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B4EST

Adaptive BREEDING for productive, sustainable and resilient FORESTs under climate change

Deliverable D4.3

Multi-trait and multi-criteria performance modelling platform for FRM

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1 Summary

In this deliverable we review and analyze how stand-level decisions can be made on which forest reproductive materials (FRM) to deploy for different European forest tree species given conditions where the FRM expected performance from the decision-maker should fulfil several criteria that are often complex, and which frequently are in trade-off relationships with each other. For some of the species and some of the traits, there is enough data to develop biological and/or statistical performance models that would aid the management of FRM deployment and to deal with the trade-offs. In other situations, trade-offs are better managed by splitting and differentiating FRM in different subclasses. In yet other instances, there exists a general knowledge about a trade-off between complex traits, but where solid sources of data nonetheless are lacking. In such cases, management decisions often need to be taken more on a case-by-case judgement basis. Alternatively, a set of criteria or a definition of performance could be established by decision-makers and stakeholder at a higher tactical or strategic level incorporating all known trait models and trade-offs characterizing the FRM. From such a process stand-level decision-making tools could be developed despite a lack of explicit models for certain traits or trade-offs.

The aim of this analysis is to develop and offer a common framework and modeling platform to tackle multi-trait and multi-criteria issues for European forest tree species. Because FRM are utilized and traded for many species in Europe we will here devote the in-depth analysis and discussion only to a select example of tree species which include Norway spruce (*Picea abies*), Poplars (*Populus spp.*) and Douglas fir (*Pseudotsuga menziesii*). The species are selected to represent contrasting situations and highlight possible differences in approach. Norway spruce represents a long rotation species with a predominantly seed orchard-based deployment system. Poplar is instead a short rotation species deployed by clonal propagation. Douglas fir serves as an example of an introduced/exotic species. Common conclusion that can be drawn is that the management of multi-trait tradeoffs is an important issue for all the studied species finding it critical that this issue dealt with properly. We also found that the prospect of climate change on the European continent will increase the importance of this multi-trait tradeoff management even more as it interacts with several of the trade-off relationships. Finally, it was also found that expectations of stakeholders varied among species thus having an impact on what characteristics and consequently FRM traits would be desirable. By describing, analyzing and discussing the specific FRM deployment conditions for each of the species included, we here propose a common framework for how successful management of multi-trait and multi-criteria trade-offs could be made.

2 Introduction

2.1 Multi-trait performance modelling of FRM given multiple desired criteria: concepts and definitions

Given the objective to regenerate forests and generate new forests at a large scale, there are several strategic choices to be made in terms of the choice of regeneration method, silviculture, choice of tree species and also the choice of forest reproductive materials (FRM) within species that is to be deployed. In this study we will focus on how choose among different FRM of the same species for

deployment at the stand level. We will in particular consider and highlight that such a choice includes the evaluation of multiple desired or undesired *traits* characterizing the FRM but also have to consider multiple *criteria* desired by stakeholders (see Figure 1 for overview). General traits such as growth, survival, stem- and wood quality and reproductivity can be characterized by breeders with relative ease but traits connected to various vulnerabilities such as abiotic and biotic threats are also often considered important. Ideally, some or all, of these traits should be modelled and integrated so that each FRM could be characterized by a specific *performance* for the establishment of a specified stand in a given geographic area.

