Spatial distribution of leaf morphological and physiological characteristics in relation to local radiation regime within the canopies of 3-year-old Populus clones in coppice culture

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Summary  Spatial distributions of leaf characteristics relevant to photosynthesis were compared within high-density coppice canopies of Populus spp. of contrasting genetic origin. We studied three clones representative of the range in growth potential, leaf morphology, coppice and canopy structure: Clone Hoogvorst (Hoo) (Populus trichocarpa Torr. & Gray × Populus deltoides Bartr. & Marsh), Clone Fritz Pauley (Fri) (Populus trichocarpa Torr. & Gray) and Clone Wolterson (Wol) (Populus nigra L.). Leaf area index ranged from 2.7 (Fri and Wol) to 3.8 (Hoo). The clones exhibited large vertical variation in leaf area density (0.02–1.42 m² m⁻³). Leaf dry mass per unit leaf area (DMₐₐ) increased with increasing light in Clones Hoo and Fri, from about 36 g m⁻² at the bottom of the canopy to 162 g m⁻² at the top. In Clone Wol, DMₐₐ varied only from 65 to 100 g m⁻², with no consistent relationship with respect to light. Conversely, nitrogen concentration on a mass basis was nearly constant (around 1.3–2.1%) within the canopies of Clones Hoo and Fri, but increased strongly with light in Clone Wol, from 1.4% at the bottom of the canopy to 4.1% at the top. As a result, nitrogen per unit leaf area (Nₐₐ) increased with light in the canopies of all clones, from 0.9 g m⁻² at the bottom to 2.9 g m⁻² at the top. Although a single linear relationship described the dependence of maximum carboxylation rate (17–93 µmol CO₂ m⁻² s⁻¹) or electron transport capacity (45–186 µmol electrons m⁻² s⁻¹) on Nₐₐ, for all clones, Clone Wol differed from Clones Hoo and Fri by exhibiting a higher dark respiration rate at low Nₐₐ (1.8 versus 0.8 µmol CO₂ m⁻² s⁻¹).

Keywords: canopy profiles, gas exchange, leaf area density, leaf irradiance, light acclimation, mass per area, nitrogen concentration, Populus spp., RATP.

Introduction

In response to concern about global climate change, the search for renewable energy sources is receiving increasing attention (Bolin 1991). Since the 1970s, the culture of woody perennial crops for fuel and fiber on rotations of less than 15 years (short-rotation woody crops, SRWC) has been the subject of much research in North America (Graham 1994, Hohenstein and Wright 1994), Europe and other parts of the world (Grassi et al. 1990). Hardwoods with good coppicing ability include species or clones of the genera Populus, Salix, Eucalyptus and Castanea (Grassi et al. 1990). Poplar (Populus spp.) is a highly productive tree crop, and has been the subject of long-term breeding efforts with superior parental trees and genetically improved clones (Stettler et al. 1996).

Under conditions of non-limiting water and nutrient availability, biomass production is directly related to: (i) the availability of photosynthetically active radiation (PAR) (see Table 1 for list of abbreviations and their definitions); (ii) the proportion of available PAR intercepted by the canopy (εᵢ); and (iii) the efficiency of light use in biomass production (εₑ) (Monteith 1981, Jarvis and Leverenz 1983, Cannell et al. 1988, Cannell 1989, Ford 1992, Medlyn 1998). Because εᵢ is directly related to canopy structure, and εₑ to leaf physiological processes, the spatial distribution of leaf morphological (i.e., area and dry mass) and physiological (i.e., photosynthetic capacity) characteristics along the vertical light gradient within a canopy are the main variables determining crop productivity (Ross 1981, Milne et al. 1992, Harrington et al. 1997). Generally, leaf dry mass (DMₐₐ), nitrogen concentration (Nₐₐ) and photosynthetic capacity per unit leaf area increase from shaded to sunlit leaves within a canopy (Field and Mooney 1986, Ellsworth and Reich 1993, Niinemets 1997c). More than half of foliar nitrogen in C₃ plants is normally invested in the photosynthetic apparatus (Field and Mooney 1986, Evans and Seemann 1989, Makino and Osmond 1991). Moreover, leaf photosynthetic properties (i.e., maximal photosynthetic carboxylation rate (V_cₗₗₗₗ), maximal photosynthetic electron transport capacity (J_cₗₗₗₗ) and mitochondrial respiration rate due to phosphorylative oxidations (R_d)) are strongly correlated with Nₐₐ (Evans 1989, Hollinger 1992, Reich et al. 1994, 1995, Le Roux et al. 1999a, 2001, Niinemets et al. 1999a). Thus, understanding and predicting tree productivity and canopy structural dynamics requires knowledge of leaf nitrogen and its spatial distribution within the canopy.
For many species, a strong and positive correlation between \( N_A \) and local radiation regime has been documented (DeJong and Doyle 1985, Evans 1989, Lemaire et al. 1991, Ellsworth and Reich 1993, Kull and Niinemets 1993, Niinemets 1997c, Le Roux et al. 1999a, 1999b). However, when expressed on a mass basis, leaf \( N \) concentration \( (N_M) \) showed positive (Kull and Niinemets 1993, Niinemets and Kull 1998), constant (Niinemets 1997c, Rosati et al. 2000, Le Roux et al. 2001) or negative (Kull and Niinemets 1993, Niinemets 1995, 1997c, Rosati et al. 2000) correlations with leaf irradiance. Because \( N_A \) is the product of \( DM_A \) and \( N_M \), as suggested by Niinemets and Tenhunen (1997) and by Le Roux et al. (1999b), the relationships observed between \( N_A \) and local radiation regime may be the result of an increase with irradiance in \( DM_A \) or \( N_M \), or both. Consequently, traditional model analyses of nitrogen effects on photosynthesis need to describe the investment in leaf dry mass per area as well as in leaf nitrogen concentration per unit mass. Variations in these processes as an expression of genetic variability must also be taken into account (Ceulemans et al. 1990, Hinckley et al. 1992).

