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Evaluation of leaf traits for indirect selection of high yielding poplar hybrids

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Abstract

Two *Populus* families growing at two sites in Europe (i.e., northern Italy versus central France) were used to investigate: (1) the relationships between various leaf structural and growth traits and biomass production, (2) the dependence of these relationships on environmental conditions and genetic background (i.e., *Populus deltoides* × *Populus nigra* family versus *P. deltoides* × *Populus trichocarpa* family), and (3) the subsequent relevance of the use of these morphophysiological traits as indirect indicators of productivity. Tree growth and leaf characteristics, as well as the links between them, were intensively studied for 3 weeks. The *P. deltoides* × *P. trichocarpa* family was more productive than the *P. deltoides* × *P. nigra* family at both sites. The two families inherited complementary leaf characteristics from their respective male parents, i.e., large leaves from *P. trichocarpa* and fast leaf production from *P. nigra*. The traits were clearly dependent on site conditions, trees being much bigger in Italy than in France. Moreover, the G × E interaction caused a significant change in the genotypic ranking between sites in terms of productivity for the *P. deltoides* × *P. trichocarpa* family, which might represent a limit for the selection of productive hybrids showing a large environmental spectrum. Three categories of leaf traits could be considered: (i) traits linked to whole tree growth irrespective of site and family (e.g., leaf area, petiole dimensions), (ii) traits for which the relationships with tree growth were dependent on site and/or family (e.g., specific leaf area, nitrogen content, leaf number increment), and (iii) traits showing no link with tree growth irrespective of site and family (e.g., chlorophyll and carbon contents).

Keywords: *Populus*; Chlorophyll; Nitrogen; Carbon; Leaf area; SLA; Heritability; Heterosis; G × E interaction

1. Introduction

Poplars are considered the fastest growing trees under temperate latitudes and are widely used in the wood industry for the production of paper, plywood, matches, and light packaging materials or for bioenergy (Hansen, 1991; Heilman et al., 1994; Zsuffa et al., 1996). The *Populus* genus is a very diverse genus in terms of the level of productivity and resistance to pathogens; many selection programmes have been developed in order to screen for the most promising genotypes. However, due to the extremely complex genetic basis for productivity, improving and maintaining plant performance under fluctuating environmental conditions remains a slow, laborious, and mostly empirical process. Progress in increasing productivity and its stability through direct selection has been hampered by the relatively low heritability of biomass production and by its large genotype × environment (G × E) interaction (Ceccarelli and Grando, 1996). Moreover, from a technical point of view, the direct estimation of plant productivity is also a time-demanding and costly process, requiring a large amount of work by the breeders.

As an alternative to the direct selection for biomass production, morphophysiological traits genetically correlated with productivity have been targeted in selection programmes pursued in collaboration between physiologists and breeders. Even if the ideotype concept (i.e., a model plant of the desirable phenotype) has been more widely used by crop breeders than by forest tree breeders (with exception of the Finnish conifer ideotype and poplar ideotype; see review by Dickmann et al., 1994), Stettler et al. (1992) suggested the use of ideotypes as one possibility for breeding in short-rotation forestry (Rönnberg-Wästljung and Gullberg, 1999). The successful application of this strategy

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requires morphophysiological traits that are cheap and easy to score, characterized by a high genetic correlation with biomass production and/or growth performances, and by heritability higher than that of productivity (Tuberosa et al., 2002). In poplar, numerous traits, both at the whole plant and leaf levels, have been examined and evaluated as potential determinants of productivity. At crown level, tree architecture, canopy density, or sylleptic branchiness have been shown to be intimately related to stand productivity in some cases (Ceulemans, 1990; Dickmann et al., 1994; Wu and Stettler, 1998; Marron et al., 2006). At the leaf level, functional and structural components generally associated with high growth rates and productivity include total and individual leaf area, internal leaf structure, stomatal morphology and behaviour, leaf growth physiology, and functional traits such as photosynthetic performance (Isebrands and Nelson, 1982; Ceulemans et al., 1988; Pellis et al., 2004; Al Afas et al., 2006). Unfortunately, only a few success stories have so far been reported for enhancing productivity by applying indirect selection.