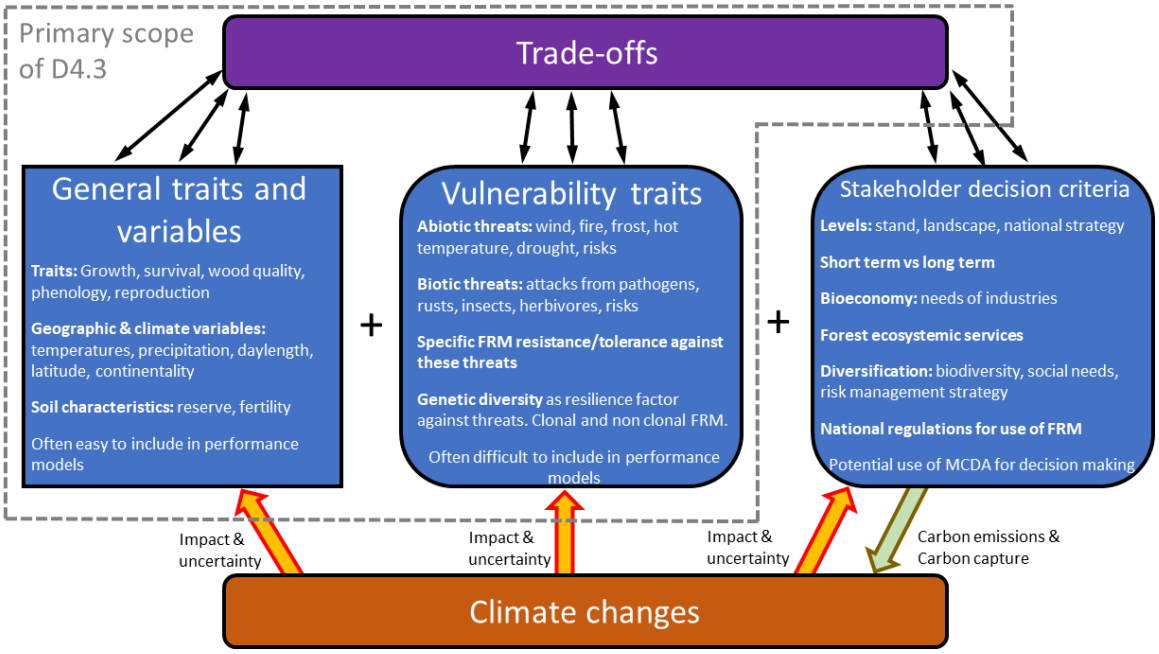


Figure 1: Schematic overview detailing traits (general and vulnerability) that potentially can be included in performance models given a set of criteria specified by stakeholders. All traits and criteria may be subject to trade-off relationships and may also be impacted by future climate change. The scope of the D4.3 study is limited to the area within the dashed lines but with attention given to the impact of external stakeholder criteria and climate change.

Furthermore, the choice of traits that ultimately are considered valuable thus contributing to *performance* is guided by multiple *criteria* desired by different stakeholders. The assessed traits and desired criteria are often very different in nature and not always favourably related with each other which can create the tricky balancing of *trade-offs* (Figure 1). Therefore, stakeholders will be faced with the question on how to prioritize among the desired criteria which could potentially be achieved by multi-criteria decision analysis (MCDA, see e.g. Blagojević et al. 2019). It should be noted that the criteria desired for any FRM, and thus the definition of performance, may vary across species, countries and geographic regions (see e.g. Deliverable 5.1). But to enable the development of guidelines and recommendations for the deployment of any FRM, it is necessary for breeders and foresters to know, not only the criteria desired by their stakeholders, but also national regulations and practical obstacles (see e.g. Deliverable 4.2) that may influence their particular situation. Thus, they would have a definition of what performance means enabling them to make informed trade-off decisions.

Complications may not only arise from a less-than-favourable biological relationships among desired traits and criteria *per se* but may also stem from differences in trait modelling methods and in the nature of trait expression. It is critical to know to what extent the individual traits are governed by heritable genetic factors or by environmental cues. For traits connected to climate adaptation it is useful to estimate reaction norms and establish universal response functions which indicate the geographic transferability of different FRM in deployment situations (see e.g. Deliverables 1.2 and 1.3). Genetic and environmental signals can moreover interact in complex ways e.g. by giving rise to differing phenotypic plasticity of FRM over a range of environments. Alternatively, specific environmental signals given at a critical timepoint during the early development of tree seeds and seedlings may regulate future genetic expression and characteristics at a later stage, so called epigenetic regulation. In the best of cases such epigenetic regulation could also be predicted and accounted for by reaction-norm-type approaches. In addition to this, the integration of multiple traits into performance will have to contend with limited data availability and difficulty of trait assessment. Nonetheless, in order to safeguard the health of future deployed forests from abiotic and biotic threats, ensure future forest growth, and to enable economically and ecologically sustainable use of the produced forest resources in an optimal way, the requirement to account for and balance multiple performance criteria will be unavoidable. As we shall see, this is particularly important given future climate changes as these will have an impact both on FRM trait expression, the desirability of certain criteria and on the trade-off relationships among different traits and criteria.

