

Maternal effects should be considered in the establishment of forestry plantations

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Abstract

Breeding strategies for plants focus on the genetic influence on their phenotypes. However, the phenotype is not only the outcome of the genotype or the environmental conditions under which plants grow. It is important to also recognise that the maternal environment has a significant effect on the phenotype of the offspring. These maternal effects represent a transgenerational form of phenotypic plasticity, transmitted to the progeny without modifications in the DNA sequence. These can influence the development, disease and pest resistance, and fitness of the offspring and subsequent development of the mature plant. In this review, we define and synthesize current understanding of maternal effects in plant reproduction and discuss evidence for the role of these effects in plants and more specifically in trees utilised for plantation forestry. We highlight the implications of the maternal environment in the management of forestry seed orchards and discuss approaches to study maternal effects in order to enhance the productivity of forestry plantations.

Keywords: Epigenetic changes; Forestry seed orchards; Fungal microbiomes; Maternal environmental effects; Phenotypic plasticity; Resistance

1 Introduction

Productivity in plantation forestry has benefitted significantly from breeding strategies. Among these strategies, interest has grown on disentangling the genetic influence on the phenotype of a plant ([Harfouche et al., 2014](#); [Linhart and Grant, 1996](#); [White et al., 2007](#)). For this reason, the study of plant genetic diversity has

become essential for the improvement of growth, wood quality, pest (including insects and microbes) resistance and other traits of plants (Harfouche et al., 2014; Linhart and Grant, 1996; White et al., 2007). There is, however, empirical evidence to show that the phenotype reflects more than only the outcome of DNA sequence variation and the environmental conditions under which plants grow. An important and often overlooked effect is the maternal environment of a plant, which can also have a significant effect on the phenotype of its offspring (Bonduriansky and Day, 2009; Herman and Sultan, 2011; Roach and Wulff, 1987).

Maternal effects represent a transgenerational form of phenotypic plasticity, transmitted to the progeny without modifications in the DNA sequence (Herman and Sultan, 2011; Holeski et al., 2012; Roach and Wulff, 1987). The maternal environment can influence the development, pest resistance, and fitness of the offspring, as well as the subsequent development of the mature plant (Agrawal, 2002; Blödner et al., 2007; Vivas et al., 2019). Moreover, maternal effects can play a significant role in the biology of plants with long generation times such as trees, enabling them to respond rapidly to changing environments (Bonduriansky and Day, 2009). In the contemporary world, it is especially important to consider these effects in environments predicted to be altered due to climate change (Miller et al., 2012; Munday et al., 2013; Salinas and Munch, 2012).

Maternal effects have relevance for forest management, which aims to enhance the productivity of forest plantations. However, the application knowledge relating to maternal effects in plantation forestry had been limited. This is despite a substantial increase in studies relating to these effects in recent years. In this review we i) define maternal effects in plant reproduction, ii) discuss evidence for the role of maternal effects in plants and specifically in tree species, iii) highlight the implications of the maternal environment in the management of forestry seed orchards, and iv) discuss the means to study maternal effects so as to enhance the value of forestry seed orchards.

2 Definition of maternal effects

Maternal effects in plants can be defined as changes expressed in the phenotype and fitness of the offspring, not caused by modifications in the DNA sequence, but rather by the environment under which the parents exist (Fig. 1) (Herman and Sultan, 2011; Roach and Wulff, 1987). In the parental generation, the induction of a stimulus or a change in the environmental conditions of a plant can cause a maternal effect. Such maternal effects will then be expressed in the progeny but possibly not in the parental generation (Jablonka and Raz, 2009). Hence, biotic or abiotic stressors in the maternal environment can play an important role in the development of the seedlings in the absence of DNA modifications (Fig. 1) (Agrawal et al., 1999; Holeski et al., 2012; Jablonka and Raz, 2009; Roach and Wulff, 1987).

