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Botanical determinants of foliage clumping and light interception in two-year-old coppice poplar canopies: assessment from 3-D plant mock-ups

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Abstract – Botanical parameters (e.g., shoot and branch inclination, petiole length, leaf phyllotaxy, size and shape) that influence light interception and foliage clumping in dense two-year-old monoclonal poplar (*Populus* spp.) coppice crops were analysed with a three-dimensional simulation model. Crop LAI varied from 1 to 2 for clone Ghoy and from 2.5 to 7.4 for clone Trichobel from May to September. Canopies were strongly clumped, with a clumping index (μ) about 0.5. Canopy light transmittance (τ) varied from 0.59 in May to 0.41 in September for clone Ghoy and from 0.42 to 0.08 for clone Trichobel, and was strongly associated with LAI. The overall effect of a simulated shift in botanical parameters was relatively small and resulted in limited changes in μ and τ by ± 0.05 and ± 0.1 , respectively. Petiole length had the most notable effect on μ and τ , while the other parameters were less effective. However, biomass cost analyses showed that actual petiole length optimised the efficiency of biomass investment into light capture.

biometry / multi-scale / canopy structure / seasonal changes / sensitivity analysis / three-dimensional model

Résumé – Déterminants botaniques de l'agrégation du feuillage et de l'interception de la lumière pour des taillis de peupliers âgés de deux ans : caractérisation à partir de maquettes 3-D. Les paramètres botaniques (angle d'inclinaison des tiges et des branches, longueur des pétioles, phyllotaxie foliaire, taille et forme des feuilles) qui influencent l'interception lumineuse et l'agrégation foliaire ont été étudiés chez des taillis de peupliers (*Populus* spp.) âgés de deux ans à partir d'un modèle de simulation tridimensionnelle. De mai à septembre, les taillis étudiés ont présenté des valeurs d'indice foliaire (LAI) variant de 1 à 2 pour le clone Ghoy et de 2.5 à 7.4 pour le clone Trichobel. Les couverts étaient fortement agrégés, avec un paramètre d'agencement (μ) proche de 0.5. La fraction de rayonnement transmis au sol (τ) a varié de 0.59 en mai à 0.41 en septembre pour le clone Ghoy et de 0.42 à 0.08 pour le clone Trichobel, et elle était fortement corrélée au LAI. Les variations apportées dans les paramètres botaniques étudiés n'ont modifié que faiblement μ (± 0.05) et τ (± 0.1). Parmi tous les paramètres botaniques étudiés, la longueur du pétiole a montré l'effet le plus notable sur μ et τ . Cependant, une analyse de sensibilité a montré que l'investissement en biomasse était optimisé pour la taille réelle des pétioles.

biométrie / multi-échelle / structure du couvert / variations saisonnières / analyse de sensibilité / modèle tridimensionnel

1. INTRODUCTION

Complex processes are involved in tree growth, which depend on the plant ability to intercept light energy and to efficiently convert it to biomass through the process of photosynthesis [1]. Light interception properties are in turn governed by total canopy leaf area and the spatial arrangement of the leaves [22]. Phyllotaxy rules, branching angle and frequency, lengths of internode and petiole and leaf shape, size and orientation have significant effects on light interception at both branch and canopy levels in various species [4, 8, 10, 17–19, 21, 25, 27]. Percy and Yang [20] and Takenaka et al. [26] also claimed that plants are optimal with respect to light capture. Although the spatial dispersion of vegetation elements is often considered to be random in dense deciduous broadleaved forest tree canopies (i.e., μ near unity, see Tab. I for list of abbreviations and their definitions), little consideration has been

given to foliage clumpiness in short rotation woody crop systems. Recently, Niinemets et al. [17] reported strong foliage aggregation and some correlation between μ and petiole length in young poplar crop canopies.

Plants in the genus *Populus* are amongst the most promising fast-growing trees for producing fuel and fibre, especially when trained as short-rotation coppice systems where crops are harvested every 3 years over a 15-year lifespan [12]. Consequently, the genus *Populus* has been extensively investigated and large genotypic differences have been demonstrated amongst spp. in terms of crop-level performances [14, 15]. This genetic variation was often governed by a combination of clonal contrasts in leaf physiological and morphological characteristics and the display of those parameters within time and space as set by the development of canopy architecture [2, 3, 15]. Since current developments in plant functional genomics and molecular genetics may provide the ability to improve productivity for those crop systems, understanding possible effects and sources of non-random foliage dispersion

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Table I. List of symbols.

Symbol	Definition
A	Axis. A1, an axis of order 1, is a shoot, and A2, an axis of order 2, is a leafy branch
A	Total leaf area per U2 (m ²)
a	Individual leaf area (m ²)
α	Inclination angle between A1 and A2 or A2 and P (°)
d	Shoot diameter (m)
θ	Phyllotactic angle (°)
Gho	Clone Ghoy (<i>Populus nigra</i> L. \times <i>Populus deltoides</i> Bartr. ex Marsh.)
I	Internode. An internode is morphologically represented as a cylinder and bounded at its two extremities by nodes
k	Canopy light extinction coefficient
l	Length (m)
L	Leaf blade
M	Metameric unit. A metameric unit consists of an I and a possibly vegetative bud, leaf or A2
μ	Clumping index ($0 < \mu < 1$) that decreases with increasing leaf aggregation
N	Node. A node consists of a possibly vegetative bud, leaf or branch
n	Number of
P	Petiole. A petiole is the slender stalk that supports the leaf blade
PAR	Photosynthetically active radiation
Q	Solar radiation level (mol PAR m ⁻² s ⁻¹)
φ	Elevation of the shoot segment (°)
S	Stool
Se	0.2-m-long segment (the curved shape of a A1U1 is described by the φ value of every consecutive Se)
τ	Canopy light transmittance
Tri	Clone Trichobel (<i>Populus trichocarpa</i> Torr. & Gray \times <i>Populus trichocarpa</i>)
U	Growth unit. U1 is the part of an axis that has lengthened during the previous growing season, U2 is the growing part of an axis during the current year
w	Width (m)

