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Light-use efficiency of native and hybrid poplar genotypes at high levels of intracanopy competition

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Abstract: In southern Wisconsin, U.S.A., tree growth and associated canopy traits were compared among five native and hybrid genotypes of poplar (*Populus* spp.) in replicated, monoclonal stands planted at a 1 × 1 m spacing. The overall objective of this study was to assess clonal suitability to cultural conditions entailing high levels of intracanopy competition (such as high-density plantations or long rotations) and to identify selection criteria suitable to such conditions. Two of the clones were *Populus deltoides* Bartr., two were *P. deltoides* × *Populus nigra* L. (DN) crosses, and the fifth was a *P. nigra* × *Populus maximowiczii* A. Henry (NM) cross. In the third year after establishment, variation in aboveground biomass gain (ANBG) was analyzed in relation to canopy light interception (IPAR) and canopy light-use efficiency (LUE) during a 31-day period when growing conditions were most favorable (late June through late July). ANBG in this interval varied by twofold among genotypes (2.76–5.78 $Mg \cdot ha^{-1}$), and it was highest in the two *P. deltoides* clones, followed by the NM and DN hybrids, respectively. Across genotypes, ANBG was unrelated to IPAR, which varied by only 5%. Instead, it was strongly and positively related ($r^2 = 0.99$) to the twofold variation in LUE (1.06–2.22 $g \cdot MJ^{-1}$). Among measured canopy traits, the best predictor of LUE ($r^2 = 0.88$) was an additive combination of factors associated to the optimization of canopy photosynthesis: LUE was negatively related to both the canopy light-extinction coefficient and compensation irradiance at the canopy base. We infer from these findings that poplar genotypes can vary considerably in LUE and, correspondingly, in the extent to which photosynthesis is optimized in dense canopies. Furthermore, the low LUE among hybrid genotypes at this level of intracanopy competition may reflect a bias in "tree improvement" efforts towards maximizing biomass production under conditions of relatively low competition.

Résumé : La croissance des arbres et les caractéristiques correspondantes du couvert ont été comparées chez cinq génotypes natifs et hybrides de peuplier (*Populus* spp.) dans des peuplements monoclonaux répliqués et plantés avec un espacement de 1 m dans le Sud du Wisconsin, aux États-Unis. L'objectif global de cette étude était de déterminer si ces clones étaient adaptés à des conditions culturales caractérisées par une forte compétition dans le couvert (comme des plantations à forte densité ou de longues rotations) et d'identifier des critères de sélection adaptés à de telles situations. Deux des clones étaient des *Populus deltoides* Bartr., deux autres clones étaient des croisements de *P. deltoides* × *Populus nigra* L. (DN), et le cinquième était un croisement de *P. nigra* × *Populus maximowizcii* A. Henry (NM). Au cours de la troisième année qui a suivi la plantation, la variation de gain en biomasse aérienne a été analysée en relation avec l'interception de la lumière par le couvert et l'efficacité d'utilisation de la lumière par le couvert, durant une période de 31 jours pendant laquelle les conditions de croissance étaient les plus favorables (de la fin juin à la fin juillet). Au cours de cette période, le gain en biomasse aérienne pouvait varier du simple au double parmi les génotypes (2,76–5,78 $Mg \cdot ha^{-1}$), et était le plus élevé pour les deux clones de *P. deltoides*, suivis respectivement par les hybrides NM et DN. Pour l'ensemble des génotypes, le gain en biomasse aérienne n'était pas corrélé avec l'interception de la lumière qui variait à peine de 5%. Au lieu de cela, il était fortement et positivement corrélé ($r^2 = 0{,}99$) avec la variation du simple au double de l'efficacité d'utilisation de la lumière (1,06–2,22 $g \cdot MJ^{-1}$). Parmi les caractéristiques du couvert qui ont été mesurées, le meilleur prédicteur de l'efficacité d'utilisation de la lumière ($r^2 = 0{,}88$) correspondait à une combinaison additive de facteurs associés à l'optimisation de la photosynthèse : l'efficacité d'utilisation de la lumière était négativement corrélée à la fois avec le coefficient d'extinction de la lumière dans le couvert et avec l'irradiance au point de compensation à la base du couvert. Nous concluons de ces faits que les génotypes de peuplier peuvent varier considérablement dans leur efficacité d'utilisation de la lumière et, par conséquent, dans la façon dont la photosynthèse est optimisée dans des couverts denses. La faible efficacité d'utilisation de la lumière chez les génotypes hybrides dans des conditions de forte compétition dans le couvert pourrait refléter un biais dans les efforts " d'amélioration des arbres " qui tendent à maximiser la production de biomasse dans des conditions de compétition relativement faible.