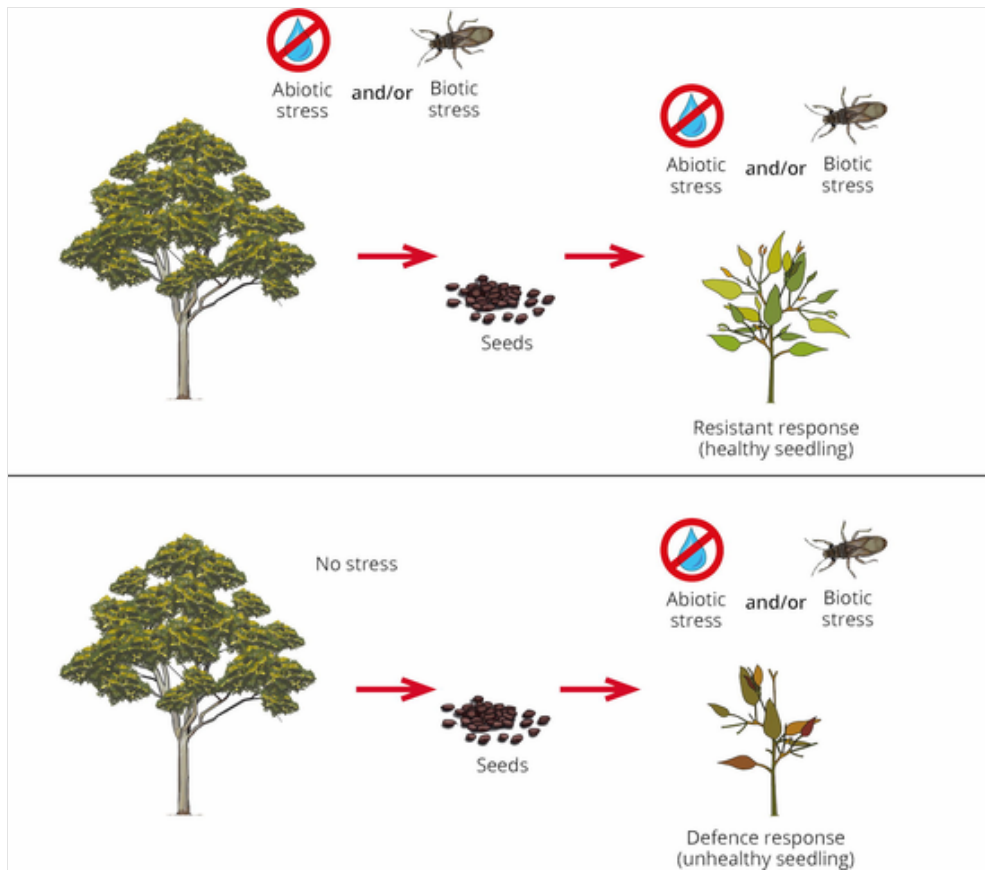


Fig. 1. Hypothetical relationships between genotype, environment of the maternal plant and environment of the progeny across two generations of trees. The figure illustrates a single mother clone subjected to contrasting biotic and abiotic conditions (maternal abiotic and/or biotic stress, above, and non-stress, below). Above: Abiotic and/or biotic stress suffered by the mother (maternal effects) may result in increased resistance in seedlings subjected to the same abiotic and/or biotic stress (healthy seedling). Below: Where the same maternal tree does not experience stressful conditions, the defence response will be triggered (unhealthy seedling) when the progeny experience stress. Thus, seedlings from maternally damaged plants are expected to respond to subsequent stress more effectively than the progeny of unstressed maternal plants.

The influence of both maternal and paternal environments can trigger maternal effects in plant offspring. However, in most plant species, the environment in which the mother grows is considered to underlie the conditions of the environment of the parent (Crean and Bonduriansky, 2014; Galloway, 2001; Roach and Wulff, 1987). There are various reasons for this. Firstly, the maternal parent provisions the seeds with biomolecules (nutrient resources, hormones, proteins and transcripts), and the quantity and quality of these resources are strongly dependent on environmental changes during seed development. Furthermore, the endosperm of the seed is triploid with two-thirds of maternal origin in angiosperms, and it is haploid with a maternal origin in gymnosperms. The embryo of the seed is diploid and one half is maternal, while the seed coat is diploid and is of maternal origin (Baskin and Baskin, 1998; Lacey et al., 1997; Singh et al., 2017; Yakovlev et al., 2012). Consequently, the maternal environment has a substantially greater influence on the phenotype of the progeny than the paternal environment (Donohue, 2009; Galloway, 2001; Yakovlev et al., 2012). In this review, we use the term maternal effects to refer interchangeably to the environmental effects of the mother or the father because the specific contribution of each partner is not always known.