2.2 Approaches of accounting for multiple traits

A mathematically and quantitatively appealing approach is to actually combine and integrate the different traits completely into a *performance index* (e.g. Berlin et al. 2019). This can be done, for instance by using product multiplication thereby emulating the logically multiplicative relationships often evident in the laws of probability, biology and physics. Given a situation where areal biomass growth over a rotation is the desired outcome, it is possible to combine growth and survival into such a performance index, as they can be expressed in a common non-monetary scale (Berlin et al. 2009; Chambers & Borralho 1997). However, also from a more general perspective, trees need to both survive and grow to constitute a forest, so a such a multiplicative index could be motivated both from economic and ecological perspectives. Within the scientific field of ecology, the term most closely corresponding to *performance* would be evolutionary *fitness* which also has been modelled for trees depending on multiple basic traits (e.g. Gàrate-Escamilla et al. 2019).

However, there may be additional traits and trade-offs that are more difficult to generate in a straightforward multiplicative way. For such traits one can instead take the statistical approach of generating an additive performance index based on adding the desired trait values together, each of them weighted by a measure of relative importance. The determination of such weights is itself often a complex task involving intensive interactions with stakeholders on how they value and prioritize among their desired target criteria. This can be done either by bioeconomic modelling or by MCDA among stakeholders. In any case, the outcome of such an evaluation may result in an *economic weights index* (Baker 1986, Hazel 1943) which may be utilized to calculate performance. Alternatively, the criteria specified by stakeholders may be translated into a set of constraints imposed on the traits based on desired and undesired outcomes (*restricted index*, Yamada et al. 1975). Candidate traits for an additive performance index are often growth, stem- and wood quality traits but there are also a few notable examples of disease resistance being included using such an approach (rust and aphid

resistance in Poplars). Using the methods of imposing constraints, genetic diversity is also often included (e.g. Brisbane & Gibson 1995; Stoehr et al. 2008; Ahlinder et al. 2014).

Finally, there may also be important traits whose nature and relationships are inadequately known and thus are too difficult to combine into any common scale performance index. However, if they are included or connected to any desired criteria, they will nonetheless have to be somehow handled, if necessary, by more subjective means using the best data available. Examples of this are often the risks of damages due to extreme events (droughts, frosts, storms and fires) or due to pests and pathogen attacks.

2.3 Objectives

- To propose an open modelling platform that could host available multiple trait models and previously developed single-trait sub-models with guidelines for their adaptation to new performance datasets.
- To facilitate the development of tools and guidelines for deployment recommendations where the knowledge developed in B4EST is used. It is important to envision this end-result/product for different species and regions and adapted to different sets of criteria specified by stakeholders. The solutions will most likely be different but have some common characteristics.

3 Results

3.1 Norway spruce (*Picea abies*)

Norway spruce was chosen as an example template of performance modelling for the Nordic region. The primary objective of tree breeding and deployment programs for Norway spruce in the Nordic region is to increase volume production per unit area (e.g. Berlin et al. 2012; Jansson 2007; Jansson et al. 2017). This objective also constitutes the expectation of most major stakeholders. But this criterion still has to be fulfilled in such a way that general forest health, climate adaptation, resilience towards biotic and abiotic threats and a certain amount of genetic diversity is safeguarded. Therefore, specific efforts of validation for this species were focused on explicitly integrating climate risks, in particular late spring frost damages, and the effect of epigenetic regulation from the seed reproductive environment. The species wide distribution in northern Europe is characterized by its immigration from refugees in Russia after the last glaciation (Figure 2), large gene flow from long distance pollen dispersal and low degree of differentiation (Tollefsrud et al. 2008, 2009, 2015; Tsuda et al. 2016). In contrast, the more scattered distributions in central Europe show a stronger degree of differentiation (Heuertz et al. 2006, Tollefsrud et al. 2008). The immigration into Scandinavia probably followed two main routes (Tollefsrud et al. 2008): one over northern Finland, around the Gulf of Bothnia and then south and westwards into Sweden and Norway. The other route was across the Baltic sea into southern Sweden and Norway.