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Introduction

Short-rotation woody crops (referred to as SRWC) may offer an economically appealing alternative to the management of natural forests for fiber and biomass production owing to the exceptional growth potential of cultivars such as hybrid poplar (DeBell et al. 1977; Isebrands and Nelson 1982; Dickmann 1985; Stettler et al. 1988; Ceulemans et al. 1992). However, the enhanced productivity of such cultivars tends to be associated with poor tolerance of competition (Dickmann 1985; Kärki and Tigerstedt 1985), and the cultivation of hybrid poplar generally requires intensive management that may offset the economic advantages of fast growth. Consequently, "tree improvement" efforts have sought to identify traits that maximize resource-use efficiency (particularly light) in specific applications based on theorized ideotypes of canopy structure, function, and phenology (Isebrands and Nelson 1982; Dickmann 1985; Cannell et al. 1988; Wu 1993), a strategy successfully used in the development of agricultural hybrids (Donald 1968; Dickmann 1985).

Strong relations exist between biomass production and light interception across a wide range of vegetation (Monteith 1972; Jarvis and Leverenz 1983; Linder 1985; Cannell et al. 1988; Russell et al. 1989; Ceulemans et al. 1992; Haxeltine and Prentice 1996; Ceulemans and Daraedt 1999; Ruimy et al. 1999), and the superior growth rates of hybrid poplars are often attributed to their rapid canopy development and high light interception (Zavitkovski et al. 1974; Isebrands and Nelson 1982; Scarascia-Mugnozza et al. 1989; Ceulemans et al. 1990; Souch and Stephens 1998; Ceulemans and Daraedt 1999). However, variation in productivity among poplar genotypes may arise from differences in either the amount of solar radiation absorbed by the canopy or the efficiency with which that absorbed energy is converted into biomass (Cannell 1989), commonly referred to as light-use efficiency (LUE, grams biomass produced per megajoule of absorbed, photosynthetically active radiation).

Differing opinions exist regarding the importance of LUE as a determinant of genotypic variation in poplar productivity. For example, Cannell et al. (1988) found similar LUEs among disparate poplar and willow genotypes, grown under favorable conditions, that varied nearly twofold in biomass production. As a result, they concluded that large improvements in biomass production would be realized in constructing ideotypes based on differences in phenology (i.e., proportion of growing season during which the canopy is photosynthetically active) and (or) biomass allocation (i.e., to aboveground vs. belowground tissues). Conversely, others have argued that rates of canopy photosynthesis (and thus, LUE) could be enhanced in hybrid poplar by manipulating canopy structure based on defined ideotypes (Isebrands and Nelson 1982; Isebrands et al. 1988; Scarascia-Mugnozza et al. 1989; Dickmann et al. 1990). Thus, there is a clear need to establish whether growth variation among poplar clones in a given context is determined principally by light interception, LUE or a combination of both (Cannell 1989; Landsberg et al. 1996), and such an examination may point to useful clone-selection criteria.

The fraction of incident photosynthetically active radiation intercepted by a canopy (IPAR) is governed primarily by the amount of foliage and its orientation (Jarvis and Leverenz 1983; Cannell 1989; Landsberg et al. 1996). In contrast, canopy LUE is largely determined by the average photosynthetic rate of its foliage (Jarvis and Leverenz 1983; Cannell et al. 1987; Medlyn 1998), which in turn is controlled by a combination of leaf structural and biochemical properties (Givnish 1988; Ellsworth and Reich 1993; Reich et al. 1998; Sims et al. 1998; Ishida et al. 1999). For example, variation in leaf photosynthetic capacity within and across species is closely linked to differences in leaf nitrogen (Field 1983; Field and Mooney 1986; Hirose and Werger 1987*b*; Anten et al. 1995; Sims et al. 1998) and leaf mass per unit area (LMA) (Reich et al. 1998; Peterson et al. 1999*a*, 1999*b*; Green and Kruger 2001). Thus, efforts to reveal the cause(s) for LUE variation should include an assessment of these photosynthetic, morphological, and biochemical attributes.

Perhaps of equal importance in determining LUE is the coordination of photosynthesis among elements in heterogeneous canopy light environments (Cannell 1989). In an "ideal" canopy, photosynthesis would respond proportionally at each microsite to changes in ambient light (Verhagen et al. 1963; Field 1983; Hirose and Werger 1987*a*; Givnish 1988; Wu 1993; Terashima and Hikosaka 1995; Haxeltine and Prentice 1996; Hikosaka and Hirose 1997). Optimization theories suggest that this "ideal" canopy should optimize both the light environment and the acclimation of each leaf's photosynthetic apparatus to that environment (Jarvis and Leverenz 1983; Hollinger 1989; Terashima and Hikosaka 1995; Hikosaka and Hirose 1997).

The optimization of canopy light environment implies that the greatest number of leaves receive sufficient energy to function near their photosynthetic potential. Furthermore, variability in canopy structure among plant genotypes may play an important role in determining light distributions (Scarascia-Mugnozza et al. 1989; Ishida et al. 1999). In particular, steep leaf angles in mid- and upper-canopy regions result in low light-extinction coefficients (k) and deeper penetration of light. This "homogenization" of the light environment is thought to enhance canopy photosynthesis at high leaf area index (Dickmann et al. 1990; Anten et al. 1995; Terashima and Hikosaka 1995; Hikosaka and Hirose 1997).