The transmission of the maternal effects to the next generation is achieved mainly by two non-exclusive mechanisms: seed provisioning or epigenetic mechanisms (Herman and Sultan, 2011). In the case of seed provisioning, cytoplasmatic or somatic factors (e.g. hormones, proteins, lipids, RNA) and nutrients (e.g. carbohydrates, mineral nutrients) are transmitted to the progeny (Roach and Wulff, 1987). These substances are allocated by the mother to the seed and used by the germinating seedling to develop the first stages of the plant (Herman and Sultan, 2011). However, this is an ephemeral mechanism that persists for only a single generation (Elwell et al., 2011). The second mechanism underpinning the transmission of maternal effects relates to epigenetic changes. These molecular processes can modify the activity of particular genes in the parental tree (Bossdorf et al., 2008) and can be transmitted to the progeny when they are maintained in the germline, commonly referred to as transgenerational epigenetic inheritance (Bonduriansky and Day, 2009). Epigenetic changes can be mediated by DNA methylation, histone modification affecting chromatin structure and/or small RNA molecules (reviewed in Bräutigam et al., 2013). Unlike seed provisioning, epigenetic mechanisms can be inherited across multiple generations (Hauser et al., 2011).

The persistence of the maternal effects between generations can provide advantages to the offspring when the changes are adaptive. Such adaptation is possible when the environmental conditions of the offspring are predictable (i.e. stable across generations or in regular rhythm) and when the changes enhance the development and fitness of the offspring (Burgess and Marshall, 2014; Galloway, 2005; Galloway and Etterson, 2007; Mousseau and Fox, 1998). Where the environments of the offspring are very different from that of their parents, the maternal effects will be non-adaptive and they can have a negative impact on the offspring (Robertson and Wolf, 2012).

The environmental conditions of the offspring can vary through space (Fox et al., 2019). This is the case, for example, in species with long-distance seed dispersal, and in which those maternal effects are less likely to occur (Galloway, 2005). Importantly, this also applies to plantation-grown trees where collected seeds are commonly established in an environment different from that of the maternal seed orchard. Also, environmental conditions can vary through time (Fox et al., 2019). It is particularly important that environmental changes through time are studied in seedling environments predicted to be altered due to climate change (Munday et al., 2013; Salinas and Munch, 2012), to better understand how seedlings might have to readapt to new environmental cues in future (reviewed in Norouzitallab et al., 2019). The extent to which maternal effects play a role in such adaptation remains unclear (Schmid et al., 2018).

3 Evidence and the role of maternal effects in plants, and trees in particular

Plants, as sessile organisms, have a greater plasticity than animals to adapt to rapidly changing environmental conditions during their lifespan (Bonduriansky and Day, 2009). This greater plasticity makes plants prone to the effects of the maternal environment (Bonduriansky and Day, 2009). For example, an increase of maternal nutrient and light levels on *Campanula americana* increased seed mass and decreased the percentage of seed germination (Galloway, 2001). *Arabidopsis thaliana* in warm environments produced progeny having more rapid germination rates, greater leaf biomass, and faster root elongation than progeny from cold parental environments (Blödner et al., 2007). Moreover, herbivory on maternal plants produced more resistant progeny

compared to control plants (Agrawal, 2002; Holeski, 2007; Rasmann et al., 2012). These examples clearly illustrate that the maternal environment can minimize the negative effects of stressful environments or even alter the development of seedlings.

There are many examples of maternal effects in annual plants (e.g. reviews by Donohue, 2009; Herman and Sultan, 2011), but the literature pertaining to forest tree species is much more limited. It is challenging to incorporate an understanding of the maternal effects into forest management practices specifically because trees are long-lived, consequently presenting serious limitations to study these effects over multiple generations. Nonetheless, there is a growing number of studies (Table 1) considering maternal effects on forest trees and illustrating how these effects influence seed and seedling (cutting) development and pest resistance (Table 1).

