



Maternal temperature during seed maturation affects seed germination and timing of bud set in seedlings of European black poplar

Sumitra Dewan^{a,*}, Kristine Vander Mijnsbrugge^b, Pieter De Frenne^{a,c}, Marijke Steenackers^b, Boudewijn Michiels^b, Kris Verheyen^a

^a Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, 9090 Gontrode, Belgium

^b Research Institute for Nature and Forest (INBO), Gaverstraat 4, 9500 Geraardsbergen, Belgium

^c Department of Plant Production, Ghent University, Proefhoevestraat 22, 9090 Melle, Belgium



ARTICLE INFO

Keywords:

Maternal temperature

Climate change

Phenology

Seedlings

Crosses

Memory effect

ABSTRACT

The maternal temperature during seed development can significantly affect seed dormancy, germination and seedling performance. While the response of germination and seedling phenology to maternal temperatures has been well studied for annuals and conifers, very few studies focus on deciduous trees. To understand the responses of seedlings to variation in maternal temperature during seed maturation, we assessed the germination, bud phenology (bud burst, bud set) and height of full sib families in a common garden. We performed three controlled crosses between three different pairs of genotypes of European black poplar (*Populus nigra*) to achieve full sib families in three experiments in warm (+10 °C) and cold (control) maternal environments during crossing and seed maturation. Warmer (+10 °C) maternal temperatures decreased the seed germination success. The seedlings from the warmer maternal environment also displayed later bud burst and earlier bud set, but only in one out of the three crossings (Proven ♀ x Horrues ♂). Our results indicate that the maternal environment can considerably impact on seed germination and the phenological responses of even two-year old seedlings suggesting the existence of a memory of maternal temperature during seed maturation. The seedlings resulting from the colder maternal environment grew taller than those from the warmer environment during the first, but not second, growing season. Our results further our understanding of the responses of deciduous forest trees to rapid climate change, but more research is needed to better understand the mechanisms behind the observed effects of maternal warming.

1. Introduction

The phenology of trees affects key forest ecosystem processes such as biomass production, carbon sequestration, plant-animal interactions and linkages with the understorey biodiversity. Leafing out (bud burst) and growth cessation and senescence (bud set) in particular are key tree phenophases at the start and end of the growing period. Many plant species advanced their spring bud burst in the last decades due to climate warming (Menzel et al., 2006; Zhang et al., 2007; Prieto et al., 2009; Yu et al., 2010). However, the response to increasing temperature varies among species and among genotypes within species (Hedhly et al., 2009; Vitasse et al., 2009; Yu et al., 2010; Fu et al., 2013). Recent findings indicate that the phenology of plants is not only controlled by environmental cues and genetic factors, but also the maternal environment during seed development may determine the phenology of progenies (Yakovlev et al., 2012; Cendán et al., 2013; Latzel et al., 2014; Penfield and MacGregor, 2017).

The temperature of the maternal environment during seed production plays a significant role and can alter the germination success, phenology, establishment and fitness of the progenies (Roach and Wulff, 1987; Fenner, 1991; Hedhly et al., 2007; Rix et al., 2012; Cendán et al., 2013; Chen et al., 2014; Lemke et al., 2015; Gruwez et al., 2016; Penfield and MacGregor, 2017). Yet, the effect of the maternal temperature during seed production on seed germination, seedling performance and phenology is complex. Whereas we know quite well how germination, growth, flowering and yield in annual crops and fruit trees are affected, very few studies focus on forest trees (El-Keblawy et al., 1996; Greenwood and Hutchison, 1996; Owens et al., 2001; Johnsen et al., 2005; Hedhly et al., 2009; Rix et al., 2012). Annual plants have relatively short life cycles. This provides them with the opportunity to adapt faster to a changing environment through natural selection while trees are limited in this respect as generation times are much longer. Trees generally only flower and fruit after 5–20 yrs, which can be longer in forest stands (up to 50 years for some species) (den Ouden

* Corresponding author.

E-mail address: Sumitra.dewan@ugent.be (S. Dewan).

Table 1
Background of the clones used for controlled crosses in both 2013 and 2014.

Sex	Clone name	Province/country	Collection site	Latitude (°N)	Longitude (°E)
♀	Proven	West-Flanders, Belgium	Proven	50.90	2.64
♂ ♀	Horrues Meers	Hainaut, Belgium Limburg, Netherlands	Thoricourt Meers	50.61 50.96	3.99 5.72
♂ ♀	Elst Oosterzele	East-Flanders, Belgium East-Flanders, Belgium	Elst Oosterzele	50.82 50.95	3.74 3.84
♂	Remicourt	Hainaut, Belgium	Twee Akren	50.73	3.87

et al., 2010). Thus, it is likely that contrasting strategies exist between annuals and trees to adapt to a rapidly changing environment.