The objectives of this study were to characterize and compare three poplar clones in terms of: (i) intra-canopy distribution of leaf area density; (ii) intra-canopy variability of leaf dry mass per area, leaf carbon and nitrogen concentrations, and values of the key parameters of the \( C_3 \) photosynthesis model; and (iii) the relationship between leaf characteristics and mean daily time-integrated leaf irradiance \( (Q_{ti}) \), as simulated by the radiation transfer part of the radiation absorption, transpiration and photosynthesis (RATP) model (Sinoquet et al. 2001). In addition, sources of variation in photosynthetic capacity within the three poplar canopies were compared by the approach proposed by Niinemets and Tenhunen (1997).

### Materials and methods

#### Plant material and plantation layout

Measurements were carried out during the third growing season (1999) in a 0.56 ha experimental field at Boom (51°05' N, 4°22' E; 5 m a.s.l.), Belgium. The plantation consists of 17 poplar clones of differing parentage and belonging to dif-

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**Table 1. List of symbols and abbreviations.**

<table>
<thead>
<tr>
<th>Symbol/abbreviation</th>
<th>Definition</th>
</tr>
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<tbody>
<tr>
<td>( A, \bar{A} )</td>
<td>Leaf area and mean leaf area (cm²), respectively</td>
</tr>
<tr>
<td>( A_a )</td>
<td>Leaf net CO₂ assimilation (µmol CO₂ m⁻² s⁻¹)</td>
</tr>
<tr>
<td>( C_a )</td>
<td>Atmospheric partial CO₂ pressure (Pa)</td>
</tr>
<tr>
<td>( C_l )</td>
<td>Sub-stomatal partial CO₂ pressure (Pa)</td>
</tr>
<tr>
<td>( C_{M, A} )</td>
<td>Leaf carbon concentration expressed per unit of leaf dry mass (g g⁻¹) and per unit of leaf area (g m⁻²)</td>
</tr>
<tr>
<td>( D, \bar{D} )</td>
<td>Individual and mean shoot diameter (mm) measured at 22 cm above the ground</td>
</tr>
<tr>
<td>( DM, DM_A )</td>
<td>Leaf dry mass (g) and leaf dry mass expressed per unit of leaf area (g m⁻²)</td>
</tr>
<tr>
<td>( \varepsilon_c )</td>
<td>Canopy light conversion efficiency</td>
</tr>
<tr>
<td>( \varepsilon_i )</td>
<td>Canopy light interception efficiency</td>
</tr>
<tr>
<td>( FM, FM_A )</td>
<td>Leaf fresh mass (g) and leaf fresh mass expressed per unit of leaf area (g m⁻²).</td>
</tr>
<tr>
<td>( Fri )</td>
<td>Clone Fritz Pauley, \textit{P. trichocarpa}</td>
</tr>
<tr>
<td>( H )</td>
<td>Shoot height (m)</td>
</tr>
<tr>
<td>( Hoo )</td>
<td>Clone Hoogvorst, \textit{P. trichocarpa} x \textit{P. deltoides}</td>
</tr>
<tr>
<td>( J_{\text{max}} )</td>
<td>Maximal photosynthetic electron transport capacity (µmol electrons m⁻² s⁻¹)</td>
</tr>
<tr>
<td>( L )</td>
<td>( L = 1 ) to 10, the horizontal layer number</td>
</tr>
<tr>
<td>( LAD )</td>
<td>Leaf area density (m² m⁻³)</td>
</tr>
<tr>
<td>( LAI )</td>
<td>Leaf area index (m² m⁻³)</td>
</tr>
<tr>
<td>( N_{M, A} )</td>
<td>Leaf nitrogen per unit dry mass (g g⁻¹) and per unit area (g m⁻²)</td>
</tr>
<tr>
<td>( NL )</td>
<td>Number of leaves</td>
</tr>
<tr>
<td>( NS )</td>
<td>Number of shoots</td>
</tr>
<tr>
<td>( O_a )</td>
<td>Atmospheric partial O₂ pressure (kPa)</td>
</tr>
<tr>
<td>( Q )</td>
<td>Incident photon flux density (µmol PAR m⁻² s⁻¹)</td>
</tr>
<tr>
<td>( Q_{ti} )</td>
<td>Mean daily intra-canopy time-integrated leaf irradiance (mol PAR m⁻² day⁻¹)</td>
</tr>
<tr>
<td>( PAR )</td>
<td>Photosynthetically active radiation</td>
</tr>
<tr>
<td>( P_{\text{max}} )</td>
<td>Maximum value of the photosynthetic activity (µmol CO₂ m⁻² s⁻¹)</td>
</tr>
<tr>
<td>( RATP )</td>
<td>Radiation absorption, transpiration and photosynthesis model (Sinoquet et al. 2001)</td>
</tr>
<tr>
<td>( R )</td>
<td>Total respiration rate (µmol CO₂ m⁻² s⁻¹, ( R = R_d + R_l ))</td>
</tr>
<tr>
<td>( R_l )</td>
<td>Photorespiration rate (µmol CO₂ m⁻² s⁻¹)</td>
</tr>
<tr>
<td>( R_d )</td>
<td>Mitochondrial respiration rate due to phosphorylative oxidations (µmol CO₂ m⁻² s⁻¹)</td>
</tr>
<tr>
<td>( SRWC )</td>
<td>Short-rotation woody crop</td>
</tr>
<tr>
<td>( V_{\text{max}} )</td>
<td>Maximal photosynthetic carboxylation rate (µmol CO₂ m⁻² s⁻¹)</td>
</tr>
<tr>
<td>( V_L )</td>
<td>Horizontal layer volume (m³), ( V_L = 36.45 ) m³ (experimental plot area) x height of layer (m)</td>
</tr>
<tr>
<td>( Wol )</td>
<td>Clone Woltersen, \textit{P. nigra}</td>
</tr>
</tbody>
</table>
ler hybrid groups (Deraedt and Ceulemans 1998). Three clones were considered in this study: Hoogvorst (Hoo) (Populus trichocarpa Torr. & Gray × Populus deltoides Bartr. & Marsh), Fritzi Pauley (Fri) (Populus trichocarpa Torr. & Gray) and Wolteron (Wol) (Populus nigra L.) (Table 2).