Canopy photosynthetic acclimation necessitates a tight coupling of each leaf's metabolism to its light environment, which entails structural and functional plasticity within dense canopies. Accordingly, intracanopy gradients in light availability are typically mirrored by shifts in leaf photosynthetic metabolism, which tend to minimize energy costs and maximize energy capture at any microsite (Field 1983; Hirose and Werger 1987*a*, 1987*b*; Givnish 1988; Hollinger 1989, 1996; Wu 1993; Anten et al. 1995; Terashima and Hikosaka 1995). These nonuniform distributions in leaf traits are particularly beneficial at high canopy densities (Hirose and Werger 1987*a*; Wu 1993). It has been suggested that, among these traits, leaf compensation irradiance (I_C, the incident light intensity required to balance dark respiration with gross photosynthesis) in the canopy interior (the region of greatest competition for light) may provide an effective index of photosynthetic acclimation to low light (Jarvis and Leverenz 1983).

The principal objective of this study, then, was to determine the proportion of variation in aboveground net woody biomass (ANBG) production related to IPAR versus LUE at

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high levels of competition (where resource-use efficiency is arguably most critical) among five native and hybrid poplar genotypes possessing dissimilar canopy structural and functional traits (e.g., leaf angle and photosynthetic capacity). Of particular interest was the potential relation between LUE and traits influencing canopy photosynthetic optimization. In stands planted at densities resulting in high light interception, we examined two hypotheses: (*i*) among clones, variation in ANBG would be more closely related to LUE than to IPAR, and (*ii*) LUE variation would be related to key leaf- and canopy-level attributes governing average rates of photosynthesis, including factors influencing the degree of canopy photosynthetic optimization (namely k and I_C).

Methods and materials

Study design and site conditions

To address our hypotheses, we established five monoculture stands of each of five poplar genotypes in May 1997 at the Arlington Agricultural Research Station of the University of Wiscsonsin-Madison, Arlington, Wis. (43.20.17°N, 89.22.49°W). Stands were generated from dormant (unrooted) stem cuttings and arranged in a randomized complete-block design. Two genotypes (252-4 and D-105) were *Populus deltoides* Bartr. varieties, and three were interspecific hybrids (NM-6 (*Populus nigra* L. × *Populus maximowiczii* A. Henry), DN-34 (*P. deltoides* × *P. nigra*), and Bucky (unknown parentage, but thought by the authors to be a *P. deltoides* × *P. nigra* hybrid)). These genotypes were chosen because of their superior growth performances and the diversity in crown structural and functional traits that they exhibited in a 1-year, multiclone growth trial conducted on the same site (2.4 × 3 m spacing) in 1996. The monoclonal stands established in 1997 consisted of 36 trees planted at a 1 × 1 m spacing to encourage rapid canopy closure and high light interception. Each stand was surrounded by a one-row border of the same genotype. In addition, a two-row border of DN-34 encircled the plantation to minimize edge effects on outer plots. In 1997 and 1998, groundcover was controlled by hand weeding and herbicide application (glyphosate). No control occurred in 1999, as the plots were nearly weed free because of the dense poplar canopy.

Our objective was to study clonal behavior under near-optimal growing conditions, thereby minimizing the extent to which environmental stress would constrain genotypic variation in productivity and its determinants (Cannell 1989; Runyon et al. 1994; Haxeltine and Prentice 1996; Landsberg et al. 1996). Thus, we established this common-garden study on a highly fertile Huntsville silt-loam soil (Cumulic Hapludoll) with an A horizon thickness of approximately 1 m (Hole 1976). Additionally, we restricted the timing of measurements to a period when growing conditions were deemed to be most optimal (June 22 through July 23). During this period, precipitation at the site (116 mm) was 27% above the 30-year mean, while average daily temperature (22.3°C) exceeded the 30-year mean by 1°C (Midwestern Climate Center 2000). This was also the interval during which canopy foliage density was at its peak and most stable. Moreover, this restricted time frame allowed us to avoid the difficulties inherent in separating clonal variation in growth rate from that in growth duration owing to differences in phenology (i.e., time of leaf flush and abscission) (DeBell et al. 1996).

