbon and allocation bookkeeping tool. Our data were all derived using young plants
337 and we did not use many parameters that might be of importance in the long run (e.g.
338 processes like sapwood turnover). Since the simulated stands refer to even-aged
339 plantations, the model assumption of horizontal homogeneity ought to hold (Mäkelä
340 1997).

341 Simulated plant height increased linearly over the first years, whereas diameter growth
342 followed an exponential trend. During the first year, small increments in diameter are
343 probably associated with the fact that roots are not yet well developed (Deckmyn et al.
344 2004, Coll et al. 2004). Juvenile growth simulations of trees with different N_{leaf} diverged
345 considerably. Those differences were particularly noticeable between trees with 1.2%
346 and 2.4% N_{leaf} confirming the rapid reaction of poplars to fertilisation, particularly to
347 nitrogen (Liu and Dickmann 1992, Heilman and Xie 1994). The simulated tree growth
348 reaction with increasing nitrogen status from 2.4 mg g⁻¹ to values of 3.6 mg g⁻¹ was
349 moderate and may respond to the existing logarithmic relation between N_{leaf} and the

350 maximum carbon assimilation capacity (A_{max}) of leaves (Evans 1983, Coll et al. 2007).
351 Increases in respiration decreased somewhat the total growth of the trees but the
352 changes in photosynthesis dominated the growth response. Simulated five-year diameter
353 and height growth of poplar clones were in the range of those presented for comparable
354 studies (Stettler et al. 1988, Zhang et al. 2003, van den Driessche et al. 2008). The
355 model slightly over- and underestimate diameter and height growth for, respectively,
356 medium and high leaf nitrogen levels (data not shown). However adequate validation of
357 the model from hybrid poplar fertilisation trials was not possible since completely
358 independent data were not available (and trees in our sites did not all present the same
359 N_{leaf} values than the ones used in our simulations). In addition, comparisons of
360 simulated results and available data from the 3 sites used in this paper would not give
361 enough insight into validity of a mean stand model such as CROBAS.
362 The CROBAS simulations suggested the positive relationship between N_{leaf} and A_{max} to
363 be the main factor explaining tree growth and biomass increases with N fertilisation,
364 whereas allocation and structural parameters played a much smaller role. Fast-growing
365 early-successional species such as poplars are known to present high photosynthetic
366 rates and to rapidly respond to resource availability changes (Bazzaz 1979). These
367 species are able to incorporate N more efficiently in compounds involved in
368 photosynthesis (i.e. leaves) compared to slow-growing ones, and then are able to rapidly
369 increase their biomass (Poorter 1989). The response of photosynthetic capacity to
370 increase in nitrogen concentrations confirms earlier results (Evans 1989). There is
371 evidence that the slope of this regression is much lower for evergreen conifers than for
372 broadleaves (Reich et al. 1995). For example, Ripullone et al. (2004) found the
373 increment of carbon assimilation rate with nitrogen to be threefold higher in poplar
374 compared to in Douglas-fir. The other N-dependent parameters had only relatively

375 small effects on simulated growth. The smaller effects of specific leaf area on growth
376 were due to the fact that photosynthesis was defined on a per ground area and per leaf
377 mass basis. Therefore changes in SLA affected only the shading inside the canopy.
378 Since poplar stands have typically low leaf area indices (Gielen et al. 2001) the effects
379 of mutual shading on canopy photosynthesis is probably limited. The fact that CROBAS
380 calculates photosynthesis on a leaf-mass basis can lead to an underestimation of the
381 effect of SLA on the growth response of plants to nitrogen. The use of individual
382 functional–structural plant models that explicitly take into account the spatial
383 distribution of the leaves (see Godin and Sinoquet 2005, Delagrange et al. 2006) would
384 probably be more appropriate to accurately analyse the above-mentioned dependencies.
385 Increasing the foliage to root mass ratio with N_{leaf} slightly increased tree growth but its
386 effect was small compared to the effect associated to A_{max} .
387 As a summary, the results of the model predicted that physiological traits rather than
388 allocational and morphological traits predominate in determining poplar plant growth.
389 This agrees with the findings of Poorter (1999) who found net assimilation rate to be the
390 main factor explaining growth differences among a number of tree species under high
391 light conditions. In addition, simulations indicated that the contribution of the different
392 parameters modulated by N_{leaf} on plant growth were additive. In other words, the
393 differences between the simulations with one N-level and another are approximated by
394 the sum of the effects of each N-varying parameter taken individually. There seems to
395 be very little interaction between each parameter. This additivity is an interesting
396 emerging property of the model simulations, since mechanisms for interactive effects
397 are built into CROBAS. For example, the photosynthetic production depends on the
398 foliage biomass, the photosynthetic capacity and the specific leaf area. The foliage
399 biomass, on the other hand, is determined to a large extent by the allocation to new