within the canopy on light interception have also to be considered [24]. However, studies linking botanical parameters to spatial distribution of leaf area and/or light interception are scarce. Actually, light interception results from complex interactions between several botanical determinants that are difficult to consider from direct observations [18].

We used 3-D CPCA (three-Dimensional Coppice Poplar Canopy Architecture) [3], a computer based model that reconstructs 3-D virtual crops of two-year-old coppice poplar canopies of clones Ghoy (Gho, *Populus nigra* L. \times *Populus deltoides* Bartr. ex Marsh., a Euramerican clone) and Trichobel (Tri, *Populus trichocarpa* Torr. & Gray \times *Populus trichocarpa*, an interamerican clone), in combination with computation of light interception to investigate foliage clumping. For both clones, the sensitivity of τ and μ was studied by numerically changing botanical parameters, namely shoot and branch inclination, petiole length, leaf phyllotaxy, size and shape, in order to:

(i) determine the contribution of any individual parameter to whole-canopy light capture and define the minimum data sets to be measured in the field for a given reconstruction quality; and

(ii) evaluate the effects of biomass investment into additional petiole length on whole-canopy light capture.

Because we used plant mock-ups built from field data rather than a process based functional-structural model, we made the prerequisite hypotheses that:

(i) changing a botanical parameter in the early stages of canopy development does not affect canopy structure along the studied growing season (hypothesis h_1); and

(ii) modifying petiole length does not affect the total plant biomass and its partitioning between above- and below-ground compartments (hypothesis h_2).

2. MATERIAL AND METHODS

2.1. 3-D poplar plant model

A multi-scale biometric methodology for describing the architecture of fast-growing short-rotation woody crops has been developed by Casella and Sinoquet (2003) to describe two-year-old poplar clones during a second rotation. The method operates at stool (S) level and describes the plant as a collection of shoots (A1) and branches (A2) decomposed into growth units (U1 and U2). Growth

Table II. List of scenarios (see Tab. I for list of abbreviations and their definitions) related to the modified botanical parameters and expected effects (? unknown; – decreasing; + increasing) on whole-canopy foliage clumping and light transmittance.

Parameter	Scenario	Definition	Effect	Reference	
Shoot (A1U1)	$\varphi_{Se_1} + 15^\circ$ $\varphi_{Se_1} - 15^\circ$	The curved shape of each A1U1 was modified by increasing or decreasing the elevation angle (φ) value of their initial 0.2-m-length segment (Se_1) by 15°	?	–	
	$l_1 = l_{A1U1}/n_M$	A unique internode length (l_1) value was applied to every consecutive meristematic unit (M) along each A1U1 by dividing its l by its number (n) of M	?	–	
Branch (A2U2)	$\alpha_{A2U2} + 15^\circ$ $\alpha_{A2U2} - 15^\circ$	The branch insertion angle (α_{A2U2}) was increased or decreased by 15°	weak	[4, 8]	
	$l_1 = l_{U2}/n_M$	A unique l_1 value was applied to every consecutive M along each U2 by dividing its l by its n_M	?	–	
	$n_L \times 0.5$ $n_L \times 2$	At constant U2 total leaf area (A) and for a fixed leaf lamina (L) shape, n_L of each U2 was multiplied by a factor of 0.5 or 2	– +	[25]	
	$a = A/n_M$	A unique leaf lamina area (a) value was applied to every consecutive L along each U2 by dividing A by n_M	?	–	
Petiole (P)	$\alpha_P = 47^\circ$ $\alpha_P = 56^\circ$	The P inclination angle (α_P) was set to an averaged value of 56° for Gho and 47° for Tri [3].	?	–	
	$\theta_P = 45^\circ$ $\theta_P = 90^\circ$	The P phyllotactic angle (θ_P) was set from a value of 141° to 90° or 45°	– –	[18, 25, 27]	
	$l_P \times 0$ $l_P \times 0.25$ $l_P \times 0.5$ $l_P \times 0.75$ $l_P \times 1.5$ $l_P \times 1.75$ $l_P \times 2$	At constant a and for a fixed L shape, l_P values were multiplied by a factor of 0, 0.25, 0.5, 0.75, 1.5, 1.75 or 2	– – – – + + +	[17, 19, 20, 21, 25, 26]	
	Leaf lamina (L)	$w_L/l_L \times 0.2$ $w_L/l_L \times 0.593$ $w_L/l_L \times 0.809$ $w_L/l_L \times 2$	At constant a and l_P , the leaf lamina length/width ratio (w_L/l_L) was set from a value of 0.809 to 2, 0.593, or 0.2 for Gho and from a value of 0.593 to 2, 0.809, or 0.2 for Tri	– ? ? +	[25]