Aboveground biomass gain

The net biomass gain of aboveground woody tissues (ANBG, $Mg \cdot ha^{-1}$) was estimated with clone-specific allometry. To ensure that allometric relations were consistent across the study site, we compared height and diameter trends among blocks for each clone. Log transformations were used to normalize the data, and the general linear models (GLM) procedure in SAS (SAS Institute Inc. 2000) was used to test for significant variation in height versus diameter relations across plots for each clone ($P > 0.12$ for plot effects on slope and intercept in all comparisons). We then conducted a 50% thinning (every other tree) in one block of trees (one plot per clone) in November of 1999. Stem diameter at 15 cm above the soil surface and height for each tree were measured prior to cutting. Ten trees of each clone were selected to represent maximum, minimum, and average sizes. Woody portions were separated into stem and branch components. Samples were then dried at 70°C to a constant mass and weighed. Clone-specific relations between aboveground woody biomass and diameter ($r^2 = 0.93$ in all cases) were subsequently used to estimate biomass gain for all trees during the period between June 22 and July 23 based on diameter measurements taken on those days. Finally, tree biomass gain was averaged across all individuals in each plot to estimate ANBG for the study period.

Canopy structure and light environment

To estimate canopy averages for leaf mass per unit area (LMA, $g \cdot m^{-2}$), foliage of each clone was collected in stands from two randomly chosen blocks in mid-July. In a stand, 10 leaves were collected within each 1-m height increment from the base to the top of the canopy. The number of increments ranged from five in the hybrids to six in the *P. deltoides* clones. Sampled leaves were measured for fresh leaf area, oven-dried at 70°C to a constant mass, and weighed. Among these samples, five were randomly selected from each stand and height interval for determination of nitrogen concentration (N_{mass}, $mg \cdot g^{-1}$). Each set of five leaves was ground and homogenized, and the resulting stand or increment samples were analyzed for total N_{mass} using a micro-Kjeldahl digestion procedure (Schulte et al. 1987). Analyses were conducted at the University of Wisconsin Soil and Plant Analysis Laboratory in Madison, Wis. All measures within a stand were averaged to estimate its canopy mean for LMA and N_{mass}.

In July, canopy averages for leaf angle were estimated in the aforementioned stands (two per clone) based on measurements taken at increments of 1 m from the base to the top of canopies using a protractor inclinometer (Norman and Campbell 1989). The lamina angle in relation to horizontal was measured on a minimum of 50 arbitrarily selected leaves per increment. Leaf angle was then averaged across height increments in each stand. The canopy light-extinction coefficient (k), which represents the fraction of leaf surface projected onto the horizontal plane, was estimated as the cosine of the average leaf angle (Ross 1981). We used k as a basis for clonal comparisons of intracanopy light distribution.

The total amount of photosynthetically-active radiation intercepted by the canopy during the 31-day study period ($IPAR_T$, $MJ \cdot m^{-2}$) was estimated in each stand using the equation $IPAR_T$ = Total PAR × $IPAR_f$, where $IPAR_f$ is the fraction of the PAR intercepted by the canopy. Total solar radiation ($MJ \cdot m^{-2}$) for the study period was measured at the Arlington Research Farms meteorological station located about 1 km from the study site. Solar radiation was converted to total PAR using a factor of 0.47 (Campbell and Norman 1998). $IPAR_f$ was calculated as $1 - PAR_B/PAR_A$, where PAR_B was the average measured below the canopy, and PAR_A was that measured simultaneously above the canopy. Measurements of PAR were conducted under both cloudy and sunny conditions in late June and mid-July using an AccuPAR portable radiometer (Decagon Devices, Pullman, Wash.) configured to record 20 point measurements spaced 4 cm apart.

To measure PAR_B, the wand was extended from the plot center in eight compass directions (45, 90, 135, 180, 225, 270, 315, and 360°) under the canopy base. PAR_A was measured simultaneously using a LI-COR LI-190 quantum sensor (LI-COR Inc, Lincoln, Nebr.) calibrated to the AccuPAR radiometer. For each plot, measurements were combined across months and sky conditions to

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Table 1. Clonal data for net gain in aboveground woody biomass (ANBG), light-use efficiency (LUE), light interception ($IPAR_f$ and $IPAR_T$), and stem basal area (BA) during the period between June 22 and July 23, 1999.

Clone	ANBG ($Mg \cdot ha^{-1}$)	LUE ($g \cdot MJ^{-1}$)	$IPAR_f$ (fraction)	$IPAR_T$ ($MJ \cdot m^{-2}$)	BA ($m^2 \cdot ha^{-1}$)
252-4	4.94 (0.25)*b*	1.82 (0.09)*b*	0.977 (0.002)*a*	272.0 (0.5)*b*	15.8 (0.5)*c*
D-105	5.78 (0.30)*a*	2.22 (0.12)*a*	0.937 (0.002)*c*	260.8 (0.5)*d*	21.5 (0.8)*a*
Bucky	3.11 (0.07)*d*	1.18 (0.02)*d*	0.945 (0.002)*b*	263.2 (0.6)*c*	18.8 (0.7)*b*
DN-34	2.76 (0.13)*d*	1.06 (0.05)*d*	0.937 (0.004)*bc*	260.9 (1.2)*cd*	18.4 (0.6)*b*
NM-6	3.84 (0.13)*c*	1.40 (0.05)*c*	0.984 (0.002)*a*	274.4 (0.2)*a*	22.8 (0.6)*a*

Note: Values are means, with SE given in parentheses (based on $n = 5$ stands). Values followed by the same letter do not differ significantly at $P = 0.05$. $IPAR_f$, fraction of photosynthetically active radiation intercepted by the canopy under sunny and cloudy conditions; $IPAR_T$, total amount of PAR intercepted by the canopy during the study period.