Table 1. Studies demonstrating maternal effects in forest trees.

Tree species	Maternal stimulus/stress	Maternal effect on the offspring	References
<i>Eucalyptus globulus</i>	Abiotic: Four genotypes as parents for a diallel crossing scheme.	Seedling germination was affected by paternal and maternal effects. Seedling response to high temperature was influenced by the maternal parent.	(Rix et al., 2012)
<i>Eucalyptus globulus</i>	Abiotic: Different environments located in north-eastern and southern Tasmania.	Seed mass presented a significant maternal effect and has a persistent carryover effect on early growth.	(Lopez et al., 2003)
<i>Eucalyptus grandis</i>	Biotic and abiotic: Two differing environments.	Seedling performance, resistance and the structure of fungal communities in the foliage were affected by the differences in the maternal environments.	(Vivas et al., 2017)
<i>Eucalyptus grandis</i>	Biotic and abiotic: Two differing environments.	Seedling relative growth rate, leaves intercellular CO ₂ , and intrinsic water use efficiency were	(Vivas et al., 2019)

		affected by the differences in the maternal environments.	
<i>Larix laricina Larix decidua Larix leptolepis</i>	Abiotic: Different environmental temperature when doing parental crosses.	Seedlings from the different crosses showed significant growth differences. In addition, it was observed segregation distortion at the chlorophyll-ah-protein locus as a function of crossing environment.	(Greenwood and Hutchinson, 1996)
<i>Picea abies</i>	Abiotic: Northern clones sown in a southern location.	Seedlings grown in a southern location were more severely damaged by frost during cold acclimation than seedlings grown in their area of origin (north). This effect was persistent for more than one growing season.	(Johnsen, 1989b)
<i>Picea abies</i>	Abiotic: Northern clones sown in a southern location.	Seedlings grown in the southern location flushed later in the spring, terminated leader shoot growth later in the summer, had higher frequencies of lamm shoots, had delayed lignification during autumn, and were taller (seven-year-old) than seedlings grown in their area of origin (north). These effects were permanent from age four to seven.	(Johnsen, 1989a)
<i>Picea abies</i>	Abiotic: Northern clones sown in a southern location.	Seedlings grown in the southern location were more severely damaged by winter frost (four-year-old seedlings) and had reduced growth (six-year-old seedlings) than seedlings grown in their area of origin (north).	(Johnsen et al., 1989)
<i>Picea abies</i>	Abiotic: Different photoperiod and temperature during microsporogenesis to anthesis.	Crosses performed at times of short day length and high temperature produced less hardy progeny than their full-sibs reproduced from a long day lengths and high or low temperature.	(Johnsen et al., 1996)
<i>Picea abies</i>	Abiotic: Contrasting temperatures under seed production.	Seedlings with warm seed production formed terminal buds later, were less hardy and expressed lower transcription levels of the phytochrome and the class IV chitinase genes, than seedlings with cold seed production.	(Johnsen et al., 2005)
<i>Picea abies</i>	Abiotic: Two different environments, cold (outdoor) and warm (inside a glasshouse).	Seedlings from a warm environment were taller and had significantly later bud set, than seedlings from a cold parental environment.	(Kvaalen and Johnsen, 2008)
<i>Picea glauca</i>	Abiotic: Two different locations.	Germination traits, number of needle primordia, height, and frost hardiness were significantly	(Stoehr et al., 1998)