A randomized block design with three replications per clone was used following a protocol prescribed by U.K. Forest Research (Armstrong 1997). In April 1996, hardwood cuttings (25 cm) were planted in a double-row design with alternating inter-row distances of 0.75 and 1.5 m, and a spacing of 0.9 m within rows, resulting in an overall density of about 10,000 stools per ha. Individual plot size was 9 × 11.5 m and contained 10 rows of 10 stools each. In December 1996, all stools were cut back to a height of 5 cm to create a multi-shoot coppice system. Measurements were taken on 36 stools in the center of one selected plot per clone.

Development of leaf area index

An LAI-2000 plant canopy analyzer (Li-Cor, Lincoln, NE) was used to estimate leaf area index (LAI) of each experimental plot every 3 weeks between April 1 (Day 91) and August 13 (Day 223). A total of 22 below-canopy measurements were made above the soil surface in different directions to account for spatial variation and planting design. Four zenith angles (from 0 to 58°) with a 270° view restrictor were used in all measurements to encompass the restricted dimensions of the plots and to occlude the operator from the view area. Above-canopy measurements were taken automatically every 15 s from a platform 8 m above the stand.

Light and CO₂ response curves

From August 16 to 22, 1999 (Days 228–234), light (Q) and CO₂ (C𝑖) response curves of leaf net photosynthesis (𝐴𝑛) were measured. As the selected plots experienced a weak water deficit period in July, all measurements were made after an 8-day rainy period to ensure that photosynthetic rate was unaffected by water deficiency. Gas exchange measurements were made on days with completely overcast sky between 0700 and 1900 h (0600–1800 h, UT). Gas exchange was measured with an infrared gas analyzer/leaf chamber system (Li-Cor LI-1900, 1500, 1000, 500, 400, 300, 200, 100, 75, 50, 25 and 0 µmol PAR m⁻² s⁻¹) while leaf temperature and water vapor pressure deficit in the cuvette were maintained at 25 ± 0.3 °C and 1 ± 0.1 kPa, respectively.

