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Physiological vs. morphological traits controlling the productivity of six aspen full-sib families

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ABSTRACT

For investigating genotypic differences in the production potential of *Populus tremula* L., we grew aspen plants of six full-sib families under optimal water and nutrient conditions and analysed more than 20 physiological and morphological traits with a potential impact on productivity. The six families were produced from controlled crossings of two male and four female trees. Despite genetic distances of 2–28%, the families showed no significant differences in photosynthetic and leaf water status parameters (photosynthetic capacity, leaf water potential and others), even though productivity differed up to twofold between the families. Hence, growth rate was not related to photosynthetic activity but showed a close association with several morphological traits, most closely with the leaf number (L) and total leaf area. Variation in L explained 70% of the growth variation across the six families, and the start of bud burst (BB) correlated with the leaf number (early-starting families produced more leaves). The between-family variation in growth-related morphological traits was much larger than that in physiological traits (coefficient of genetic variation 4–29% vs. 0–4%). Even though the genetic constitution had a significant effect on eight morphological (leaf and root-related) traits, we found no relation between the genetic differences between any two families and the corresponding growth differences. We conclude that the timing of bud burst and the resulting total number of leaves developed are the determinants of growth in *P. tremula*. Selection programmes should focus on the considerable intraspecific variation in L and BB in order to increase yield.

1. Introduction

The interplay of genetic variation and productivity is of prime importance for forest industries, because it offers the potential to increase biomass gain for global renewable energy needs. There is an urgent need to improve the properties and increase the productivity of high-yielding woody plantation systems (e.g. short-rotation coppice) in order to satisfy the market

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demand on a long-term basis [1]. At present, bioenergy and fibre production within short-rotation forestry in Europe and North America is based mainly on poplar species and their cultivars [2–4]. A recent focus of ecological research is to disentangle the relationship between biodiversity and ecosystem functioning [5–7] and to understand the conditions under which plant species diversity has a positive effect on productivity e.g. [8,9]. In contrast, the role of plant genotype diversity for ecosystem functioning is not well studied and probably underestimated. Even though the variation between genotypes may be smaller than the variation between species, the impact on the productivity of the populations may be large enough to affect ecosystem structures and functions. In the recent past, empirical evidence for plant genotypic diversity increasing productivity has become available [10], but a deeper understanding of the functional role of intraspecific genetic diversity is still lacking.

In this study, we focus on *Populus tremula* L. plantings in short-rotation coppice, one of the important tree species for the energy wood industries [11–13]. Many selection programmes have been developed in order to screen for the most promising aspen and poplar genotypes in terms of productivity [14–16]. Yet, the contribution of intraspecific genetic variation to differences in productivity is not sufficiently understood [17]. For estimating the production potential, detailed knowledge of a plant's yield components together with the genetic variation in the available plants is required [13]. Aspen are successful pioneer species with a large geographic range [18]. Because of their high fecundity and wind dispersed pollen and seeds, aspen species have a high level of inter- and intra-population diversity [19]. As typical colonizer species, they also reproduce clonally via root suckers. Hence, newly established aspen populations at open sites and on barren land typically consist of numerous closely related genetic individuals [20]. We tried to simulate this situation by investigating several closely related progenies (full-sibs) which are the offspring derived by pair-crossing from a few colonising mother and father trees. The high level of genetic diversity and the valued resource for short-rotation coppice makes *P. tremula* a well suited study object for examining the role of genetic variation for productivity.

In the current study, we characterize six different full-sib families of *P. tremula* by a broad set of morphological and physiological traits in order to understand the potential of intraspecific variation for growth promotion in aspen and to identify traits associated with productivity. We attempted to minimise the influence of a variable environment setting up an experiment under natural light and optimal growing conditions (favourable water supply and fertile soil substrate) with plants of defined genetic constitution. While uniform and non-limiting growing conditions do not represent natural field conditions, they enable relating the productivity performance to physiological and morphological traits inherent to the full-sib families. This is important information to be used in selection programmes. We hypothesize that (i), even under uniform environmental conditions, yield and growth-related morphological and physiological traits differ significantly from each other in a group of aspen progenies with closely related genetic constitution, and (ii) this variation is related to the genetic variation.

2. Materials and methods

2.1. Aspen full-sib families

The plants used in this study belong to six full-sib families of trembling aspen (*P. tremula*) bred by controlled crossing. The parent tree material originates from 30-year-old trees selected in Göttingen-Geismar, Central Germany (51°32′N, 9°56′E). Two male trees were used as pollen donors (Geismar #3 and 5) and four served as mother plants (Geismar # 2, 4, 8, 9). Cropped shoots of the parent trees were used and the crossings 2 × 3, 2 × 5, 4 × 5, 8 × 5, 9 × 3 and 9 × 5 (full-sib families) were carried out under laboratory conditions. Seeds were germinated on moist Vermiculite (3–8 mm grain size, Deutsche Vermiculite Dämmstoff GmbH, Sprockhövel, Germany). The offspring was raised in 10-L pots (Fruhsdorfer soil, type N, Fruhsdorf, Germany) by the group of Forest Genetics and Tree Breeding at the University of Göttingen in 2000. The trees were cultivated outdoors and watered as necessary. Twenty-four progenies per family were selected for the experiment.

2.2. Experimental design

The experiment was conducted in the outdoor area of the Department of Forest Botany and Tree Physiology at the University of Göttingen. In April 2008, 8-year-old progenies from the six full-sib families were transplanted in two blocks of 10 m × 2 m, with each block being composed of four plots. Each plot included three aspen saplings of each family which were randomly placed at a distance of 50 cm. The eight plots were treated as replicates, because ANOVA revealed no significant plot effects. To provide uniform and optimal growing conditions, the used soil substrate was nutrient-rich humus, and the trees were regularly watered. Every plot was bordered by a single row of trees that were not used for the physiological and morphological measurements. This row served as a buffer zone to avoid the potential impact of edge effects on the target plants. Due to inherent differences in relative growth rate between the six families, the plants had reached different tree heights, total twig lengths and shoot diameters at the beginning of the experiment. To account for these size differences, initial tree height was used as a covariable in the statistical analyses (ANCOVA).

2.3. Molecular analyses

In order to characterize the genetic differences between the six full-sib families, DNA of the progenies was analysed using five nuclear encoded microsatellite markers. The total DNA from young leaves was extracted using the DNeasyPlant Minikit (Qiagen, Hilden, Germany). For microsatellite analyses the primers PMS14, PMS16 [21], PTR2, PTR4 [22] and PTR5 [23] were used. PCR amplification was performed in a 12.5 mm^3 volume containing 10 ng template DNA, 10 mmol Tris/HCl pH 9.0, 0.2 mmol of each dNTP, 1.5 mmol Mg Cl2, 50 mmol KCI, 0.2 μM each of forward and reverse primers and 1 U of Tag polymerase (Qiagen, Hot Star Master Mix, Hilden, Germany). All amplifications were performed in a Peltier Thermal Cycler (PTC-0200 version 4.0, MJ Research) with a heated lid under the