units are themselves defined as a collection of elementary units (internode, I; petiole, P and leaf blade, L). Branching and connections between elementary units and their spatial location, orientation, size and shape describe the plant architecture. The methodology has been used to describe the plant architecture of poplar clones Gho (Gho) and Trichobel (Tri) from 15 selected stools per clone over a five month-period (May-September 2001). On individual stools, shoots have been selected from three classes spanning the diameter distribution range. Using a multi-scale approach [11], monthly empirical allometric relationships have been developed to parameterise and/or explain the topological relationships and geometry of plant units. The empirical functions form the basis for the 3-D CPCA model that recreates the 3-D architecture of the coppice at plot scale. The quality of the reconstruction method was tested. Tests indicated an adequate predictive ability of the 3-D CPCA model: model outputs compared

well with in situ measurements for features such as the individual components of a plant (e.g., total number of leaves) or light interception properties assessed from fisheye photographs [3]. Results of this work were used in the present study to generate actual and modified plant mock-ups of the two clones (i.e., with the same topological and geometrical properties as the measured plants and after changing a botanical parameter in the digitized mock-up, respectively).

2.2. Numerically modified plants

Modified plants were reconstructed by numerically changing a botanical parameter according to different scenarios (see Tab. II for list of scenarios and their definitions). According to hypothesis h_1 , the effects of non-random foliage dispersion within canopies on light

capture were investigated by changing the geometry of the shoots (scenarios $\varphi_{Se1} \pm 15^\circ$), branches ($\alpha_{A2U2} \pm 15^\circ$) (Fig. 1) or leaves ($\theta_p = 45^\circ$ or 90° , l_p variable or w_L/l_L variable) (Fig. 1) or the number of leaves ($n_L \times 0.5$ or 2). Effects of changing distributions in internode length (scenario $l_1 = l_A/n_M$), petiole inclination angle (α_p constant) or leaf lamina area ($a = A/n_M$) within shoots or branches were tested in order to define the minimum data sets required for a given reconstruction quality. As a result of the modelling process, individual l_1 and/or l_p , l_L , w_L and a values have been recomputed according to variations in n_M for scenarios $n_L \times 0.5$ or 2 and/or in l_L for scenario $a = A/n_M$.

2.3. Generation and description of canopy structures

For a given date, clone and plant type (actual or modified), a virtual crop structure was generated by the 3-D CPCA modelling process, according to Casella and Sinoquet [3]. A crop structure (9×11.25 m) mimicking actual planting pattern consists of 10 north-south oriented rows of 10 plants each with alternating inter-row distances of 0.75 m and 1.5 m, and a within row spacing of 0.9 m, to yield a planting density of 1 plant m^{-2} . From model outputs, basic structural plant dimensions and canopy LAI were computed. Average basic structural plant dimensions (e.g., l , w , a) of elementary units (e.g., L, P) were calculated over all 36 plants (i.e., 6×6) localised in the centre of each actual crop.

2.4. Computation of light interception and foliage clumping

Using the method defined by Casella and Sinoquet [3], a set of ten virtual hemispherical images were computer-generated from each actual or modified crop mock-up with the POV-Ray™ ray-tracing software program (Persistence of Vision™ Raytracer) (Fig. 1). At 0.15 m above ground, five hemispherical images were simulated along the central row of the 36 plants in the crop centre and five from one of its adjacent inter-rows. Each virtual hemispherical image was processed using the HemiView canopy analysis software (Delta-T Devices Ltd, Cambridge, Version 2.1) to compute an effective leaf area index (LAI), a hypothetical value based on the assumption that leaf dispersion was random [7]) and the diffuse solar radiation level below the canopy (Q , from 48 sky sectors covering the entire hemisphere). Standard overcast sky conditions were used for the simulation of diffuse light transmittance. For each crop, τ was computed as:

$$\tau = \bar{Q}/Q_0 \quad (1)$$

where $\bar{Q} = \sum_{i=1}^{10} Q_i/10$; where Q_i is the diffuse solar radiation below the canopy computed from hemispherical image i and Q_0 is the solar radiation above the canopy.

This was used to estimate a monthly average daily-integrated amount of photosynthetically active radiation (Q_{int} , mol PAR $m^{-2} d^{-1}$) intercepted by each canopy vegetation as:

$$Q_{int} = (1 - \tau) \times Q_{int,0} \quad (2)$$

where $Q_{int,0}$ is the monthly average daily-integrated incident quantum flux density calculated from recorded PAR quantum flux density (BF2 sunshine sensor, Delta-T Devices Ltd, Cambridge) during the 2001 growing season ($Q_{int,0} = 39.9, 44.7, 41.5, 32.9$ and

23.2 mol PAR $m^{-2} d^{-1}$ from May-September, respectively). Concurrently, μ was derived [7] from LAI computation:

$$\mu = \overline{LAI}/LAI_{actual} \quad (3)$$

where $\overline{LAI} = \sum_{i=1}^{10} LAI_i/10$; LAI_i is LAI computed from hemispherical image i and LAI_{actual} is the LAI computed from the corresponding actual crop mock-up.

