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Genotypic variation and heritability of growth and adaptive traits, and adaptation of young poplar hybrids at northern margins of natural distribution of *Populus nigra* in Europe

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ABSTRACT

The study aimed at estimating the adaptation, genotypic variation and heritability of growth and other adaptive traits of poplar hybrids at the northern margins of the natural distribution of *Populus nigra* in Europe, and to compare with the performance of native aspen hybrids from the middle of their geographic ranges. A set of 105 clones of poplar hybrids originated from crossing *Populus deltoides*, *P. nigra*, *Populus trichocarpa*, *Populus maximowiczii* and *Populus balsamifera* and aspen hybrids obtained from crossing *Populus tremula*, *Populus tremuloides and Populus alba* were studied in two juvenile clonal trials in Lithuania. ANOVA revealed a significant hybrid effect for growth traits and bud flush phenology. *P. maximowiczii* × *trichocarpa* had the highest height increment followed by *P. tremuloides* × *tremula*. Most adaptive traits were under strong genetic control, with 0.61–0.94 heritability. Genotypic variation for height increment ranged 19.40–58.10%. Hybrid × site interaction was significant for height growth. The highest plasticity was found in *P. balsamifera* × *trichocarpa* and *P. nigra*, with ecovalences reaching 21.4–24.7%. The low inter-site (B-type) genotypic correlations and significant clone × site interaction found for most growth traits and autumn phenology indicated a presence of genotypic variation in plasticity/response of clones. Negative correlations between autumn leaf shed phenology and tree condition and survival indicate that clones with late growth cessation suffer from adaptation problems. Thus poplar breeding in Northern Europe has to incorporate hardy species from harsher climates of North America to maximize both tree growth and survival to match phenology to local climates.

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1. Introduction

Because recent restructuring of European agriculture reduces traditional agricultural production and withdraws large areas of arable land from crop cultivation, there is a great potential for establishing short rotation forestry (SRF) and short rotation coppice (SRC) plantations on agricultural lands [1]. In 2011, hybrid poplar plantations in Europe covered a total area of 9402 km^2 [2,3]. The poplar roundwood annually produced in the European countries amounts to an average of 8.0 hm^3 and it is used for the production of plywood/veneers (40%), sawn timber (31%), pulp-paper-card-board (15%), and fuelwood-bioenergy (1%) [2]. Hybrids between *Populus deltoides* Bartr. ex Marsh and *Populus nigra* L. (*Populus* × *euramericana* Guin.) are the most widely planted hybrids in Europe and in the north-eastern regions of North America, where they perform well in several site conditions and show good commercial potential. Although, in many countries, cultivation of hybrid poplar is based on a small number of clones [2–4]. Clone I-214, which was bred in 1979 is grown on about 80% of poplar plantations in Europe. These monoclonal or oligoclonal plantations have low genetic diversity and therefore are vulnerable to disease or insect outbreaks and to changing or extreme climatic conditions. Multiclonal plantations, although they require the breeding and selection of multiple hybrids and clones, provide an alternative solution that limits these risks [5].