In Sweden the breeding and deployment of Norway spruce divided is into a southern and a northern part. This division runs along a cultural and climatological border (sometimes denoted *Limes Norrlandicus*) that divides the boreal from the boreo-nemoral forests and roughly runs along an east-west line between latitudes 60°N and 61°N (Fries 1948). The biologic and economic effects of this division is most pronounced in Sweden which has considerable landmass both north and south of the border, whereas it is less important in Norway and Finland whose forests are situated mostly in the

northern part. North of this division, there are three main gradients of adaptation, from south to north, from the oceanic Atlantic climate in West of Norway towards the continent, and the elevational gradients from sea level up to 1200 m elevation.

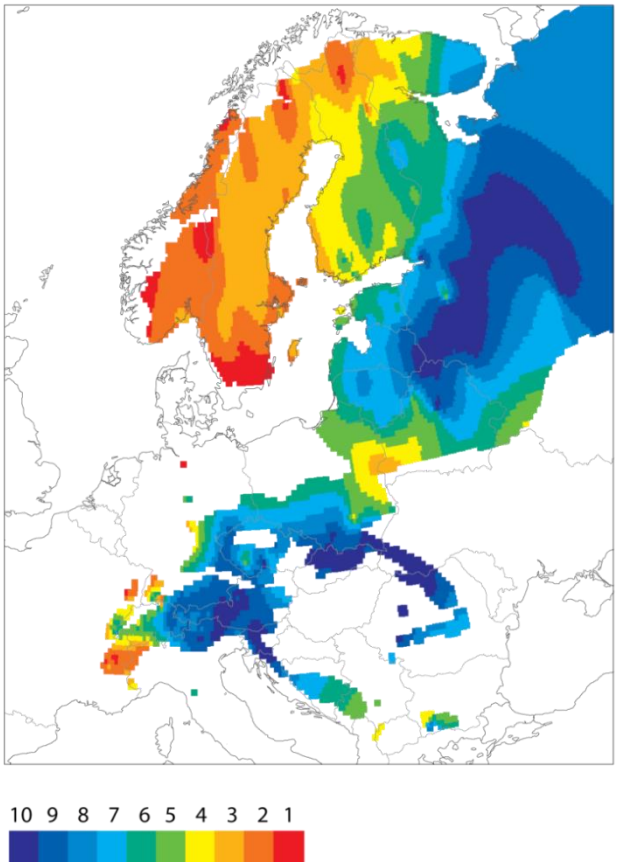


Figure 2 : Map showing the estimated age of pollen fossils in intervals of 1000 years indicating the history of immigration from glacial refugees. Map by C. Sperisen based on data from Tollefsrud et al. (2008).

3.1.1 Main traits, growth and survival

For Norway spruce, *Universal Response Function* (URF) modelling efforts conducted in deliverable 1.3 involved height growth and survival at 580 test sites in Sweden, Norway, Finland, Denmark and the Baltic states. These two traits are critical for tree health and for the total area production over the rotation which is the primary desired criterion of stakeholders in Scandinavia. In short, these traits were modelled separately by URF transfer models which are frequently used for seed orchard-based deployment systems based on the average performance of each provenance within each trial. The provenance origins ranged across the whole Nordic region and substantial parts of the European continent. The field trial data was paired with climate indices from the EOBS climate data (Swedish Metereological institute, downscaled 5.5×5.5 km grid) and the CRUTS/UKCP18 climate data (downscaled 1×1 km grid). For height growth (*H*) the best URF-model so far included factors such as tree age at height measurement (*AGE*), annual temperature sum above 5˚C at the site (*TS*), precipitation at the site during April to October (*PRC*) and the latitudinal transfer of any given provenance to the experimental site (*ΔLAT*). The model formulation was given as:

$$\ln(H) = \alpha_0 + \alpha_1 \frac{1}{AGE} + \alpha_2 TS + \alpha_3 PRC + \alpha_4 PRC^2 + \beta_1 \Delta LAT + \beta_2 \Delta LAT^2 + \gamma_1 TS \times \Delta LAT^2 + \delta + \varepsilon$$

where, apart from the factor combinations and their respective coefficients, α_0 is the intercept, δ is a random site effect and ε is the residual. The proportion variance explained by this model was ~60% (R^2).