2.5. Biomass

During 2001, 15–20 shoots per clone were harvested monthly from nearby experimental crops. The diameter (d) at 0.1 m above the point at which a shoot (A1) joins a stool and the length (l) of each shoot were measured after leaf collection. Petioles (P) were subsampled and individual l was recorded. For each clone and date, sampled plant fractions were oven dried at $75^\circ C$ for at least 48 h and their dry masses (DM) measured. Allometric relationships between shoot volume index ($d^2 l_{A1}$) and DM_{A1+A2} and between l_p and DM_p were computed (Fig. 2). These functions were used to estimate monthly values of $\overline{DM}_{A1+A2,actual}$ and $\overline{DM}_{P,actual}$ or $\overline{DM}_{P,modified}$ (i.e., when applying a scenario with changed l_p) at plant level. This was computed (i) from a set of d and l_{A1} data collected during the 2001 growing season on 15 selected plants within each described field crop [3] and (ii) by the 3-D CPCA modelling process:

$$\overline{DM}_{A1+A2,actual} = \sum_{k=1}^{15} \left(\sum_{j=1}^{n_{A1U1}} DM_{A1+A2,actual,j} \right) / 15 \quad (4)$$

$$\overline{DM}_{P,actual/modified} = \sum_{k=1}^{36} \left(\sum_{j=1}^{n_{A1U1}} \left(\sum_{i=1}^{n_{U2}} \left(\sum_{h=1}^{n_M} DM_{P,actual/modified,h} \right) \right) \right) / 36 \quad (5)$$

where $DM_{P,actual} = f(l_{p,actual}) = f(l_{L,actual})$, $DM_{P,modified} = f(l_{p,modified})$, $h = 1, \dots, n_M$ is the M number at the U2 scale, $i = 1, \dots, n_{U2}$ is the U2 number at the A1U1 scale, $j = 1, \dots, n_{A1U1}$ is the A1U1 number at the plant scale and $k = 1, \dots, 15$ or 36 the plant number at the crop scale.

3. RESULTS

3.1. Geometrical characteristics of actual canopies

Compared with clone Trichobel (Tri), plants of clone Ghoj (Gho) were on average 1.6 times shorter but displayed 1.5 times more leaves (Tab. III). Leaves of Gho were characterised by a triangular shape ($\bar{w}_L = 0.809 \times \bar{l}_L$) compared to the ovate shape in Tri ($\bar{w}_L = 0.593 \times \bar{l}_L$). \bar{a} was on average 5 times smaller in Gho than in Tri and, contrasting with a relatively horizontal position for Tri, leaf blades of Gho were highly angled. However, the two clones displayed similar values in \bar{l}_p . At crop level (Fig. 3), low values of LAI and a weak canopy closure dynamic characterised Gho, while the quick and strong canopy closure of Tri resulted in a high LAI. As a result, there were strong relationships between τ and LAI, showing clonal differences in the estimated light extinction coefficient (k). Concurrently, μ computations showed strong foliage clumpiness in the early stages of both canopies (to a lesser extent for Gho than for Tri), which slightly increased with time (Fig. 3).