Table 2. Clonal data on canopy structural and functional traits obtained in two of the five blocks.

Clone	LMA ($g \cdot m^{-2}$)	A_{area} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	A_{mass} ($nmol \cdot g^{-1} \cdot s^{-1}$)	N_{mass} ($mg \cdot g^{-1}$)	Leaf angle (°)	k	I_C ($\mu mol \cdot m^{-2} \cdot s^{-1}$)
252-4	61.2 (1.4)*c*	29.0 (0.3)*a*	345 (4)*a*	32.0 (0.3)*b*	48.1 (0.2)*b*	0.668 (0.003)*c*	17.9 (1.7)*a*
D-105	66.7 (0.5)*bc*	24.4 (0.3)*bc*	297 (4)*b*	33.5 (1.2)*ab*	56.3 (1.1)*a*	0.555 (0.016)*d*	33.4 (3.8)*b*
Bucky	68.6 (1.2)*abc*	23.4 (0.4)*cd*	270 (8)*bc*	34.3 (0.1)*a*	45.9 (1.7)*bc*	0.696 (0.022)*bc*	51.1 (2.5)*c*
DN-34	72.3 (1.2)*ab*	22.6 (0.3)*d*	250 (4)*cd*	32.6 (0.9)*abc*	38.9 (0.5)*c*	0.779 (0.006)*b*	58.5 (0.7)*c*
NM-6	75.8 (1.9)*a*	22.9 (0.3)*d*	221 (7)*d*	29.0 (0.3)*c*	23.5 (0.1)*d*	0.917 (0.001)*a*	22.5 (0.7)*a*

Note: Values are means with SE given in parentheses (based on $n = 2$ stands). Values followed by the same letter do not differ significantly at $P = 0.05$. Canopy attributes include light-saturated photosynthesis per unit leaf area and leaf mass in the upper canopy (A_{area} and A_{mass}, respectively), and canopy averages for leaf mass per unit area (LMA), leaf nitrogen concentration (N_{mass}), leaf angle from horizontal and light-extinction coefficient (k), and leaf compensation irradiance at the canopy base (I_C).

provide an average $IPAR_f$ for the study period. Depending upon leaf angle distributions, this method might have underestimated $IPAR_T$ for some clones and overestimated it for others because of interactions between leaf angle and solar angle during the day (Ross 1981; Campbell and Norman 1998). Nevertheless, it was likely an accurate estimate of $IPAR_T$ during the hours of high solar angle and maximal photosynthetic activity (e.g., 09:00–15:00; Dickmann et al. 1990; Michael et al. 1990).

Leaf function

The acclimation of photosynthetic metabolism to light availability in the canopy interior was assessed using leaf compensation irradiance (I_C, $\mu mol \cdot m^{-2} \cdot s^{-1}$) at the canopy base. In early July 1999, photosynthetic light response was measured in situ on leaves at the base of the two aforementioned canopies per clone using a LI-COR 6400 Portable Photosynthesis System (LI-COR Inc., Lincoln, Nebr.). Photosynthesis was measured on each of five leaves per canopy through a descending PAR series (1000, 500, 200, 100, 50, 25, amd 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Leaf temperature was maintained at 20°C during measurement periods to simulate the cooler environments typical in shaded canopy regions (Sullivan et al. 1996). Photosynthetic light responses were characterized using the nonlinear model published by Hanson et al. (1988). This model generates key functional parameters including I_C.

In the upper third of each of the same canopies, light-saturated net photosynthesis (A_{area}, $\mu mol \cdot m^{-2} \cdot s^{-1}$) was measured at a PAR of 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ on fully expanded leaves using the LI-COR 6400 under the same conditions described above, except that leaf temperature was maintained at 25°C. Measurements were conducted in early July. Sampled leaves were measured for fresh leaf area, oven-dried at 70°C to a constant mass, and weighed to determine LMA, which was used to calculate light-saturated photosynthesis per unit leaf mass (A_{mass}, $nmol \cdot g^{-1} \cdot s^{-1}$).

Statistical analysis

Relationships among ANBG, LUE, and canopy traits were examined by linear regression using the GLM procedure in SAS (SAS Institute Inc. 2000). Stand was the experimental unit in all regressions. The GLM procedure was also employed to conduct multivariate regressions between ANBG, LUE, and all combinations of measured canopy traits. The significance of differences in clonal means for ANBG, LUE, $IPAR_f$, $IPAR_T$, and all canopy traits were tested using Fisher's least-squares difference test ($\alpha = 0.05$). The analysis of variance (ANOVA) procedure in SAS was used to test for significant block effects on ANBG and LUE. In no analysis did we detect a significant block effect.