		affected by the location of the maternal environment.	
<i>Picea glauca</i> × <i>engelmannii</i>	Abiotic: Two temperature regimes during reproductive development of seed and pollen cones.	Seed cone development and the adaptive properties of the progeny (seed yields, cotyledon emergence and germination) showed differences depending on the temperature regime of seed and pollen development.	(Webber et al., 2005)
<i>Pinus aristata</i> <i>Pinus flexilis</i>	Abiotic: Local annual weather conditions over multiple years.	Seedlings sourced over multiple years showed significant differences in twig growth characteristics, seed size, and seedling performance.	(Borgman et al., 2014)
<i>Pinus pinaster</i>	Abiotic: Two contrasting environments (favourable vs unfavourable).	Seeds from a favourable environment germinated earlier and showed higher germination percentages than seeds from an unfavourable environment.	(Cendán et al., 2013)
<i>Pinus pinaster</i>	Abiotic: Two contrasting environments (favourable vs unfavourable).	Seedling height, diameter and pathogen resistance were higher in progenies grown from a favourable maternal environment in comparison with an unfavourable maternal environment.	(Vivas et al., 2013)
<i>Pinus pinaster</i>	Abiotic: Two contrasting environments (favourable vs unfavourable).	After pathogen inoculation, seedling glucose was higher and uronic acid lower in progenies from a favourable maternal environment in comparison with an unfavourable maternal environment.	(Vivas et al., 2014a)
<i>Pinus pinaster</i>	Abiotic: Two contrasting environments (favourable vs unfavourable).	The relationship between seedling antioxidant activity and stem necrosis caused by pathogen inoculation differed significantly between maternal environments.	(Vivas et al., 2014b)
<i>Pinus pinaster</i>	Abiotic: Two contrasting environments (favourable vs unfavourable).	Cone and seed size, seed mass variability, seedling height and root/shoot ratio were determined by the maternal environment.	(Zas et al., 2013)
<i>Pinus pinaster</i>	Abiotic: Two contrasting environments (favourable vs unfavourable).	Cone and seed weight means and within-individual variation in seed weight were influenced by the maternal environment.	(Zas and Sampedro, 2015)

<i>Pinus sylvestris</i>	Abiotic: Soil treatments.	Seedling epicotyl length showed a positive relationship with maternal N needle content. And autumn frost hardiness of the seedling related to maternal soil treatment.	(Andersson, 1989)
<i>Pinus sylvestris</i>	Abiotic: Three geographic locations.	Seedlings from maternal environments at northern localities were hardier than seedlings from maternal trees at southern localities.	(Andersson, 1994)
<i>Pinus sylvestris</i>	Abiotic: Environments located at three different latitudes.	Seedlings from the different paternal environments showed differences in seed weight and height development in two growth periods. There was also an effect of autumn frost hardiness during the first growth period.	(Dormling and Johnsen, 1992)
<i>Pinus sylvestris</i>	Abiotic: Environments located at three different latitudes.	Seedlings showed different heights and mortality depending on the maternal latitude.	(Lindgren and Wei, 1994)
<i>Pinus thunbergii</i>	Abiotic: Different age and stand density.	Seedling biomass allocation and growth were influenced by maternal age. Seed germination and seedling growth were influenced by stand density of the mother tree.	(Mao et al., 2014)
<i>Populus angustifolia</i> <i>Populus fremontii</i> and their F1 hybrids	Biotic: Herbivory.	Phytochemical content and concentration of phytochemical resistance decreased in seedlings with maternal herbivory, relative to undamaged maternal seedlings.	(Holeski et al., 2013)
<i>Populus deltoids</i> <i>Populus trichocarpa</i>	Abiotic: Different temperature and photoperiod (different geographic locations).	The temperatures experienced by the parent tree altered the bud flush of the cuttings.	(Dewan et al., 2018a)
<i>Populus nigra</i>	Abiotic: Warm and cold environment during crossing and seed maturation.	Warmer maternal temperatures decreased seed germination. Seedlings from the colder maternal environment were taller than those from the warmer environment, during the first growing season.	(Dewan et al., 2018b)
<i>Populus nigra</i> cv. <i>Italica</i> Duroi	Abiotic: Different environments.	Phenology of bud set at the end of the growing season was correlated with climate variables experience by the mother trees.	(Vanden Broeck et al., 2018)
<i>Populus trichocarpa</i>	Abiotic: Two locations with different	Stem cutting growth was affected by the maternal environment. The differences were associated with different levels of methylation and amounts of miRNAs.	(Schönberger et al., 2016)

	phosphorous availability.		
<i>Populus</i> hybrid clones: – <i>P. deltoides</i> × <i>P. nigra</i> – Walker [<i>P. deltoides</i> var. <i>occidentalis</i> × (<i>P. laurifolia</i> × <i>P. nigra</i>)]– Walker × (<i>P. laurifolia</i> × <i>P. nigra</i>)	Abiotic: Two different locations.	Seedling drought showed differences in transcript abundance patterns and genome-wide DNA methylation based on differences in geographic origin for two of the three clones.	(Raj et al., 2011)