Modeling was also attempted for survival. But because survival was generally satisfactory (>80%) across the vast majority of investigated field trials it could be concluded that its influence over the target area (volume) production over a rotation would be marginal. Observations of general high survival rates have been made in studies both with improved and unimproved Norway spruce FRM (Roiko-Jokela 1980; Pohtila & Pohjola 1983; Ruotsalainen & Nikkanen 1998; Napola 2004; Haapanen 2020). However, certain extreme conditions during winter cause severe mortality among seedlings (e.g. Rolandsen 2015), and research on survival in the context of risk management to extreme events is required to corroborate the tendencies so far observed. Further research is also motivated for the very northern margins of the species distribution where there are indications of deteriorated survival (Ruotsalainen 1987) but where data is still lacking.

Nonetheless, given the current observations our working assumption within this deliverable is that height growth would act as the sole primary factor underlying the key performance index and that the impact of the survival rate can be considered negligible. For Norway spruce this performance index is exemplified with the Planter's guide tool.

3.1.2 Phenology and frost risk

Apart from height growth and survival *per se*, there are good reasons to follow traits related to abiotic and biotic threats which still are difficult to include explicitly in URF models. For Norway spruce, shoot phenology traits are among such traits because of their connection to risk of frost damage to the newly developed tissue in spring and fall. Such damages may result in reduced growth, impaired tree health in general, stem quality defects and even mortality in extreme cases. It should be noted that phenology and hardiness development in late summer and fall is probably also linked to winter survival. The timing of phenology events in Norway spruce is under strong genetic control (e.g. Skrøppa & Steffenrem 2016) regulated by temperature and photoperiodic cues. Growth onset is primarily regulated by accumulated temperature sum whereas growth cessation is a result of the combined effect of photoperiod and temperature (e.g. Koski & Sievänen 1985; Partanen 2004).

Trees with growth rhythm adapted to the planting site will combine a high growth potential with avoidance of damages by late spring and early autumn frosts. In practice, the situation is more complex and a direct connection between phenology and growth has been difficult to develop due to the stochastic nature and timing of frost events, and lack of standardized assessments of such damages in the field. In addition, young trees are more susceptible to detrimental damages and damages have to be repeated over several subsequent years to heavily affect growth and survival. However, the timing and duration of the growth period seems to be important for the accumulated growth. The general impression is that when the sites are not too climatically severe, FRM with a slightly delayed growth initiation and cessation perform better than the "local FRM". This is probably primarily due to a more optimal utilization of the growing conditions during the season, but also avoidance of spring frost (Skrøppa 2021, Skrøppa & Steffenrem 2019). At sites closer to the climatic margins in the north, the situation might be the opposite as early hardiness development in the fall might be more important for long term productivity (Skrøppa & Steffenrem 2020). At sites in the lowland, prone to spring frost, late flushing materials perform better (Skrøppa & Steffenrem 2016; Lundströmer et al 2020).