Results

Production of aboveground woody biomass and light-use efficiency

Estimates of ANBG between June 22 and July 23 varied nearly twofold among genotypes (2.76–5.78 $Mg \cdot ha^{-1}$; Table 1). The *P. deltoides* clones grew the fastest, while the hybrid clones were grouped at the low end. Within genotypes, variation in ANBG was quite small. The LUE ($g \cdot MJ^{-1}$) of each plot was calculated by taking the quotient of ANBG and $IPAR_T$ for the study period. LUE during the study period spanned a twofold range (1.06–2.22 $g \cdot MJ^{-1}$) among clones (Table 1), and again, *P. deltoides* clones had the highest LUE values. As with ANBG, within-clone variation in LUE was comparatively small.

Canopy function, structure, and light environment

Light-saturated photosynthesis in the upper canopy was highest among *P. deltoides* clones (Table 2). Relatively speaking, clonal variation in A_{mass} was twice that observed for A_{area} (56 vs. 28%, respectively). The I_C in the lower canopy spanned more than a threefold range, and it was substantially higher in the DN hybrids than in NM-6 or the *P. deltoides* clones (Table 2). Canopy averages for LMA were greatest among the hybrids (Table 2), with the highest average (in NM-6) exceeding the lowest (in 252-4) by about 24%. Can-

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Table 3. Relations between net gain in aboveground woody biomass (ANBG, Mg·ha^{-1}), light-use efficiency (LUE, g·MJ^{-1}), and measured canopy traits.

y	x	n	r^2	P	a	b
ANBG	LUE	25	0.99	<0.0001	0.06	2.63
ANBG	LMA	10	0.52	0.02	15.19	–0.16
ANBG	A_{area}	10	0.56	0.01	–4.67	0.35
ANBG	A_{mass}	10	0.58	0.01	–1.16	0.02
ANBG	k	10	0.39	0.05	8.35	–5.88
ANBG	I_C	10	0.47	0.03	5.88	–0.05
LUE	LMA	10	0.53	0.02	5.75	–0.06
LUE	A_{area}	10	0.52	0.02	–1.65	0.13
LUE	A_{mass}	10	0.57	0.01	–0.44	0.01
LUE	k	10	0.45	0.03	3.26	–2.38
LUE	I_C	10	0.40	0.05	2.16	–0.02

Note: Canopy attributes include light-saturated photosynthesis in the upper canopy (A_{area}, μmol·m^{-2}·s^{-1}; A_{mass}, nmol·g^{-1}·s^{-1}) and canopy averages for leaf mass per unit area (LMA, g·m^{-2}), light-extinction coefficient (k), and leaf compensation irradiance at the canopy base (I_C, μmol·m^{-2}·s^{-1}). All regressions are in the form $y = bx + a$. For the ANBG versus LUE relation, data from all five stands per clone were used.

opy averages for N_{mass} also varied significantly among clones, but the extent of variation (29.0–34.3 mg·g^{-1}) was modest. Average leaf angle ranged from nearly planophile in NM-6; to plagiophile in 252-4, Bucky, and DN-34; to more erectophile in D-105 (Table 2). As a result, the k of NM-6 was about 70% greater than that of D-105. Among clones, the IPAR$_f$ ranged between 0.937 and 0.984 (Table 1), and consequently, IPAR$_T$ varied by only 5%.