400 foliage, which depends on plant size, the pipe model parameters and the allocation to
401 fine roots. If this additivity is confirmed in further studies, it would facilitate our
402 understanding of the effects of fertilisation since more simple models could be used.
403 This study constitutes a first attempt to analyse independently the role played by
404 different morphological and physiological parameters modulated by N_{leaf} on hybrid
405 poplar growth. The model gives us the opportunity to understand the relative
406 importance of the different acclimation of plant functioning and structure to nitrogen.
407 Furthermore, the relationships that underlie the model (i.e. the pipe model and the
408 functional balance) are solid and seem to be consistent across treatments. Hence the
409 model acts more as a “simple carbon tracking tool”. We suggested that physiological
410 responses to N-fertilisation are much more important in affecting poplar tree growth
411 than structural changes when light is not limiting. The effects of parameter changes are
412 additive showing that simple models might be used to estimate short term effects of
413 changes in plant nutrition.

414

415

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

	Nitrogen invariant				Nitrogen dependent							
Equation	Eq. 2a	Eq. 2b	Eq. 3		Eq. 1		Eq. 4		Eq. 5 (SLA)		Eq. 5 (p0)	
Parameter	α_s	α_t	β_0	z	β_0	β_1	β_0	β_1	β_0	β_1	β_0	β_1
(code, mean, SE)	322.01	187.44	-4.07	2.04	283.53	-29.34	-0.71	-0.72	91.05	14.06	11.18	12.56
	(13.39)	(6.92)	(0.67)	(0.32)	(14.93)	(5.35)	(0.31)	(0.18)	(0.99)	(1.81)	(0.24)	(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	

589 **Figure captions**

590

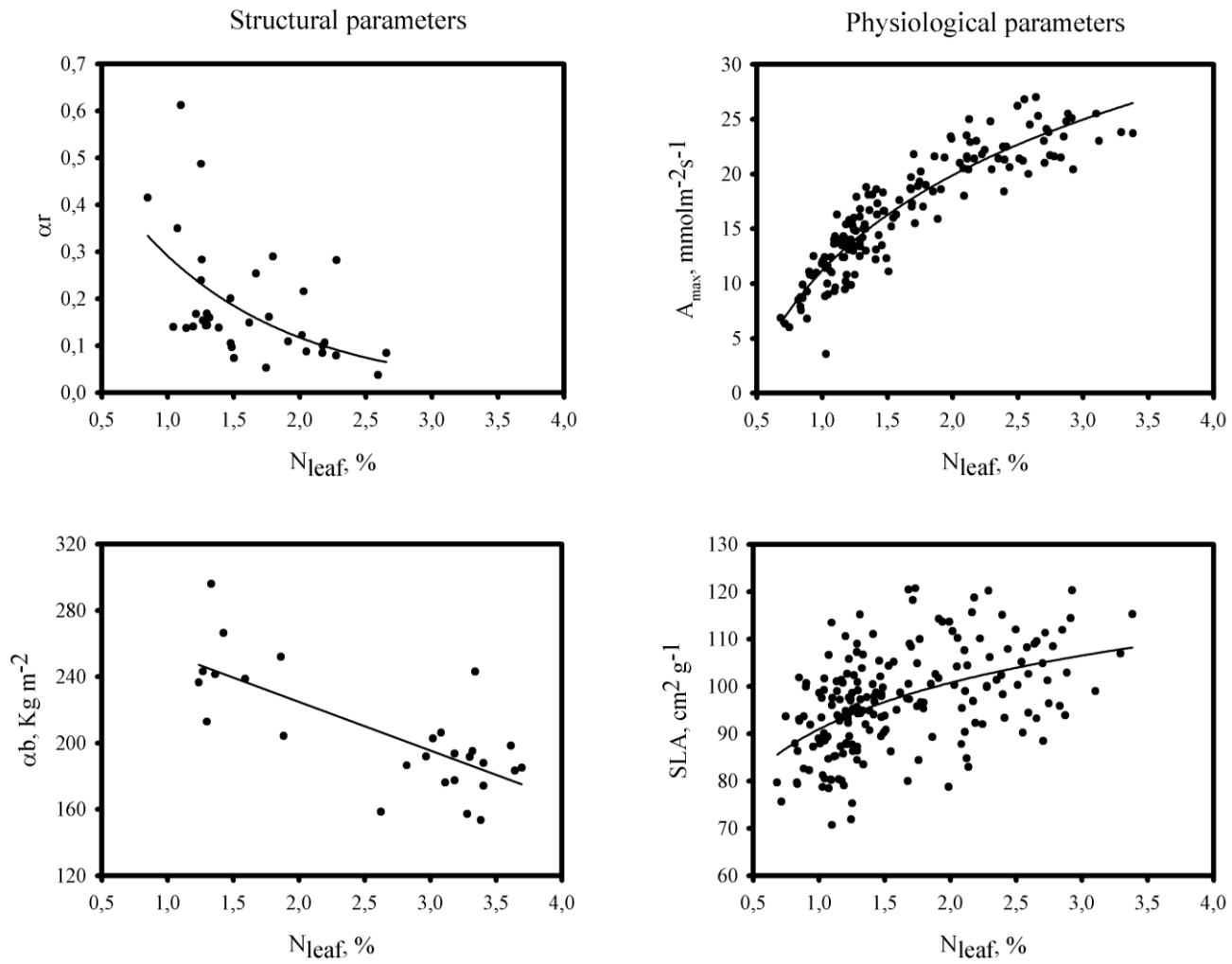
591 **Figure 1.** Effect of foliar nitrogen concentration on structural (α_b : foliage biomass to
592 branch basal area ratio, α_r : fine root biomass to foliage biomass ratio) and physiological
593 parameters (A_{max} : maximum steady-state net photosynthetic rates at light saturation,
594 SLA: specific leaf area)