At each canopy height, three 𝐴𝑛–𝐶𝑖 response curves were measured at saturating Q and low atmospheric partial O₂ pressure (𝑂₂) (Q = 1500 µmol PAR m⁻² s⁻¹, O₂ = 2 kPa). Similarly, three 𝐴𝑛–Q response curves were measured at high atmospheric partial CO₂ pressure (𝐶𝑖) and normal O₂ (𝐶𝑖 = 100 Pa, O₂ = 21 kPa). The data were used to estimate best-fit values of 𝑉_{max} (from the 𝐴𝑛–𝐶𝑖 response curves) and 𝐼_{max} (from the 𝐴𝑛–Q response curves) by nonlinear least squares regression. For each response curve, a new leaf was used. Values of 𝑅_{p}, resulting from processes other than photorespiration, were estimated from the 𝐴𝑛–Q response curves at high O₂ and from the 𝐴𝑛–𝐶𝑖 response curves at low O₂. To test the potential effects of stress resulting from the 𝐴𝑛–𝐶𝑖 measurements made at low O₂, two successive 𝐴𝑛–𝐶𝑖 response curves were measured at low and normal O₂ on the same leaf at 4 and 5 m above the soil surface for Clone Wol and for Clones Hoo and Fri, respectively. For all curves, 9 to 12 measurements were acquired (𝐶𝑖 = 150, 100, 75, 50, 35, 20, 15, 10 and 5 Pa, and Q = 2000, 1500, 1000, 500, 400, 300, 200, 100, 75, 50, 25 and 0 µmol PAR m⁻² s⁻¹) while leaf temperature and water vapor pressure deficit in the cuvette were maintained at 25 ± 0.3 °C and 1 ± 0.1 kPa, respectively.

After each gas exchange measurement, the leaf was collected and placed on ice. Leaf area (A) was measured in the laboratory with a laser area meter (CI-203, CID, Vancouver, WA). The leaf was then dried (70 °C for 48 h) and nitrogen concentration on a mass basis (N₀₀₃) was determined with a dynamic flush combustion method using an NC 2100 soil autoanalyzer (Carlo Erba Strumentazione, Rodano, Italy).

Profiles of leaf area and leaf area density

On August 22 (Day 234), 1999, LAI of the three experimental plots was measured with an LAI-2000 plant canopy analyzer. Thereafter, the vertical profile of leaf area density (LAD) of each canopy was estimated by a scaling-up approach. The diameter (𝐷) of all shoots per plot was measured at 22 cm above the ground with a digital calliper (Absolute Digimatic, Mitutoyo, U.K.) and the cumulated basal area was calculated. For each clone, the cumulated basal area was divided into three equal classes (𝐶𝑖) and the mean diameter of each class (𝑀𝑖) was calculated (Table 3). One shoot with a diameter close to the 𝑀𝑖 was selected from the inside border

<table>
<thead>
<tr>
<th>Name</th>
<th>Code number</th>
<th>Sex</th>
<th>Parentage</th>
<th>Parental code number</th>
<th>Provenance</th>
<th>Country</th>
<th>State or province</th>
<th>Latitude</th>
<th>Longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hoogvorst</td>
<td>69.038-6</td>
<td>F</td>
<td>P. trichocarpa × P. deltoides</td>
<td>V.235 × S.620-225</td>
<td>USA</td>
<td>Michigan</td>
<td>Washington</td>
<td>49°N</td>
<td>122°30’W</td>
</tr>
<tr>
<td>Fritzi Pauley</td>
<td>V.235</td>
<td>F</td>
<td>P. trichocarpa</td>
<td>–</td>
<td>USA</td>
<td>Washington</td>
<td>49°N</td>
<td>122°30’W</td>
<td></td>
</tr>
<tr>
<td>Wolteron</td>
<td>1026</td>
<td>F</td>
<td>P. nigra</td>
<td>–</td>
<td>The Netherlands</td>
<td>Doesburg (IJsel river)</td>
<td>51°59’N</td>
<td>6°06’E</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Clonal name, code number, sex, parentage and place of origin of the three Populus clones used in this study.
rows of the plot. Each selected shoot was divided into horizontal layers \((L)\) of 0.5 or 1.0 m height (from the soil surface to the top of the canopy), and all leaves of each layer were harvested. For each layer, the number of leaves \((NL_{CL})\), total leaf area \((A_{CL})\) and total fresh mass \((FM_{CL})\) were measured with a laser area meter and an electronic scale, respectively (Table 4). Total leaf dry mass \((DM_{CL})\) was determined for each harvest after 48 h at 70 °C. The LAD of each canopy layer \((LAD_L)\) was estimated by scaling-up from the measured value of \(A_{CL}\) to estimate the total leaf area per layer and per experimental plot area \((A_L)\). For each layer, \(A_L\) was estimated by multiplying \(A_{CL}\) by the number of shoots \((NS_{CL})\) in the corresponding shoot diameter class, and summing over all classes. The LAD\(_L\) value was then calculated by dividing \(A_L\) by the volume of the corresponding layer:

\[
LAD_L = \frac{\sum_{CL=1}^{CL=3} A_{CL} \cdot NS_{CL}}{V_L},
\]

where \(V_L = \text{experimental plot area} \times \text{height of layer}\).

The number of leaves per unit of ground area \((NL_L)\) (Equation 2) and the leaf fresh and dry masses per unit of leaf area \((FM_{AL}, DM_{AL})\), respectively) (Equation 3) were estimated per layer by the same method:

\[
NL_L = \frac{\sum_{CL=1}^{CL=3} NL_{CL} \cdot NS_{CL}}{36.45},
\]

where 36.45 is the experimental plot area \((m^2)\), and

\[
\alpha M_{AL} = \frac{\sum_{CL=1}^{CL=3} \alpha M \cdot NS_{CL}}{\sum_{CL=1}^{CL=3} A_{CL} \cdot NS_{CL}},
\]

where \(\alpha M\) denotes FM or DM for fresh or dry mass, respectively.