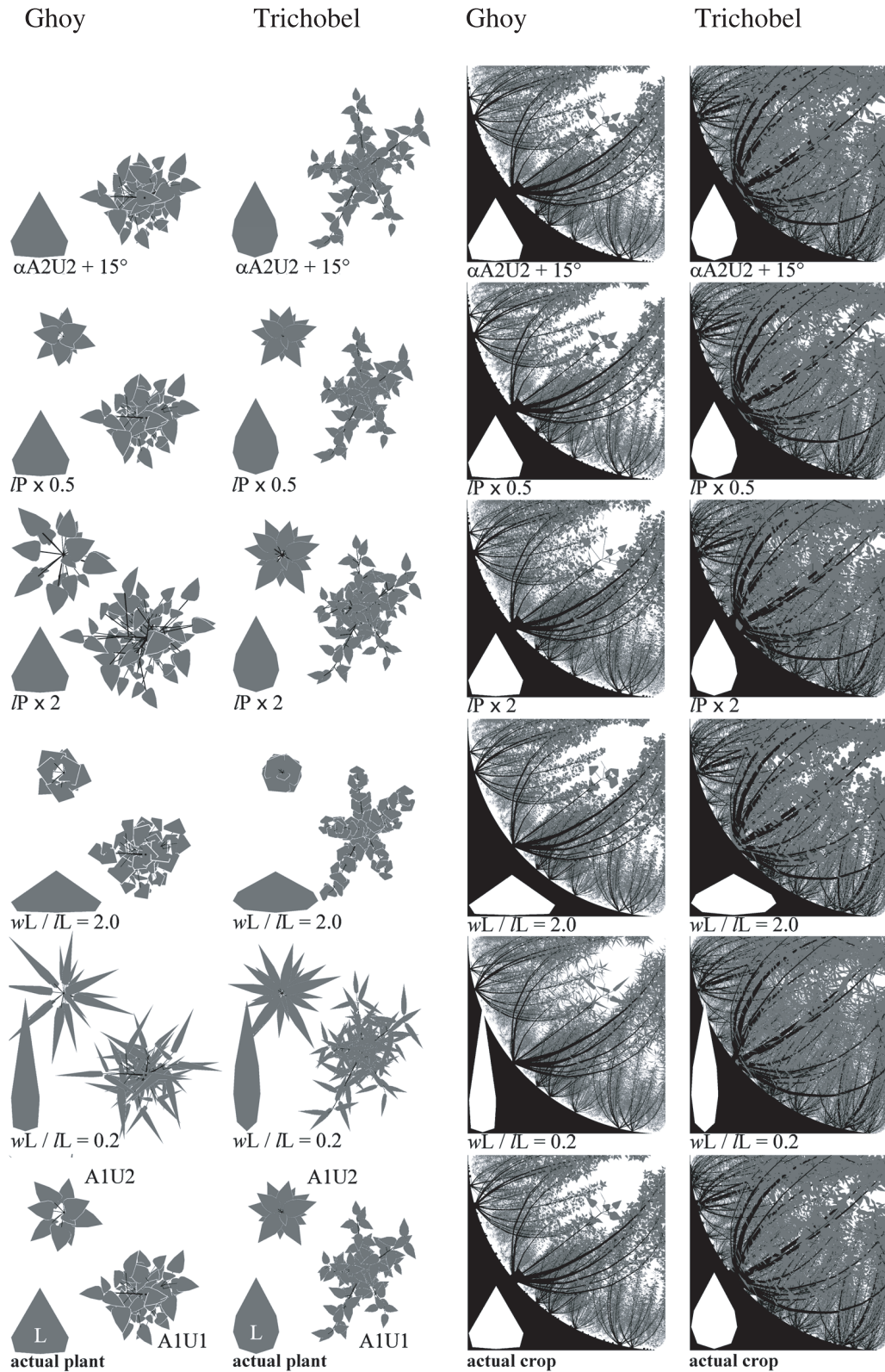


Figure 1. Examples of visual comparisons between computer-generated branched shoot (A1U1), shoot leader (A1U2), leaf blade (L) (left) and hemispherical images (right) before (actual plant) and after numerically changing botanical parameters for poplar clone Ghoy and Trichobel. Definitions of symbols are given in Table I.

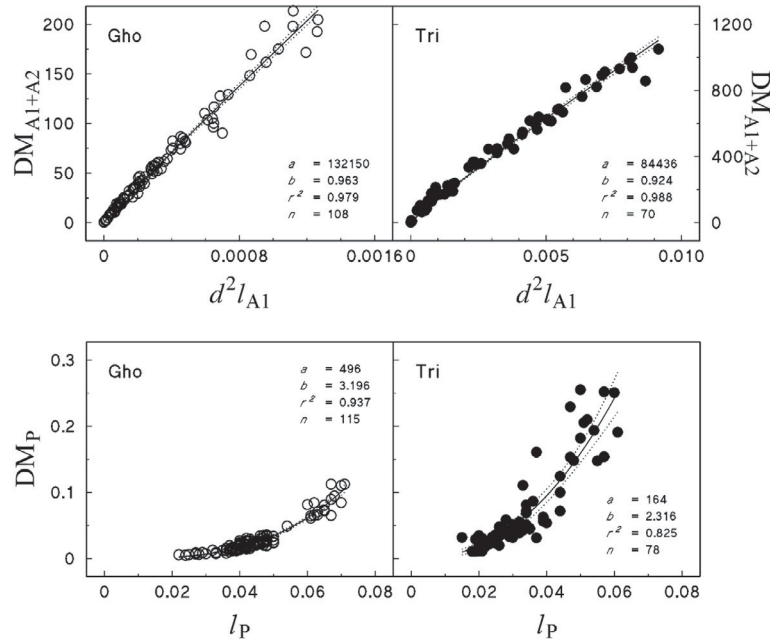


Figure 2. Sample allometric relationships between (above) shoot volume index ($d^2 l_{A1}$, m^3) and shoot dry mass (DM_{A1+A2} , g) and (below) petiole length (l_p , m) and petiole dry mass (DM_p , g) for poplar clones Gho (Gho, \circ) and Trichobel (Tri, \bullet). Relationships between DM and $d^2 l_{A1}$ and l_p were fit to the following regression: $y = a \times x^b$. Dotted lines depict the confidence interval at $P < 0.05$. Definitions of symbols are given in Table I.

Table III. Seasonal change in basic actual plant parameters derived from the 3-D CPCA model outputs (sim.) and field measurements (mes.) for poplar clones Gho and Trichobel. Maximum shoot height (l_{A1}) and mean plant parameters (see Tab. I for list of abbreviations and their definitions) were obtained from a population of 15 (mes.) and 36 (sim.) plants per clone and per date.

Clone	Date	n_{A1}	l_{A1}	\bar{n}_L	\bar{l}_L	\bar{w}_L	\bar{a}	$\bar{\varphi}_L$ / inclination angle	\bar{l}_p	\overline{DM}_{A1+A2}	\overline{DM}_p
			sim.	sim.	sim.	sim.	sim.	sim.	mes.	sim.	mes.
			(m)	(m)	(m)	(m)	(m^2)	($^\circ$)	(m)	(g per plant)	(g per plant)
Gho	May	25	2.2	1704	0.033	0.027	0.00059	-10 / 37	0.024	0287	09
	June		2.2	2189	0.034	0.027	0.00061	-11 / 38	0.025	0323	13
	July		2.4	2478	0.035	0.029	0.00067	-12 / 38	0.026	0430	17
	August		2.5	2589	0.037	0.030	0.00074	-12 / 38	0.027	0547	20
	September		2.5	2640	0.037	0.030	0.00075	-12 / 38	0.028	0563	20
Trichobel	May	22	3.3	1000	0.077	0.045	0.00251	-52 / 53	0.024	0688	41
	June		3.6	1486	0.080	0.047	0.00265	-29 / 30	0.025	0811	63
	July		4.0	1747	0.088	0.052	0.00328	-6 / 19	0.028	1040	84
	August		4.3	1847	0.092	0.054	0.00365	-6 / 19	0.029	1323	89
	September		4.8	1903	0.095	0.056	0.00390	-6 / 19	0.029	1648	89

3.2. Effects of changing botanical parameters on light interception and foliage clumpiness

In both clones, changing botanical parameters resulted in reverse changes in τ and μ but with low effects (Fig. 4). τ and μ were generally more sensitive to the tested scenarios in Gho than in Tri. Additionally, decreasing effects over time in μ rather than in τ for Gho and in τ rather than in μ for Tri, were found in all scenarios. When testing the scenarios on

canopy PAR interception (Fig. 4), an overall decreasing effect throughout the growing season was found for both clones due to canopy closure.