595

596 **Figure 2.** CROBAS predictions for juvenile hybrid poplar growth.

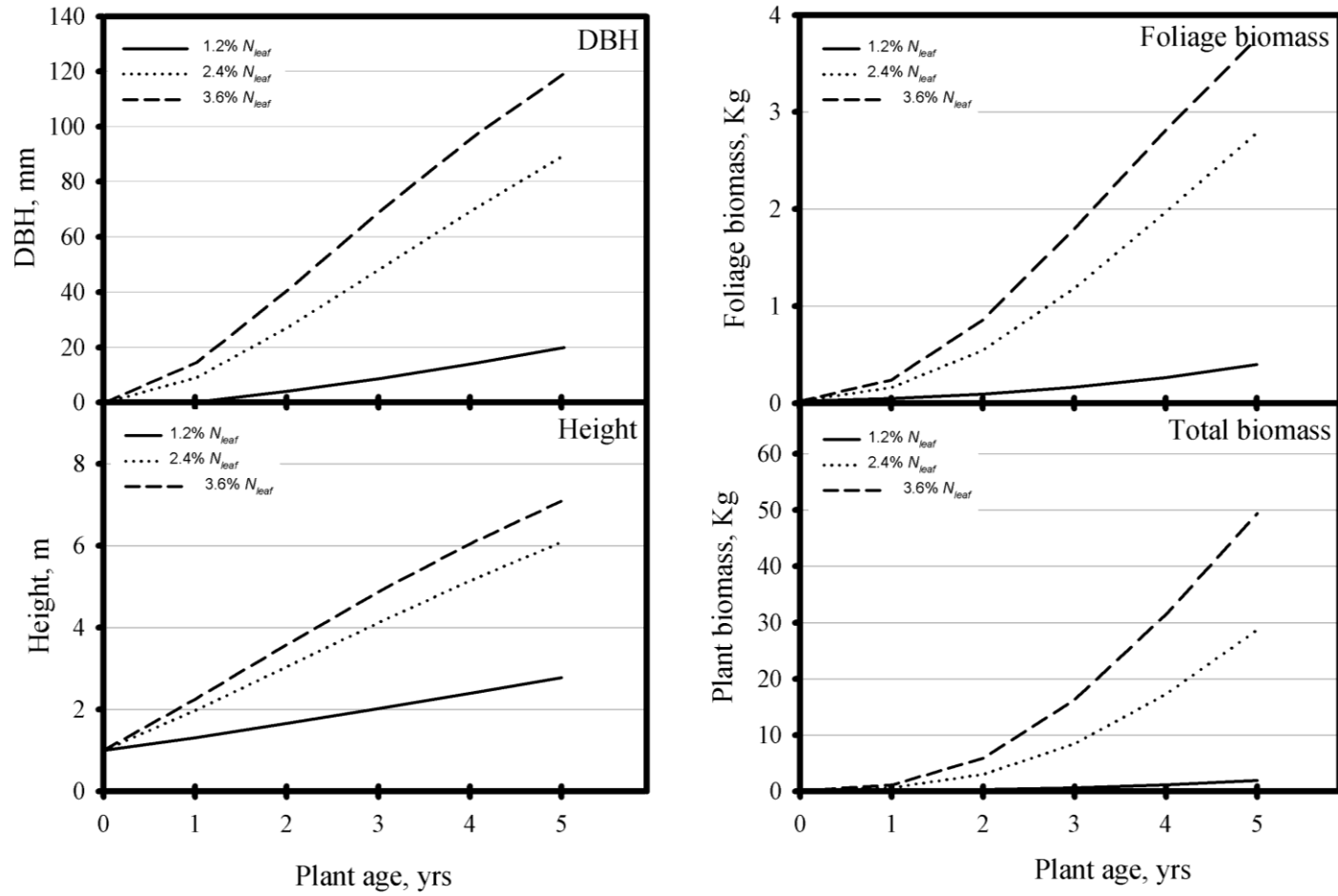
597

598 **Figure 3.** Individual effects of N-dependent parameter changes in different tree
599 variables (A) diameter at breast height, (B) total height and (C) total tree biomass. The
600 bars show the increment or decrease of the variables when each individual parameter (y-
601 axis) was entered in the model with its value corresponding to the next N_{leaf} level
602 (above 3.6% or below 1.2%), while maintaining the rest of the parameters to the
603 baseline level (2.4 %). Parameter abbreviations are: Resp (specific respiration rates of
604 active tissues), P_0 (annual photosynthetic production of a thick (leaf area saturated)