Finally, from August 23 to 25, 1999 (Days 235–237), leaves were sampled at 0.5- or 1.0-m intervals along three transects: South–North, East–West, and bottom–top in the canopy for each clone. Samples were collected between 1300 and 1500 h, UT. The three transects intersected at a common point in the center of the canopy. For each 1-m horizontal segment, 10 leaves (for each segment located below 5 m height above the soil surface; all clones) or three to five leaves (for each segment located above 5 m height above the soil surface; all clones) were collected.
ment located at 5 and 6 m height above the soil surface; Clones Hoo and Fri) were harvested and pooled. For each segment, only leaves that made contact with a string demarcating the transect were sampled, excluding the oldest leaves. Leaf material was placed on ice immediately after sampling. For each sample, individual A and total FM were measured in the laboratory. Thereafter, sampled leaves were dried at 70 °C for 48 h and the total leaf DM and N_M were determined.

Simulated radiation regime within the canopy

Estimated spatial radiation distribution within the canopy was computed by means of a three-dimensional (3-D) version of the RATP model (Sinoquet et al. 2001). This is an improved version of the radiation interception in row intercropping (RIRI) model (Sinoquet et al. 1997) developed by Sinoquet and Bonhomme (1992). The 3-D radiative transfer part of the RATP model is able to calculate canopy light interception based on the turbid medium analogy and deals with direct and diffuse incident radiation as well as with scattered radiation. The model also uses canopy architecture, leaf optical properties, and leaf inclination distribution as input parameters (for more details, see Sinoquet et al. 2001).

The space occupied by the canopy of each clone was divided into horizontal layers (12 for Clone Hoo, 14 for Clone Fri and 10 for Clone Wol). Each layer had dimensions of 36.45 m² × 0.5 m height, consistent with the experimental plot dimensions and with the LAD measurements. Leaf angle distributions were measured with a clinometer (PM-5/360 PC, Suunto, Finland) on a set of 20 leaves per layer. The RATP model was run for the entire diurnal period with a 30-min time step, using incident radiation data measured during a 1-week period before the sampling date (Day 234).

Results

Development of LAI

At the canopy scale, the measured values of LAI showed that the growing season for Clones Hoo and Fri began about 15 days earlier than for Clone Wol (Figure 1). All clones showed a similar development in mean LAI during the first month of growth (+2.3, on average). The mean maximum LAI, measured during the first 15 days of July (Days 183 and 198), showed that Clone Hoo had reached a maximum LAI of 5.1 (± 0.5) compared with values of 4.1 (± 0.3) and 3.9 (± 0.3) for Clones Fri and Wol, respectively.

As a result of a slight water deficit in July, indicated by leaf abscission in the lower part of the canopies, mean values of LAI decreased by 1 in all clones on August 13 (Day 223) (Figure 1). Given the small size of the plots, the LAI-2000 plant canopy analyzer could have underestimated LAI, because the amount of diffuse radiation arriving through the plot edges was increased as a result of the drought-induced leaf abscission.

Leaf area and LAD clonal canopy characteristics

In mid-August, Clone Wol had three times more leaves than...
Clones Hoo and Fri, but with a mean leaf area ($A$) that was less than one-third that of the other clones (Table 4). The vertical distribution of NL (Equation 2 and Table 4) and $A$ (Table 4) showed that for all clones: (i) 60 to 70% of the leaves were located in the central part of the canopy (between heights of 3 and 5, 2 and 4, and 2 and 3.5 m for clones Hoo, Fri and Wol, respectively); and (ii) $A$ increased with height. In terms of spatial distribution of LAD (Equation 1 and Figure 2), Clones Hoo and Wol had a larger range of values than Clone Fri (0.11–1.42 versus 0.02–0.78).

Profiles of leaf fresh and dry mass per area
The range of leaf fresh mass per unit leaf area ($F_M$) and $D_M$ within the canopy profile was larger for Clones Hoo and Fri than for Clone Wol (Figure 3). For each clone, the results obtained by scaling-up (Equation 3) and by the transect method showed similar vertical profiles of $F_M$ and $D_M$. Results for the South–North and the East–West transects also compared well. For Clones Hoo and Fri, $F_M$ and $D_M$ increased with height, as determined by the transect method (Figure 3). In contrast, for the top three layers in the canopy of Clone Wol, $F_M$ was constant and $D_M$ decreased with height. The results obtained by scaling-up showed similar trends for the top canopy layers of Clones Hoo and Fri (Figure 3).