The maternal effects on offspring phenotypes of trees have been studied since the late 1980's (Table 1). The influence of the maternal environment was first demonstrated in *Pinus* and *Picea* (Andersson, 1989; Johnsen, 1989a,b; Johnsen et al., 1989). That work provided an important foundation for this field of research. Yet, only a few tree genera have been considered in these studies and they remain mainly focused on conifers (Table 1). Maternal effect studies have also mostly been restricted to species that have an economic value in forestry plantations and that have short rotation periods (mostly conifers and poplars). Although the influence of maternal effects on seedling resistance against pests and pathogens has been investigated (Alonso et al., 2019), the majority of studies on forest trees have focused on abiotic characteristics of the maternal environments (Table 1). And importantly, all of the research on trees has investigated maternal effects in only one generation, most likely and understandably due to the length of time needed for many tree species to reach maturity and produce seed.

4 Implications of maternal effects for the management of forestry seed orchards

At present, breeding strategies to improve the productivity of forestry seed orchards attempt to disentangle the genetic component and its effects on the phenotype of the trees (Harfouche et al., 2014). However, the studies discussed in the previous section (Table 1) demonstrate that maternal effects can also have practical implications for tree breeding and seed production. Specifically, maternal effects can (i) improve the development, physiology and resistance to pests and pathogens in the progeny of forestry trees, (ii) be inherited across generations, and (iii) develop a rapid adaptation to stress in seedlings used in forestry plantations.

Maternal effects can improve the phenotype and fitness of the tree progenies directly (as discussed above; Table 1) or indirectly (Vivas et al., 2015). A recent study (Vivas et al., 2017) has shown that the maternal environment can modify the structure of fungal communities of the seedlings. Tree associated microbiota can also protect trees against diseases and promote their growth (Peñuelas and Terradas, 2014). Therefore, the maternal environment can indirectly influence the development, physiology and resistance of these progeny by impacting on the structure and composition of microbial communities. Results of these studies reveal that direct and indirect maternal effects can be exploited to improve the development, physiology and resistance of seedlings against biotic or abiotic stressors in any breeding program.

Forest tree breeding programs aim to improve tree characteristic in the short and long term. In the long term, the heritability of the maternal effects should be recognized as a system of heritable variation, similar to

genetic variation (Bossdorf et al., 2008). The fact that the effects caused by the maternal environment can be inherited across generations suggests that they need to be considered in breeding projects and seed production. For example, the maternal environment can be managed to pre-adapt the offspring against pathogens or to transmit inducible defences (Agrawal et al., 1999). In this regard, it is important to provide seedlings with similar environmental conditions as the maternal environment in order for the inherited maternal effects to have positive fitness effects on the offspring (Baker et al., 2018). At the very least, it should be recognised that the environment in which mother plants grow in seed orchards could have an effect on plants emerging from the produced seed.

In forest trees, maternal effects can increase the potential of the offspring to respond to abiotic and biotic stresses, and in this way make it possible for the plant to adapt rapidly in a changing environment. It is known that the ability of the parents for adaptation to different environmental cues can regulate the plasticity of the subsequent generation to those specific cues (Norouzitallab et al., 2019). What makes maternal effects unique is that, unlike genetic variation, they are triggered on a short time scale by the environment. Maternal effects, therefore, provide more rapid means to develop phenotypic variation, in comparison with genetic variation (Yakovlev et al., 2012), favouring phenotypic variability of the plants against stressors. In clonal forestry plantations, where the genotypes of the trees are identical or similar, the effect of the maternal environment can play a particularly important role in the adaptation of the offspring to stressful conditions. Although the extent to which maternal effects influence adaptation is unclear, these effects can buy time for seedlings when environmental conditions in the progeny change during the time (reviewed in Fox et al., 2019).