Determinants of ANBG and LUE

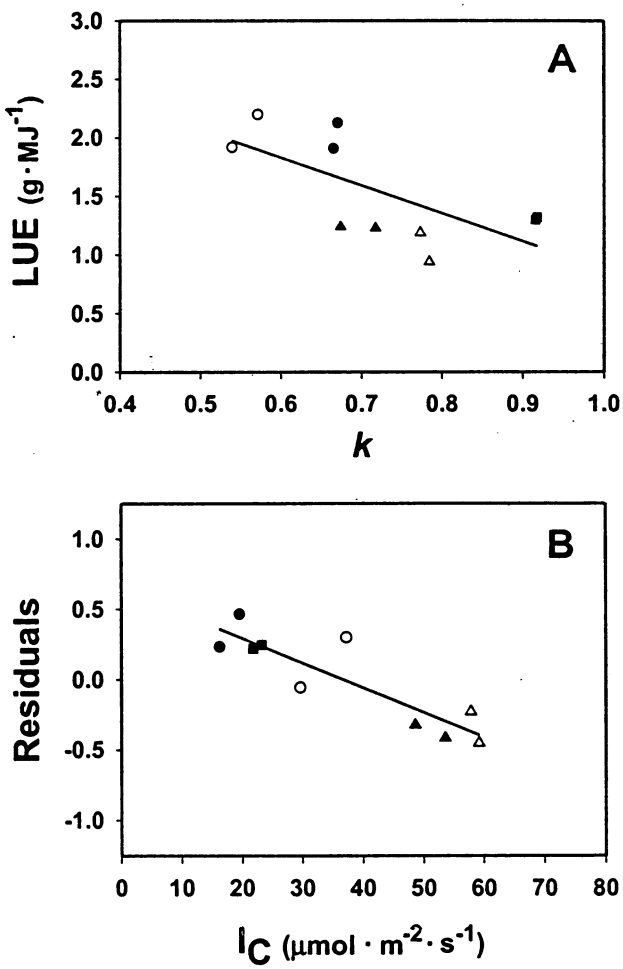
ANBG and LUE were strongly and positively correlated among genotypes (Table 3). In addition, because of the small range in IPAR$_T$, ANBG and LUE were highly proportional. Among genotypes, neither ANBG nor LUE was related to light interception (IPAR$_f$ or IPAR$_T$). Both ANBG and LUE, however, were positively related to A_{area} and A_{mass} and negatively related to canopy averages of LMA, k, and I_C (Table 3). ANBG and LUE were most strongly related to the additive combination of canopy average k and I_C, which explained 89% of the variation in ANBG (data not shown, P = 0.0004) and 88% of the variation in LUE (Fig. 1; P = 0.0006). Each variable's influence was negative (ANBG = 10.35 – 6.10(k) – 0.05(I_C); LUE = 3.95 – 2.45(k) – 0.02(I_C)), and the contributions of both k and I_C were highly significant (P < 0.0016 in all cases). Additionally, there was no interaction between k and I_C (P = 0.89), nor were k and I_C correlated (P = 0.92). In none of the other regressions in Table 3 did the addition of a second variable significantly enhance the model fit.

Discussion

LUE variation may indicate differential suitability to high levels of competition

Given the modest variation in poplar LUE reported in previous studies (e.g., Cannell et al. 1988), the wide range in ANBG and LUE that we observed among genotypes with similar IPAR was somewhat surprising. Based on these results, it appears that LUE was the key determinant of woody biomass production among these clones at high levels of competition.

Fig. 1. Relations between (A) light-use efficiency (LUE) and canopy light-extinction coefficient (k) (r^2 = 0.45, P = 0.03), and between (B) residuals of the LUE versus k regression and leaf-compensation irradiance at the canopy base (I_C) (r^2 = 0.78, P = 0.0007). Genotype symbols: 252-4, solid circles; D-105, open circles; Bucky, solid triangles; DN-34, open triangles; NM-6, solid squares.



While clonal differences in carbon allocation may have played a role here (Cannell 1989), root excavations conducted at the end of the 1998 and 1999 growing seasons indicated that belowground partitioning to woody biomass was similar among clones and years. Belowground woody biomass comprised between 0.18 and 0.22 of total woody biomass among all clones (D.S. Green, unpublished data), and values tended to be lowest among hybrid genotypes. Thus, we have no evidence that allocational differences confounded our interpretations regarding the dependence of ANBG on LUE. The favorable growing conditions that existed during our midseason measurements (i.e., fertile soil, above-average precipitation, near optimal temperatures) should have allowed all genotypes to approach their full productive potential at high levels of intracanopy competition. Furthermore, there were no indications that water availability appreciably limited LUE during the study period. In particular, average

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stomatal conductance in the upper canopy foliage measured at the beginning of the study was quite high among all clones (0.77–0.96 $mol \cdot m^{-2} \cdot s^{-1}$), and it remained so through the end of measurement period (D.S. Green, unpublished data).

While our objective was to compare "maximum" growth among clones, the actual field performance of any clone is subject to the dampening influence of environmental stresses. Thus, efforts to provide selection guidelines should also consider a genotype's capacity to tolerate environmental stress, its susceptibility to insect defoliation and pathogens, its rooting habit, its leaf phenology, and other key factors. Nevertheless, the observed behavior of these genotypes may be typical for high-density plantings on productive sites, and the differences in LUE among these "superior" clones may indicate differential adaptation to such conditions. In addition, elucidating the determinants of LUE could enhance the selection of clone attributes for similar conditions in poplar cultivation (e.g., high-density cultivation, lower density cultivation following canopy closure).

LUE as an expression of canopy optimization

Among all traits and their combinations, only the additive model including k and I_C produced a compelling predictor of LUE. We do not, however, infer that the influences of other traits, such as leaf photosynthetic potential and LMA, were unimportant. Rather, we were unable to assess their contribution in a multivariate model with k and I_C because of the limited sample size (i.e., lack of degrees of freedom) in this study.