Leaf carbon and nitrogen profiles
The distribution of total leaf carbon (results not shown) and total leaf nitrogen (Figure 4) expressed per unit of dry mass ($C_M$ and $N_M$, respectively) and per unit of leaf area ($C_A$ and $N_A$, respectively), showed similar vertical profiles in both the South–North and the East–West transects. Values of $C_M$ were constant for the entire canopy of all clones (43.5 ± 0.7, 44.5 ± 0.7 and 43.8 ± 0.9 for Clones Hoo, Fri and Wol, respectively) and $C_A$ profiles were similar to $D_M$ profiles. Moreover, in contrast to the low variability in the vertical distribution of $N_M$ for Clones Hoo and Fri, $N_M$ in the canopy of Clone Wol ranged widely (Figure 4). However, when expressed per unit of leaf area, the canopies of all clones showed similar ranges and similar vertical profiles between $N_A$ and height (Figure 4).

Correlation between leaf characteristics and the local radiation regime
As simulated by the RATP model over a 1-week period (Table 4), $Q_{Ti}$ ranged from 1.2 (at the bottom of the canopy) to 22.3 mol PAR m$^{-2}$ day$^{-1}$ (at the canopy top) for Clone Hoo,
and from 3.1 to 21.8 mol PAR m⁻² day⁻¹ and 3.3 to 22.5 mol PAR m⁻² day⁻¹ for Clones Fri and Wol, respectively. The DMₐ increased nonlinearly with \( Q_{\text{ti}} \) in Clones Hoo and Fri, but not in Clone Wol (Figure 5). The correlation between \( N_{\text{M}} \) and \( Q_{\text{ti}} \) (Figure 5) was pronounced and nonlinear for Clone Wol (from 1.4, near the bottom, to 4.1%, near the top of the canopy), but was weak and linear for Clones Hoo and Fri. Leaf nitrogen per unit area increased nonlinearly with \( Q_{\text{ti}} \) (Figure 5) and the clones showed a similar shape for the \( N_{\text{A}}-Q_{\text{ti}} \) relationships, with similar profiles for Clones Fri and Wol.

**Profiles of photosynthetic capacity**

Figure 6 shows the \( A_{\text{L}-C} \) response curves obtained at partial \( O_2 \) pressures of 2 and 21 kPa. There was no effect of low \( O_2 \) on the maximum value of the photosynthetic activity (Figure 6) or on \( V_{\text{cmax}} \) (Figure 6 and 7). For each clone, photosynthetic capacity varied strongly within the canopy (Figure 7). Values of \( V_{\text{cmax}} \) and \( J_{\text{max}} \) ranged from 17 µmol electrons m⁻² s⁻¹ (near the bottom of the canopy) to 93 µmol CO₂ m⁻² s⁻¹ (near the top), and from 45 to 186 µmol electrons m⁻² s⁻¹, respectively. Values of \( R_3 \) ranged from 0.81 µmol CO₂ m⁻² s⁻¹ (near the bottom of the canopy) to 2.79 µmol CO₂ m⁻² s⁻¹ (near the top) for Clones Hoo and Fri, and from 1.79 to 2.72 µmol CO₂ m⁻² s⁻¹ for Clone Wol. For all clones, these variables were highly correlated (\( r^2 > 0.83, P < 0.0001 \)) with \( N_{\text{A}} \) (Figure 7). A single linear relationship described the dependence of \( V_{\text{cmax}} \) or \( J_{\text{max}} \) on \( N_{\text{A}} \) for all clones. However, two linear relationships between \( R_3 \) and \( N_{\text{A}} \) were observed, one for Clone Wol and another for Clones Hoo and Fri combined (Figure 7).

**Discussion**

**Light effects on leaf size and on LAD profiles**

Despite differences in coppice structure (in terms of density and mean size of the shoots) (Table 3) and canopy morphology (in terms of number and geometry of leaves) (Table 4), the three poplar clones studied showed a similar \( Q_{\text{ti}} \) profile in their canopies (1.2–22.5 mol PAR m⁻² day⁻¹). For all clones, individual mean leaf area per layer \( (\bar{A}_L) \) increased with increasing \( Q_{\text{ti}} \) (Table 4). However, the middle part of the canopy had the largest total number of leaves, leaf area and thus the largest LAD (Table 4 and Figure 2). This foliar distribution pattern within a canopy is characteristic of the majority of deciduous trees (Greitner et al. 1994, Ross and Ross 1996, Mandre et al.)
1998) and corresponds to a part of the canopy where the largest total mass of branches and leaves is present (Mandre et al. 1998).

Light effects on DM_A, N_M and N_A profiles

The canopies of Clones Hoo and Fri differed from the canopy of Clone Wol in DM_A and N_M profiles. Clones Hoo and Fri showed high variability in their DM_A profile with Q_{ti}, in contrast with the small effect of increasing Q_{ti} on DM_A of Clone Wol (Figure 5). The latter pattern is in agreement with the results reported for Populus tremula L. (Mandre et al. 1998, Niinemets and Kull 1999, Niinemets et al. 1999b). As in P. tremula (Ninemets and Kull 1999), there were rather weak variations in the N_M profile of Clones Hoo and Fri with increasing Q_{ti}, contrasting with the high variation for Clone Wol (Figure 5).