Extensive breeding of hybrid poplars is being conducted in Canada, the United States, Italy, the Netherlands, Hungary, the United Kingdom, Sweden, Iceland and other countries in order to develop new locally adapted cultivars with the best features [6,7]. Initially, inter-specific hybrids of poplars were intended to be grown primarily for production of pulp and paper products, but now solid wood products have been considered as well, which increases the importance of improving stem and wood quality in breeding hybrid poplars [8,2,3]. In general, hybrid poplar breeding programmes emphasize improvements of tree growth, adaptability, stem form, biomass allocation, wood density, and disease resistance [9–12,3,6]. Genetically-improved hybrid poplar clones in eastern Canada reach sawlog size in 15 years with annual yields of 8–15 $m^3\ ha^{-1}\ y^{-1}$ [9]. The Poplar Regional Testing Program of the North-Central United States showed that poplar plantations can yield 27–45 $m^3\ ha^{-1}\ y^{-1}$ [12]. In western Washington hybrid poplar biomass production reached up to 35 $t\ ha^{-1}\ y^{-1}$ [10]. Among poplar species, *P. deltoides* has substantial potential value as a fibre and biofuel crop and is most often used as a parent in inter-specific hybridizations. Inter-specific hybridization of the *Populus x canadensis* taxon and recurrent breeding of parental species *P. deltoides* and *P. nigra* are central to the Italian programme [13]. Under the commercial breeding programme which started in Italy in 1990s, using the best *P. deltoides* and *P. nigra* parents selected on the basis of progeny testing and combining ability, a number of clones are at different stages of selection [2]. New varieties/cultivars already have been developed (e.g. Neva, Dvina, Nova, Saligo, Taro, Oglio, etc.) which are more productive than cultivar I-214 and have better wood quality and higher disease resistance [2]. Many clones from hybrids between *P. deltoides*, *P. nigra*, *Populus trichocarpa* Torr. & Gray., *Populus maximowiczii* A. Henry, and *Populus balsamifera* L. have been tested for growth, cold hardiness, and insect and disease resistance, and the best have been selected for specific ecological regions in North America and Europe [9,2,3]. Lithuania is situated at the northern limit of the natural distribution of *P. nigra* [14]. Therefore this tree species can be considered as a native and its hybrids have potential for wide use in short-rotation forestry, thus supplementing the extensive cultivation of hybrid aspen.

In Northern Europe, hybrid aspen has been the most intensively studied and cultivated hybrids, and here it has proved to be one of the fastest-growing hardwoods suitable for the production of pulp- and energy-wood in short-rotation forestry [6]. During recent decades over 4500 ha of hybrid aspen plantations have been planted in Northern Europe. Hybrid aspen is already mass propagated *in vitro* and is most commonly used to establish short-rotation plantations in Lithuania [6]. Breeding programmes have resulted in hybrid aspen clones with mean annual increment of stem wood reaching 20–25 $m^3\ ha^{-1}\ y^{-1}$ during 20- to 30-y rotations ([15,6] etc). Current annual increment on fertile sites reaches 30.0–46.4 $m^3\ ha^{-1}\ y^{-1}$ [15–18].

Timing/phenology of bud set and bud flush are important adaptive traits in forest trees. These traits in provenance/progeny trials show association with the photoperiod at the population/genotype's site of origin. In general, genotypes from northern latitudes which have shorter growing seasons, stop growing and set bud earlier [19–22]. Genotypes that stop growing and set bud late in the growing season are prone to frost damage [20,23,24]. Temperature at the end of the growing season can alter the timing of photoperiodically controlled growth cessation and bud set in poplars and even alter timing of bud flush in next spring [25–28].

Typically, the timing of bud flushing is controlled by the sum of active temperatures which is inherited based on adaptation to local climatic conditions at the site of origin of populations or species and timing correlates strongly with the latitude of origin [29–31,24]. Day length or other factors can influence bud flush only in very unusual cases, e.g., when winter chilling has been insufficient [32]. In general, transfer of a genotype from the latitude of its origin northward into a cooler climate delays the time of bud flush relative to locally adapted genotypes because more days are needed to accumulate sum of active temperatures. This shortens the growth period and decreases the growth of trees. Transfer of genotypes southward causes earlier flushing, which increases spring frost risk/damages (e.g. Refs. [33,34]).

A number of studies have been performed on inter- and intra-clonal variation of growth and adaptive traits in poplar species [35–39,31] or in single poplar hybrids [24,40,27]. Less research has been done on the variation among different poplar hybrids [41–47]. Selected cultivars only with the best ability to adapt to the local environmental conditions are suitable and are able to reach the greatest biomass possible and provide the best quality of wood [48–50]. However, still little information exists on ecological sensitivity, reaction norms and phenotypic plasticity of poplar clones and hybrids. Insufficient information is available on genetic parameters of different traits, their dependence upon site conditions, and on genetic interrelations among growth, adaptedness and other traits of poplar hybrids under different environmental