Variation in maternal temperature during seed development first affects seed dormancy and germination and later the phenology and growth of the seedlings (Roach and Wulff, 1987; Greenwood and Hutchison, 1996; Chen et al., 2014; Penfield and MacGregor, 2017). Maternal effects on the seedlings can occur also via direct transmission of cytoplasmic DNA (Roach and Wulff, 1987). Other maternal effects can also originate via the endosperm (Roach and Wulff, 1987). The endosperm contains enzymes that are important for germination and that provide nutrients to the developing embryo (Roach and Wulff, 1987). A zygote may inherit epigenetic states from the mother plant which are affected by temperature in the tissues of the seed (Penfield and MacGregor, 2017). In *Arabidopsis thaliana*, it has been shown that seed dormancy and germination is controlled via a long-term temperature memory, which is established before seed fertilization and is integrated in the tissue of the fruit (silique) (Chen et al., 2014). There are also interactions between the maternal and zygotic environment that influence embryo development and seed germination (Evans and Kermicle, 2001; Penfield and MacGregor, 2017). Germination of seeds then links the pathway from mother plant to offspring.

In conifers, it has been shown that the phenology is affected by the so-called adaptive epigenetic memory, the memory from the time of embryo development and seed maturation. These effects are known to persist for up to 20 years after germination (Yakovlev et al., 2012). Johnsen et al. (2005) reported that warmer maternal environments during embryogenesis delay the formation of terminal buds of the next generation in Norway spruce (*Picea abies*) through epigenetic variation, a change in gene expression without any change in DNA structure. Greenwood and Hutchinson (1996) also observed similar epigenetic effects on the growth (height) induced by maternal temperature in *Larix* spp. However, many differences exist between gymnosperms and angiosperms in their life cycle, megasporangium structure and seed development (Yakovlev et al., 2012). Considering their contrasting life histories and ecology, we can question whether the performance (germination and height) and phenological responses of broadleaves to the maternal temperature would display similar responses as conifers or not.

To understand the responses of tree seedlings to the maternal temperature during seed development and maturation, we here assessed the phenological responses (bud burst and bud set) and performance (germination and growth) of seedlings of black poplar (*Populus nigra*). Poplar is a dioecious species providing the opportunity to perform controlled crosses in specific environmental conditions, enabling us to study of the response of full-sib families to environmental variation, and eliminating the potential variation caused by genetic diversity. Since the prevailing maternal environment during embryogenesis and seed maturation may influence the performance of the progenies, application of different temperatures during crossing and seed maturation may result in deviating phenological responses and performance in the progenies (seedlings). To assess the response of full-sib families to temperature, we performed controlled crosses in warm (+10 °C, W)

and cold (control, C) maternal environments. Following these different temperature treatments during seed maturation, we sowed all the seeds in a common garden and assessed the performance of the resulting seedlings.

We hypothesised that (i) seed germination success of poplar seeds depends on the maternal environment during seed development, (ii) the seedlings of black poplar generated from the seeds of warmer maternal environments will display earlier bud burst and later bud set, (iii) the height of the seedlings will vary due to the variation in timing of bud burst and bud set.

2. Materials and methods

2.1. Study species

European black poplar (*Populus nigra*) is a keystone species of riparian ecosystems in Europe. It has a wide distribution in Europe and is found in northern Africa and central and western Asia as well (Vanden Broeck, 2003). Black poplar is an important species for the breeding program of hybrid poplar clones in western Europe, that are planted for wood and biomass production, windbreaks, and soil protection (Vanden Broeck, 2004; Vanden-Broeck et al., 2012). In Europe, the hybrid poplar plantations cover circa 800,000 ha and among them, nearly 50% are for industrial production of round wood; 12% are for environmental protection such as windbreaks, to control soil erosion (FAO, 2012).

2.2. Crosses

In two succeeding years, we performed crosses between three pairs of Black poplar genotypes (Proven ♀ x Horrues ♂ - Cross 1, Meers ♀ x Elst ♂ - Cross 2, Oosterzele ♀ x Remicourt ♂ - Cross 3, see Table 1) in three different experiments using grafts taken from trees that were growing in the field that were grafted on potted rootstocks in 2013 and 2014. We wanted to test whether the response of the offspring to maternal temperature would be similar across genotypes. That is why in experiment 3 during the second year, we performed crosses with the same temperature treatments but with different pairs of genotypes. The rootstocks were potted into 5L-pots using standard potting soil (Sanilor pro, NPK 12-14-24). The preparation of plant materials (grafts), performance of controlled crosses and subsequent monitoring were done at the Institute of Forest and Nature (INBO), Geraardsbergen, Belgium (50.763°N, 3.879°E; 19.8 m above sea level). The controlled crosses and production of clonal grafts were performed following (Vanden-Broeck et al., 2012).

2.2.1. Experiment 1: Cold and warm fertilization and seed maturation

In the beginning of February 2013, we produced the clonal grafts. After a couple of weeks, we performed the first controlled crosses in the greenhouse starting from 21 February between the clones Proven and Horrues (Cross 1) in warm (W) and cold (C) conditions. The mean temperature difference between warm and cold conditions was 10 °C during day and night. We used two separate glasshouse compartments

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