Increasing petiole length (l_p) by a factor 2 was the key scenario resulting in enhanced light interception by the vegetation (+7.9% for Gho and +2.9% for Tri on average for the entire growing season) (Fig. 4). Increasing branch inclination angle (α_{A2U2}) by 15° or decreasing the leaf lamina width/length ratio (w_L/l_L) to 0.2 only poorly affected annual light interception in

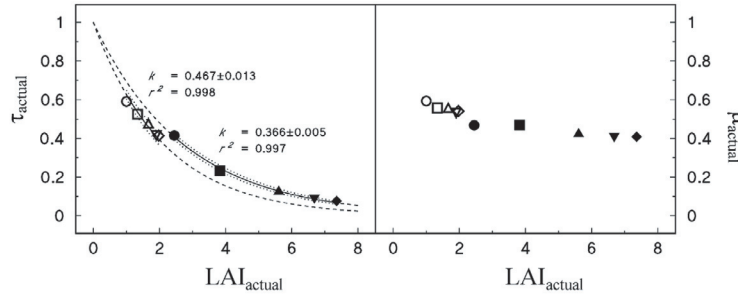


Figure 3. Seasonal changes (\circ, \bullet = May; \square, \blacksquare = June; $\triangle, \blacktriangle$ = July; $\nabla, \blacktriangledown$ = August; \diamond, \blacklozenge = September) in canopy light transmittance (τ_{actual} , Eq. (1)) and clumping index (μ_{actual} , Eq. (3)) as a function of leaf area index ($\text{LAI}_{\text{actual}}$) for the actual crops of poplar clones Ghoy (Gho, open symbols) and Trichobel (Tri, closed symbols). Relationships between τ_{actual} and $\text{LAI}_{\text{actual}}$ were fit to the following regression: $y = \exp[-k(\pm SD) \times x]$. Dotted lines depict the confidence interval at $P < 0.05$. Definitions of symbols are given in Table I.

both canopies (+1.6 and +2.8% for Gho and +1.3 and +2.1% for Tri). Combining the three last parameters (scenario 1+2+3, Fig. 4) resulted in smaller changes in annual canopy interception than the arithmetical sum of the three independent scenarios (−16% for Gho and −27% for Tri). Results from all other scenarios showed weak effects or decreases in canopy interception (e.g., −11.5% and −6.2% for Gho and Tri, respectively when l_p was set at 0).

3.3. Biomass cost analyses

For both clones, strong empirical functions explained variations in shoot dry mass ($\overline{\text{DM}}_{\text{A1+A2}}$) and in petiole dry mass (DM_p) versus shoot volume index ($d^2 l_{\text{A1}}$) and petiole length (l_p), respectively (Fig. 2). Contrasting with the relatively low effect of changing l_p on canopy interception (Fig. 5), potential effects found on standing plant biomass were strong and similar patterns characterised the two clones. Increasing l_p by a factor 1.25–2 decreased $\overline{\text{DM}}_{\text{A1+A2}}$ by about 5% to 30%, while weak effects were found when decreasing l_p . However, decreasing l_p of Tri by a factor 2, which decreased the annual canopy light interception by about 2%, increased $\overline{\text{DM}}_{\text{A1+A2}}$ by about 5% (on average for the entire growing season). In contrast, a substantial increase of about 3% in $\overline{\text{DM}}_{\text{A1+A2}}$ for a decrease of about 6% in the level of light intercepted by its vegetation was found when the same scenario was applied to Gho.

4. DISCUSSION

4.1. Determinants of light capture properties in the actual crops

Like previously detailed by Casella and Sinoquet [3], the two studied poplar crops displayed markedly different canopy structure and growth patterns (Tab. III). The authors also reported a high quality of the reconstructed mock-ups to render light interception properties of the real canopies even if the 3-D CPCA reconstruction method did not consider leaf abscission along the vegetative period. Actually, leaf longevity

of most poplar clones is around 90–120 days [6, 28]. However, as significant clonal variation exists in canopy architecture in poplar [3, 4] (e.g., branching pattern, leaf size and shape and the display of those parameters within space), differences in canopy light interception may be found within this species. Heilman et al. [13] reported a strong clonal variability in τ versus LAI from one-year-old poplar canopies of *P. trichocarpa* and *P. deltoides* clones and their hybrids. Seasonal averaged light extinction coefficients (k) ranging between 0.23 for *P. trichocarpa* \times *P. deltoides* hybrid clone Beaupré to 0.38 for *P. trichocarpa* clone Fritzi Pauley have been estimated from a two-year-old field trial by Ceulemans et al. [5]. Conversely, LAI was reported to be only weakly associated with τ by Niinemets et al. [17] from 13 one-year-old coppice poplar crops of contrasting parentage and hybrid groups, although they observed that μ decreased (from about 0.7–0.3) with increasing LAI (from 2.9–7, respectively). We observed clonal-specific dependencies between τ and LAI but an overall poor correlation was found between μ and LAI in both clones (Fig. 3). As our results show, a high degree of foliage aggregation was quickly achieved by both clones during early spring, revealing that changes in canopy LAI rather than in μ was the determinant factor driving light interception during a large fraction of the growing season. This is in agreement with the observations by Niinemets et al. [17] suggesting that μ should progressively decrease with increasing LAI as a result of an enhanced leaf clumpiness during the entire establishment year of those crop systems, but also during the early stages of crop development for the following growing seasons (Fig. 3).