Because N_A is the product of DM_A and N_M, variations in DM_A or N_M, or both, can explain within-canopy variations in N_A with local radiation regime. All clones showed similar non-linear N_A profiles related to Q_{ti} (Figure 5). For Clones Hoo and Fri, intra-canopy variation in N_A resulted mainly from changes in DM_A and to a lesser extent from changes in N_M (Figure 5). In contrast to Clones Hoo and Fri and to several reports for various shade-intolerant species (Fagus sylvatica L. (Ninemets 1995), Acer platanoides L. (Ninemets 1997c), Picea abies L. (Ninemets 1997a, 1997b), P. tremula, Fraxinus excelsior L. (Ninemets and Kull 1998, Ninemets et al. 1999b), Juglans regia L. (Le Roux et al. 1999b) and Prunus persica L. (DeJong and Doyle 1985, Rosati et al. 2000, Le Roux et al. 2001)), Clone Wol exhibited an exponential N_M profile and a decrease in N_A with increasing Q_{ti}.

Figure 5. Leaf dry mass per unit area (DM_A), leaf nitrogen concentration expressed on a mass basis (N_M) or an area basis (N_A) versus daily time-integrated leaf irradiance (Q_{ti}) for clones Hoogvorst (○), Fritzi Pauley (■) and Wolterson (▲). The vertical bars depict the standard deviation of the mean.

Figure 6. Representative CO_2 (C_i) response curves of net photosynthesis (A_n) obtained at low (2 kPa; open symbols) or high (21 kPa; closed symbols) O_2 atmospheric partial pressure (O_{a}) at 5 m height above the soil surface for Clones Hoogvorst (○; Hoo) and Fritzi Pauley (■; Fri) and at 4 m for Clone Wolterson (▲; Wol). Measurements were made in August 1999, and each curve was fit according to the Farquhar et al. (1980) model. For each response curve, the corresponding values for maximum photosynthetic activity (P_{max}), maximum rate of carboxylation (V_{cmax}) and total respiration rate (R = R_d + R_l) are presented.
in $DM_A$ (100–73 g m$^{-2}$) at $Q_A$, higher than 10–12 µmol PAR m$^{-2}$ day$^{-1}$ (Figure 5). This is in accordance with results reported for various shade-tolerant species (e.g., *Populus cordata* L. and *Corylus avellana* L. (Niinemets and Kull 1998)) as well as for some shade-intolerant species (*Eucalyptus grandis* W. (Leuning et al. 1995) and *L. and data*). In our clones, $N_A$ was nonlinearly related to $Q_A$. Niinemets and Kull (1999) and Le Roux et al. (2001) observed a curvilinear relationship between $DM_A$ and $N_A$ versus $Q_A$ in *Tilia cordata* Mill and *P. persica*, respectively. Lemaire et al. (1991) reported similar results for a dense canopy of lucerne. In contrast, DeJong and Doyle (1985), Rosati et al. (2000) and Le Roux et al. (2001) observed a linear relationship between $N_A$ and $Q_A$ if $Q_A$ was expressed as hours per day at PAR higher than 100 µmol m$^{-2}$ s$^{-1}$. Additionally, in our study, because only the number of leaves, mean leaf area and leaf angle distributions per shoot diameter class were assessed and scaled-up per horizontal canopy layer, a spatially random distribution of the foliage had been assumed for simulating the vertical profile of $Q_A$ within the canopies. However, the average probability of diffuse and direct radiation transmittance to a forest floor can be about 10% larger from a three-dimensional model simulation (i.e., taking into account the clumping of canopy elements) than if a random distribution of the foliage is assumed (Law et al. 2001). So, the assumption of random distribution of the foliage at the horizontal canopy layer level could be violated especially for the top part of our canopies, because of the presence of long unbranching shoot leaders with closely aggregated leaves in the top 6–8 m height layers (Table 4, Figure 2). This may have resulted in over- and underestimated simulated $Q_A$ values for the higher and lower parts of the canopies, respectively. Taking these limitations into account, our results, as confirmed by the similar nonlinear relationships between $N_A$ and $Q_A$ for all three clones (Figure 5), have shown the relative importance of changes in $DM_A$ or in $N_M$ in explaining intra-canopy variations in $N_A$.

**Sources of variation in photosynthetic capacity within the three poplar canopies**

Photosynthetic capacities of leaves measured under standard conditions varied strongly within the canopy, but are in agreement with results reported for *Populus* spp. (Ceulemans and Isebrands 1996) and for *P. tremula* (Niinemets et al. 1998, 1999a). Results obtained by Niinemets et al. (1998) ranged from around 24 to 68 µmol CO$_2$ m$^{-2}$ s$^{-1}$ for $V_{\text{cmax}}$ and from around 54 to 175 µmol CO$_2$ m$^{-2}$ s$^{-1}$ for $J_{\text{cmax}}$. Although a single linear relationship described the dependence of $V_{\text{cmax}}$ or $I_{\text{cmax}}$ on $N_A$ for all clones (Figure 7), Clone Wol differed from Clones Hoo and Fri by having a higher dark respiration rate at low $N_A$. In general, respiration rates are higher in shade-intolerant species than in shade-tolerant species (Grime 1966). Mean annual dry mass yield estimations from the 3-year-old shoots of all clones showed that biomass production of Clone Wol was 30 and 40% lower than biomass production of Clones Fri and Hoo, respectively (Laureysens et al. 2001).