Failure to consider the contribution of the maternal effects can lead to misinterpretations of the results of genetic studies, most likely overestimating the genetic differences between the plants (Sow et al., 2018). Taking the influence of the maternal environment into account can improve our understanding of the phenotypic variations not explained by DNA sequences or the environment of the progeny. Thus, studying maternal effects would provide forest researchers and managers with more effective information to assess the potential impact of abiotic and biotic stresses on their seed orchards.

5 How to study and utilize maternal effects for forest management

It is not only challenging to study maternal effects in forestry plantations but also to apply this knowledge to increase productivity in tree breeding programs. Ideally, maternal effects phenomena should be studied in plantations using common garden experiments. This makes it possible to predict optimal zones for tree planting that take into consideration the maternal environmental conditions (Fig. 2). The aim of a common garden study is to distinguish seedling plasticity triggered by the maternal environment and the plasticity caused by genotype or environment of the seedlings. Such common garden studies would include three phases (Bossdorf et al., 2008). These are (i) selection of the maternal environment, (ii) collection of the seed material and (iii) determination of the fitness of the seedlings (Fig. 2).

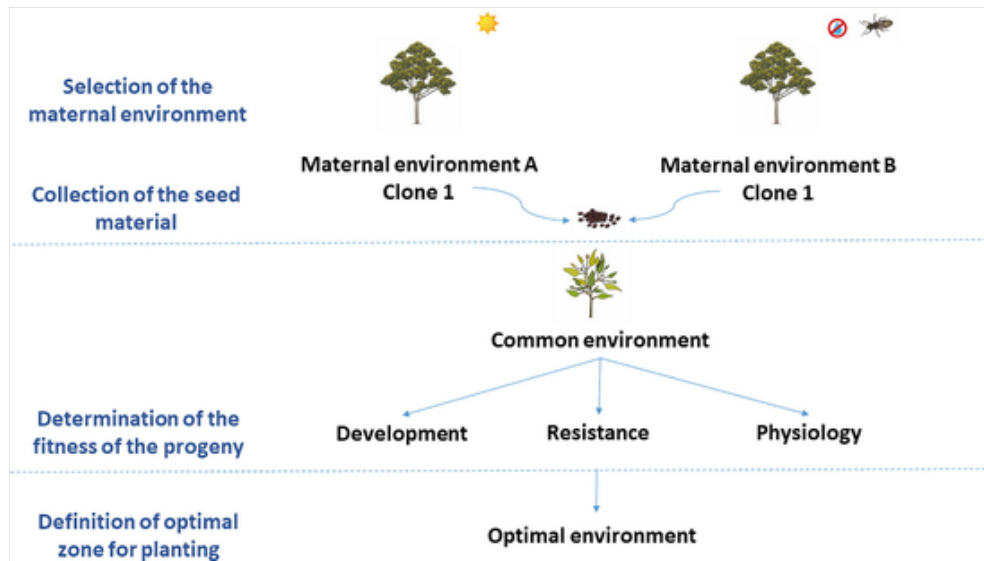


Fig. 2. Common garden experiment. This figure illustrates a hypothetical common garden experiment including three phases: (i) selection of the maternal environment, (ii) collection of the seed material and (iii) determination of the fitness of the seedling. A single mother clone (Clone 1) is selected in two contrasting environments (A and B). From the selected clone, seeds or cuttings are collected. The plant material is developed in a common environment and the differences in development, resistance and physiology of the seedlings are determined. Once the fitness is determined, it becomes possible to define optimal zones for planting the material.

To design a common garden study, it is necessary to select or establish seed orchards having different environments that are of relevance to the objectives of the breeding programs being considered. Forest trees are usually spread over large areas having different ecological conditions. It is thus necessary to clearly define the phenomena or the area of interest to be studied. The seed orchards should include the same genetic material to allow for comparisons. In forestry, the use of clones to establish plantations is a common strategy to develop the breeding populations, making this requirement generally easy to fulfil.