As suggested earlier, a genotype's LUE may reflect its canopy optimization potential in a given context; the strong relation between LUE and the combination of k and I_C among clones in this study is consistent with the stated theory that efficient canopies optimize both the distribution of light and leaf-level acclimation of the photosynthetic apparatus to that distribution (Hollinger 1989; Terashima and Hikosaka 1995; Hikosaka and Hirose 1997), particularly at high levels of intracanopy competition. For instance, both D-105 and 252-4 had a significantly lower k compared with other clones with a similar $IPAR_f$ (DN-34 and NM-6, respectively). The more even dispersal of light in canopies with low k at high $IPAR_f$ should enhance canopy photosynthesis (and overall suitability) by reducing the amount of light-saturated foliage in the upper canopy and increasing the portion of foliage functioning at levels nearer to light saturation in middle and lower canopy regions (Cannell 1989; Sprugel 1989; Medlyn 1998). Additionally, physiological acclimation to light availability appears to differ among clones. D-105 and DN-34, for instance, had the same $IPAR_f$, but D-105 had a significantly lower I_C. This disparity indicates that a more favorable balance between leaf metabolism and light environment existed in the canopy of D-105 compared with that of DN-34, at least in the region of greatest light competition.

Using canopy trait combinations as suitability indicators

Based on our results, both gradual light attenuation (low k) and pronounced physiological acclimation to low light (low I_C) appear to be highly adaptive in dense canopies, at least among fast-growing genotypes. Yet different combinations of k and I_C may be adaptive to other cultural conditions. For example, "light-demanding" genotypes may be suited to either high or low levels of competition, depending upon trait combinations. As we observed with D-105, a moderately high metabolic demand for light in the canopy interior could be met in a relatively dense, closed canopy if light attenuation was low. However, high I_C (and its associated high photosynthetic capacity) in the lower canopy may be beneficial in sparse or open canopy conditions, even if structural characteristics favored high light attenuation. DN-34, which appears to be maladapted to high levels of competition, may be well suited to more open conditions. Indeed, it is generally considered to be a highly productive genotype (Dickmann et al. 1990). In open, "high-light" conditions ($IPAR_f$ well below the levels in this study), the importance of photosynthetic acclimation to light (e.g., basal I_C) may diminish in the additive model because of the increased light availability to all canopy positions (Hirose and Werger 1987*a*).

Consequently, the influence of k and I_C may not be additive at low $IPAR_f$, wherein efficient light interception (high k, high $IPAR_T$) would likely be the key determinant of productivity (Wu 1993). High k at low levels of canopy competition maximizes energy harvesting for photosynthesis in conditions where light availability is often higher in the canopy interior (Hikosaka and Hirose 1997). During the establishment year of this study (1997, prior to canopy closure), variation in ANBG was almost entirely explained by k among all clones ($r^2 = 0.99$, $P < 0.0001$; D.S. Green, unpublished data). There appears to be an interaction between k and canopy competition, and as we suggested previously, there may also be an interaction between I_C and canopy competition. Thus, some indicator of canopy density (e.g., $IPAR_f$) could make the additive model a more robust predictor of ANBG and LUE across a greater range of conditions. The potential benefit of such a competition scalar or index would likely be most useful where canopy density spans a wide range.

Assessing genotype plasticity

It is likely that a particular poplar genotype approaches maximum productivity within a specific range of planting densities owing to the various expressions of the traits discussed above, which may maximize ANBG at different stocking levels. However, it is not clear how much trait plasticity exists among genotypes, and this will likely determine the optimal planting density range, and ultimately the rotation length, for a given clone. For instance, if traits such as leaf angle and leaf photosynthetic acclimation to light environment are relatively fixed, then the associated optimal planting density range may be quite narrow; however, a lack of plasticity may make it fairly simple to develop screening protocols that would aid in clone selection for given applications. Conversely, if key traits are more plastic in some clones, then their planting density range and (or) potential rotation length should be correspondingly greater.

Hybrid poplars may present a unique challenge. Among native genotypes, we may expect to see a strong capacity to acclimate to different conditions because of the evolutionary selection of traits that has occurred under varying levels of competition (Rosen 1967; Givnish 1986; Bazzaz 1996; Wu 1993). However, "tree improvement" efforts may be selecting traits that favor high individual plant growth rates under

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conditions of low to moderate competition based on ideotypes of optimal canopy structure and function (Kärki and Tigerstedt 1985; Wu 1993). In addition, the typically short rotations of hybrid poplar under high-density cultivation (Ceulemens and Deraedt 1999) suggest that these traits may be maladapted to the intense competition that emerges after canopy closure. Thus, the optimal environments for hybrid genotypes need to be clarified, as high leaf area or light interception are not necessarily good indicators of a clone's ultimate potential following canopy closure.

Consequently, identifying optimal matches between poplar genotypes and growth conditions necessitates consideration of the various levels of competition that will be encountered during a rotation (Kärki and Tigerstedt 1985). Furthermore, the response in LUE over the course of a rotation may provide an effective means to assess the canopy optimization potential of a genotype under various conditions. Such information should help to identify conditions that render the optimal balance between high growth rate and rotation length for a given genotype, which, ultimately, should improve the cost–benefit tradeoff in biomass production applications. In addition, the breeding of new cultivars may utilize such information to target specific traits for different applications (e.g., maximizing area-based biomass production vs. maximizing individual tree biomass production).

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