4.2. Botanical determinants of foliage clumpiness and light harvesting

Studies linking botanical parameters to spatial distribution of leaf area and/or light interception at branch and/or canopy levels were addressed within real plant canopies [4, 17] and by using geometrical models that generate virtual plants of defined architecture [8, 10, 18, 19, 21, 25, 27]. Part of the variability in foliage clumping within poplar canopies was associated with clonal differences in branching patterns [4, 8].

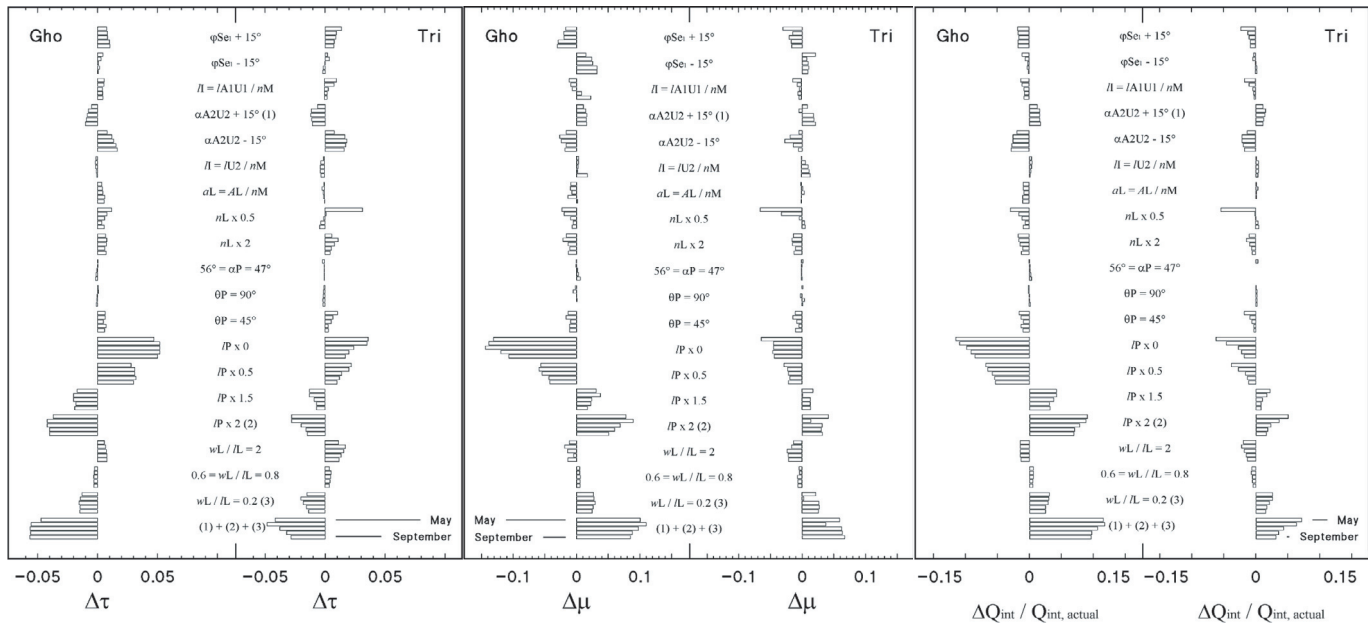


Figure 4. Absolute (left) and relative (right) effects of changing botanical parameters in canopy light transmittance ($\Delta\tau = \tau_{\text{modified}} - \tau_{\text{actual}}$) (Eq. (1)), light interception ($\Delta Q_{\text{int}} / Q_{\text{int,actual}}$, where $\Delta Q_{\text{int}} = Q_{\text{int,modified}} - Q_{\text{int,actual}}$) (Eq. (2)) and clumping index ($\Delta\mu = \mu_{\text{modified}} - \mu_{\text{actual}}$) (Eq. (3)) for poplar clone Gho (Gho) and Trichobel (Tri). Definitions of scenarios are given in Table II.

Chen (1992) reported that canopies with wider branch angles appear to have larger daily light interception, but suggested that this effect should be less important in dense crops than in stands where there are gaps between plant crowns. Here indeed we found that wider branch inclination angles only weakly improved light interception for both canopies (Figs. 1 and 4). For other tree species, simulations revealed that plants with alternate leaf arrangements in spiral phyllotaxies with a phyllotactic angle approaching 135° should be the most efficient species in term of light interception as a result of the optimisation of the distance between leaves that overlap in the vertical projection [18, 25, 27]. However, Gálves and Pearcy [10] demonstrated that actual leaf lamina display largely departs from expectations related to phyllotaxy, due to petiole reorientation. Although leaf size itself may affect leaf aggregation in canopies, decreasing the leaf size by increasing the number of leaves should inevitably intensify self-shading [25]. Both a narrow leaf blade and a long petiole reduce the degree of leaf aggregation around stems or branches and, consequently, shading among the leaves [17, 19–21, 25, 26]. But, even though narrow blades benefit plants in light interception efficiency, greater construction costs should be required for petioles and/or robust midribs to support long and narrow leaf blades [16, 19]. Pearcy and Yang [20] and Takenaka et al. [26] also demonstrated an optimal partitioning between leaf blades and petioles maximising light interception and C gain at plant level. According to our results, leaves with a longer petiole and/or a narrow blade benefit both clones in light interception by reducing the degree of leaf aggregation within canopies (Fig. 4). However, a greater construction cost in terms of biomass will be required for longer petioles in both clones (Fig. 5). Results from all other scenarios showed weak effects