When identifying improved genotypes and potential cultivars, plant breeders routinely practice selection for genotypes that display stability for a given trait or set of traits across different environments. The need to develop well-buffered cultivars has led to a greater emphasis on phenotypic stability in breeding programs (Lin et al., 1986). Eberhart and Russell (1966) defined stability as the ability to show a minimum interaction with the environment. Hence, the stability of genotype performance is directly related to the effect of G × E interactions. G × E interactions are defined as the differential response of a genotype or cultivar for a given trait across environments, and they are important and essential components of plant breeding programmes dedicated to cultivar development.

To obtain information on G × E interactions and on the genetic background of the ecophysiological yield determinants in poplar, five inter- and intraspecific *Populus* hybrid families were planted at three sites in Europe (i.e., northern Italy, central France, and southern England) within the framework of an EC-funded research program (POPYOMICs; http://www.soton.ac.uk/~popyomic/). Two of these families are full-sib families resulting from controlled crosses of the female parent *P. deltoides* ‘S9-2’ with *P. nigra* ‘Ghoy’ and *P. trichocarpa* ‘V-24’, respectively (Cervera et al., 2001). These two families were chosen because the genetic maps of the three parents are currently being established. Moreover, hybrids produced from these two interspecific crosses are of commercial importance. Indeed, most of the commercial clones planted throughout Europe and North America are derived from interspecific crosses between *P. deltoides* and *P. nigra*, or between *P. deltoides* and *P. trichocarpa* or their backcrosses, mainly because of the positive and high heterosis (superiority of the hybrids over the parents) often exhibited by the hybrids between these species (Dickmann and Stuart, 1983; Stettler et al., 1996; Cervera et al., 2001).

In a previous study, biomass production was shown to be tightly linked to the leaf number increment and to the area of the largest leaf along the stem in a subset of genotypes belonging to the *P. deltoides* × *P. nigra* family at the intermediate French site (Marron and Ceulemans, 2006). However, the afore-mentioned study was conducted at one site and with one of the two families only. In these conditions, it is difficult to know whether the observed relationships between productivity and its potential leaf determinant are robust and can be used across environments and for contrasted genetic background. In this context, the objective of the present study was to estimate the environmental, temporal, and genetic stability of the leaf determinants of productivity by relating differences in productivity among the hybrids to differences in leaf morphological and physiological traits for: (1) the two poplar families, (2) different environmental conditions (i.e., central France and northern Italy), and (3) different growing seasons (i.e., second growing season from Marron and Ceulemans (2006) and first growing season after coppicing in the present study). Furthermore, the replication of the experiment at the two sites allowed us to estimate the impact of the genotype × site (G × S) interactions on leaf growth, morphology, and physiology as well as on their links with tree productivity for the two families.

2. Materials and methods

2.1. Plant material

Two full-sib families resulting from controlled crosses and sharing the same female parent were used in this experiment. One family consisted of 180 genotypes (F_1) resulting from an interspecific cross between *P. deltoides* (Bartr. ex Marsh.) ‘S9-2’ and *P. nigra* (L.) ‘Ghoy’ (D × N family) (Cervera et al., 1996, 2001). The second family was composed of 182 genotypes and was generated from an interspecific cross involving *P. deltoides* ‘S9-2’ and *P. trichocarpa* (Torr. and Gray) ‘V-24’ (D × T family) (Marron et al., 2006). Both crosses were realized by the Institute of Forestry and Game Management (IBW, Geraardsbergen, Belgium) in 1987 and repeated in 1995 to enlarge the progeny. A sample of 31 genotypes of each family was selected to be representative of the genetic variation in the second-year biomass production. At least four replicates of each selected F_1 genotype were alive at each site.

2.2. Experimental design

The two experimental plantations were established in April 2003 from 25 cm uniform hardwood cuttings. The initial spacing was 0.75 m × 2 m, accommodating an overall plant density of 6670 trees ha^{-1}. The experimental plantations were established according to a randomized block design (Marron et al., 2006). Six blocks were defined, and one replicate of each F_1 genotype and each parent was randomly allocated to each block. To reduce the border effects (Zavitkovski, 1981; Van Hecke et al., 1995), a double border row was planted around the plantations. The plantation management included irrigation, and the use of insecticides and fungicides as needed throughout the three growing seasons.