605 canopy), SLA (specific leaf area), α_r (fine root biomass to foliage biomass ratio) and α_b
606 (foliage biomass to branch basal area ratio).



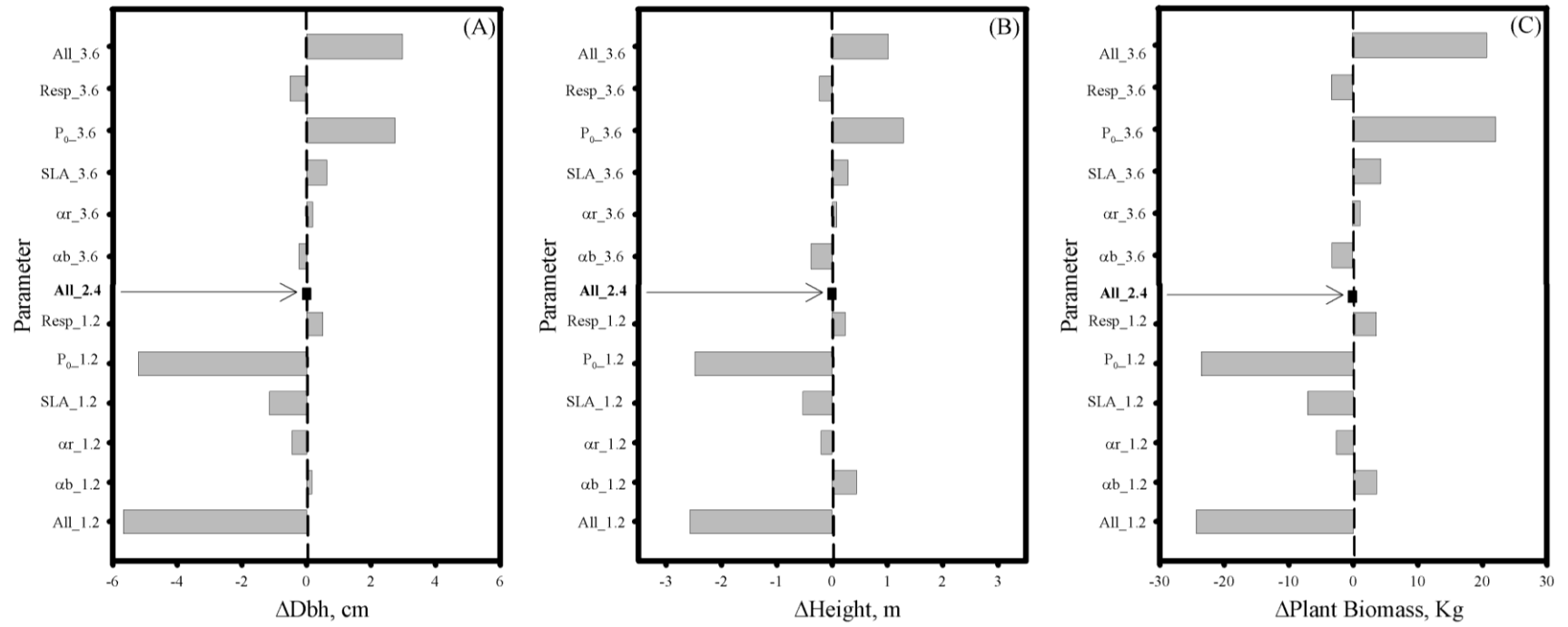
609 **Figure 2**

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611

612 **Figure 3**



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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	
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 FEM	300	Kg m ⁻³
ρ_b	wood density of branches	Pliura et al. 2007 FEM	300	Kg m ⁻³
ρ_t	wood density of transport roots	Pliura et al. 2007 FEM	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	$year^{-1}$

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