![Figure 7. Relationships between the three principal parameters of the photosynthesis model: maximum rate of carboxylation ($V_{\text{cmax}}$), light-saturated rate of electron transport ($J_{\text{cmax}}$), and dark respiration rate ($R_d$) versus leaf nitrogen concentration expressed on an area basis ($N_A$) for poplar clones Hoogvorst (●), Fritzi Pauley (▲) and Woltersen (●). Measurements were performed on leaves along the bottom–top transects at 2, 3 and 4 m height above ground for Clone Woltersen and at 3, 4 and 5 m height above ground for Clones Hoogvorst and Fritzi Pauley, and modeled from A$_n$–C$_i$ response curves at 2 kPa of O$_2$ and from A$_n$–Q response curves at 21 kPa of O$_2$. Open symbols denote values obtained from the A$_n$–C$_i$ response curves at 21 kPa of O$_2$ at 4 m height above ground for Clone Woltersen and at 5 m above ground for Clones Hoogvorst and Fritzi Pauley (see Figure 6). Relationships between $N_A$ and $V_{\text{cmax}}$, $J_{\text{cmax}}$ and $R_d$ were fit to the following linear regressions: $y = a (\pm \text{SE}) x + b (\pm \text{SE})$ for $P < 0.0001$.](http://heronpublishing.com)
that developed under sun conditions and experienced progres-
vation (between –80 and +80° against –40 to +40° for Clones
leaves; (iv) a weaker leaf area profile within the canopy; and
Clones Hoo and Fri, Clone Wol had strongly different coppice
shade leaves reflected a change in DMA rather than in
who initially. In contrast to
Clones Hoo and Fri, the light regime simulated
new leaves formed later
ontogeny. Generally, poplar spp. are fast-growing and produce
the relationships observed between \( N_M \) and \( Q_a \) may be the re-
during leaf irradiance; and (ii) traditional model analyses of nitrogen ef-
s the investment in leaf dry mass per area as well as in leaf nitrogen concentration per

changes in \( N_M \) (+24%, +26%). In contrast, for Clone Wol, the spatial variations in \( V_{\text{cmax}} \) (+149%) resulted mainly from changes in \( N_M \) (+73% against +18% for DMA) (Table 5, Figure 5). Results obtained for Clones Hoo and Fri are consistent with those reported for other tree species (Niinemets et al. 1998, Le Roux et al. 1999a, 1999b, 2001, Rosati et al. 1999).

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Table 5. Characteristics and comparison of concurrent changes in maximum carboxylation rate (\( V_{\text{cmax}} \)), leaf dry mass per area (\( \text{DMA} \)), and leaf nitrogen concentration on a mass basis (\( N_M \)) along mean daily intra-canopy time-integrated leaf irradiance gradients (\( Q_a \); mol PAR m\(^{-2}\) day\(^{-1}\)) in poplar canopies. Results were computed from equations given in Figures 5 and 7.

<table>
<thead>
<tr>
<th>Clone</th>
<th>( Q_a = 3 )</th>
<th>( Q_a = 15 )</th>
<th>( (Q_a = 15)/(Q_a = 3) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hoogvorst</td>
<td>46.3</td>
<td>81.9</td>
<td>1.77</td>
</tr>
<tr>
<td>DM(_A) (g m(^{-2}))</td>
<td>97.8</td>
<td>141.6</td>
<td>1.45</td>
</tr>
<tr>
<td>( N_M ) (%)</td>
<td>1.64</td>
<td>2.04</td>
<td>1.24</td>
</tr>
<tr>
<td>Fritzi Paudey</td>
<td>30.3</td>
<td>75.5</td>
<td>2.49</td>
</tr>
<tr>
<td>DM(_A) (g m(^{-2}))</td>
<td>74.2</td>
<td>151.7</td>
<td>2.04</td>
</tr>
<tr>
<td>( N_M ) (%)</td>
<td>1.33</td>
<td>1.67</td>
<td>1.26</td>
</tr>
<tr>
<td>Wolterson</td>
<td>30.3</td>
<td>75.5</td>
<td>2.49</td>
</tr>
<tr>
<td>DM(_A) (g m(^{-2}))</td>
<td>80.5</td>
<td>95.3</td>
<td>1.18</td>
</tr>
<tr>
<td>( N_M ) (%)</td>
<td>1.61</td>
<td>2.78</td>
<td>1.73</td>
</tr>
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</table>

In conclusion, our results confirm the suggestions of Niinemets and Tenhunen (1997) and Le Roux et al. (1999b) that: (i) the relationships observed between \( N_M \) and \( Q_a \) may be the result of an increase in \( \text{DMA} \) or \( N_M \) with increasing leaf irradiance; and (ii) traditional model analyses of nitrogen effects on photosynthesis need to describe the investment in leaf dry mass per area as well as in leaf nitrogen concentration per mass.

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