or decreases in canopy light interception (Fig. 4), revealing that (i) light interception was weakly sensitive to shoot geometry, leaf size and phyllotaxy; and (ii) the quality of our reconstructed mock-ups to render light interception was only weakly affected by setting equidistant distribution of branches along shoots and leaves along branches, and constant values in α_P within plant vegetation and in leaf area within branches. However, effects of varying botanical parameters in τ and μ were affected by the total vegetation area (Fig. 4). Actually, the sensitivity of the canopy of Gho to the tested scenarios was generally greater than that of Tri, and decreasing effects over time in μ rather than in τ for Gho and in τ rather than in μ for Tri, were found in all scenarios (Fig. 4). These results suggest a potential to improve canopy-level light interception by changing botanical parameters of canopies characterised by low LAI only (e.g., by changing the leaf shape in Gho).

4.3. Implications for short-rotation coppice poplar crop productivity

Based on the hypothesis h_1 , we found that numerically changing leaf shape from deltoid or ovate to narrow lanceolated is likely to give us the ability to increase productivity of high-density coppice poplar crop systems by improving their light interception. In fact, narrow leaves are expected to improve light harvesting during both the establishment year [17] and the early stages of crop development over the following growing seasons (Fig. 4). This advantage was sustainable during the entire growing season for Gho rather than for Tri (Fig. 4) because of low LAI (Fig. 3). According to hypothesis h_2 , we also pointed out that decreasing rather than

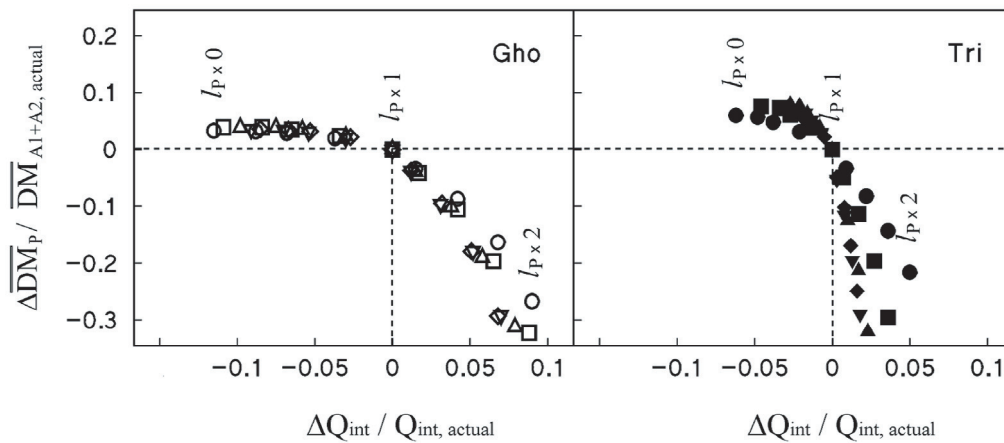


Figure 5. Computed relative effects on potential standing plant biomass ($\Delta \overline{DM}_P / \overline{DM}_{A1+A2, \text{actual}}$, where $\Delta \overline{DM}_P = \overline{DM}_{P, \text{actual}} - \overline{DM}_{P, \text{modified}}$) (Eqs. (4) and (5)) as a function of relative variations in canopy light interception ($\Delta Q_{\text{int}} / Q_{\text{int, actual}}$, where $\Delta Q_{\text{int}} = Q_{\text{int, modified}} - Q_{\text{int, actual}}$) (Eq. (2)) after numerically changing petiole lengths ($l_p \times i$, $i = 0, \dots, 2$) for poplar clone Ghoy (Gho, open symbols) and Trichobel (Tri, closed symbols). Results are given for five consecutive months ($\circ, \bullet =$ May; $\square, \blacksquare =$ June; $\triangle, \blacktriangle =$ July; $\nabla, \blacktriangledown =$ August; $\diamond, \blacklozenge =$ September). Definitions of symbols are given in Table I.

increasing l_p should benefit crop performances of highly productive poplar (e.g., Tri, characterised by big and horizontal leaves) rather than less productive ones (e.g., Gho, characterised by small and highly angled leaves) by optimising C allocation to shoots and/or branches rather than in petioles (Fig. 5). Management options should also be considered since increasing the plant spacing within rows of crops of highly productive poplar is likely to increase their light interception efficiency, while increasing plant densities should benefit less productive ones because of their weak potential in canopy closure dynamic. This is in agreement with previous work reporting that productive poplar plants in wide spacings produce more growth later in the season than did those in dense spacings as a result of a larger proportion of biomass allocated to branches [9].

However, a current limitation of this study is that models like 3-D CPCA address only canopy architecture in its current environment (e.g., hypotheses h_1 and h_2) and not the developmental processes underlying canopy formation and its growth dynamic plasticity in response to changes in light interception. Thus, 3-D CPCA should be linked to developmental-rule process-based models [23] in order to better understand and describe the consequences of a particular arrangement of leaves within space on photosynthetic C gain and allocation to organs [10].

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