From the selected seed orchards, it is necessary to collect seeds having the same genetic background to represent the contrasting environments. Or, where possible, to collect leaves, stems or roots and vegetatively propagate cuttings (Bräutigam et al., 2013). Propagation by tissue culture provides a more rapid alternative than seed to control the genetic background of the maternal trees because it allows the production of genetically identical plants without any bias of the paternal influence. The use of plants genetically identical to their mothers (such as stem cuttings) would simplify maternal effect studies in comparison with studies using seeds (Hung et al., 2018). However, care should be taken, as propagation by plant tissue culture may cause traumatic stresses to plant cell triggering genetic and/or epigenetic alterations (McClintock, 1984; Wang et al., 2013).

The development and resistance of the seedlings or cuttings representing the different maternal environments need to be determined in a common environment. The differences can then be studied comparing the phenotypic or physiological changes of the seedlings from different maternal environments, and/or implementing epigenetic studies (i.e. Yakovlev et al., 2011, 2012). In general, these studies are focused on disentangling the morpho-physiological strategies of the seedlings in a common environment. As an example, in a Eucalyptus study, *Eucalyptus grandis* seedlings in a common environment showed 21% increase seedling

height and 23% greater pathogen damage depending on the maternal environmental conditions (Vivas et al., 2017). Where feasible, it can also be useful to simulate similar conditions of the maternal environment as a control (i.e. Raj et al., 2011).

In addition, assessing phenotypic changes epigenetic studies can be conducted on the maternal material that has been collected or the offspring derived from it (reviewed in Bräutigam et al., 2013). Methods for studying specific epigenetic modifications, such as DNA methylation, are now well established (Bossdorf et al., 2008; Verhoeven et al., 2016). The most common DNA methylation in plants is cytosine methylation (Martienssen and Colt, 2001). Methylation can cause heritable changes in gene expression without modification in the DNA nucleotide sequence. Thus, such epigenetic studies also contribute knowledge regarding the heritability of maternal effects.

Once the fitness of a plant has been determined, it becomes possible to define optimal zones for planting the different sources of the seeds or cuttings. Optimal zones for planting are environments where the material (seeds or cuttings) from a seed orchard can be used to exploit the possible benefits of the maternal effects. In order for the maternal environment to contribute an advantage in development or resistance, seedlings should develop in more or less the same temperature, daylight conditions as the mother plants (Yakovlev et al., 2012). The range of the optimal zone for planting could be informed by the outcome of the maternal effects identified in the common garden studies. These outcomes result from a complex interaction of multiple abiotic and biotic conditions. Finding an optimal environment does not imply that each of the individuals of the progeny will have enhanced characteristics. However, application of maternal effect studies along with knowledge of the genotype and environment can improve tree phenotype, thus increasing productivity in tree breeding programs.

6 Conclusions

In this review, we have explored how maternal effects can improve our understanding of the mechanisms underlying phenotypic changes and responses of plant offspring. Although disentangling maternal effects from genotypes and environmental influence is complex, there is an urgent need to further increase the empirical evidence regarding maternal effects in forestry for various reasons. Importantly, maternal effects can enhance the development (growth) and resistance (pests, stress) of offspring plants. This will become increasingly important in the face of rapidly changing environmental conditions. A lack of appreciation for the importance of maternal effects will have a negative impact on the adaptability and performance of trees used to establish plantations. And in this regard, breeding programs should include the impacts of maternal effects in order to reach their goals and without overestimating genetic differences.

There are many unanswered questions that remain to be addressed to enable the common application of maternal effects in forest tree breeding and management. For example, the prevalence of the maternal effects for more than one or two generations in trees is not understood. There is also a very limited understanding of the influence of the parental effect. Yet, despite these uncertainties, it is crucial to integrate an understanding of the influence of the maternal environment in breeding programs. Breeders should use common garden studies and define optimal zones for planting, thus to begin unravelling the impact of genotype, environment and maternal environment on the response of plants derived from orchards established in different environments.

These maternal effects will need to be evaluated for different species and different environments, so as to identify the most suitable environments in which to produce tree progeny.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Highlights

- The effects of the maternal environment on forestry plantations are reviewed.
- Maternal effects can improve the phenotype in the progeny of forestry trees.
- Maternal effects should be studied in common garden experiments.
- Breeding programs should include the impacts of maternal effects.
- An understanding of maternal effects could increase forestry productivity.