The patterns of variation in adaptive traits seem to be somewhat different in the northern and southern parts of the Nordic countries. Studies with trials and provenances simultaneously covering the southern and northern areas suggest that a latitudinal cline becomes more pronounced somewhere north of latitude 60-61°N (Dietrichson 1977; Persson & Persson 1992; Dæhlen et al. 1995; Solvin & Steffenrem 2019). A pronounced latitudinal clinal trend in the timing of phenological events have been observed in both greenhouse and common-garden trials that include a wide range of populations. Spruce origins from the north both start and cease their growth before materials with a more southern origin when grown in similar conditions (Heikinheimo 1954; Beuker 1994, Partanen 2004, Skrøppa & Magnussen 1993; Kohmann 2003, Skrøppa & Steffenrem 2020, Skrøppa & Steffenrem 2019, Hannerz 1996; Hannerz & Westin 2000), thus making them more tolerant to earlier frosts episodes in fall (Dæhlen et al. 1995). In Norway, a similar elevational pattern has been found (Skrøppa & Steffenrem 2019; Solvin & Steffenrem 2019) and studies of provenances in northern Sweden have shown that although the main factor affecting growth and vitality is transfer in latitude, there are also indications of an effect of altitude (Remröd 1975; Rosvall & Ericsson 1981). Consequently, in the current Swedish deployment recommendations a transfer from lower to higher altitudes is translated into a northward transfer at latitudes above 59°N (Berlin et al. 2014). Provenances from southern Finland reach the same level of winter hardiness up to one month later than northern Finnish provenances (Beuker et al. 1998). Leinonen & Hänninen (2002) used computer simulations to study the timing of phenological events in different climatic conditions. They concluded that in the circumstances of a short growing period, early onset of growth becomes evolutionarily more important than avoidance of frost damage. There is also considerable genetic variation within natural populations and families. In Mid-Norway, natural populations from near the sea level comprise variation overlapping with populations at 500 m elevation (Skrøppa & Steffenrem 2019). Further, the range of variation in frost hardiness in autumn among progenies from 10 trees from the same natural stand is similar to the variation found between provenances varying 400 m in elevation or three latitudes difference (Johnsen & Østreng 1994; Skrøppa 1991).

As both the timing of bud burst and occurrence of frost events is so clearly connected to the temperature climate, the question arises what effect future climatic conditions will have. Several studies have shown that the risk of spring frost damages will actually increase in southern Sweden under future climate conditions and that those risks are provenance specific (related to timing of bud burst) (Jönsson & Bärring 2004; 2011; Langvall 2011; Svustyn et al. *submitted*).

Models to predict the timing of bud burst of specific provenance origins have been developed in several studies (for example within B4EST, see MS25). But for Norway spruce in our conditions, simple linear models based on temperature sum seem to perform robustly and equally good or better than more complicated models e.g. including chilling or photoperiod (e.g. Hannerz 1999; Svustyn et al. *submitted*). For example, the chilling requirement (although theoretically affecting the timing of bud burst) is most probably fulfilled during the early winter in the Nordic region for all relevant provenances used in operational forestry (Hannerz et al. 2003; Svustyn et al. *submitted*). It is, however, likely that timing of flushing is affected by the temperature during bud set in the previous year (Søgaard et al. 2008) but the practical importance has been little explored so far.

Varis et al. (2012) and Pulkkinen & Varis (2012) studied autumn frost hardiness of Norway spruce seedlings in artificial conditions that corresponded to future climate scenarios for Finland. In the climate prevailing in 2100, winter hardiness would be achieved one to three weeks later than in the

current climate. The hardiness of Central European spruce provenances appeared to be even poorer in the predicted warmer climate of the future than it was in the current climate. Partanen et al. (1998) found that very little ontogenetic development toward bud burst takes place in Norway spruce during mild periods before the winter solstice. This prevents premature onset of growth and may protect native spruce populations from frost damages under warmer conditions of the future.

In addition to its importance for spring and autumn frost damage and consequential loss in growth, phenology has been found to correlate with the occurrence of lammas shoots, which in turn may cause damages in the leader shoot and later stem defects in saplings and young trees (Skrøppa & Steffenrem 2017, Helmersson & Westin 2018). At the population level (e.g. provenance level), "early phenology" has been shown to be associated with low occurrence of lammas shoots . At the family level, however, the relationship with phenology is the opposite; families with an early onset and cessation of growth have more lammas shoots (Skrøppa & Steffenrem 2017; 2019).

In summary, there is a need to develop models that can predict provenance (and in the end FRM) specific frost risk at an arbitrarily selected planting site. To do so, the relationship between climatic conditions (temperature sum in our case) ↔ growth rhythm (bud burst) ↔ risk of frost damage must be developed and generalizable (1-3 in Figure 3). This work is currently being done in B4EST (see model work in MS25 for further details about the technical approach) and is also intimately related to a study just finalized (Svustyn et al *submitted*).

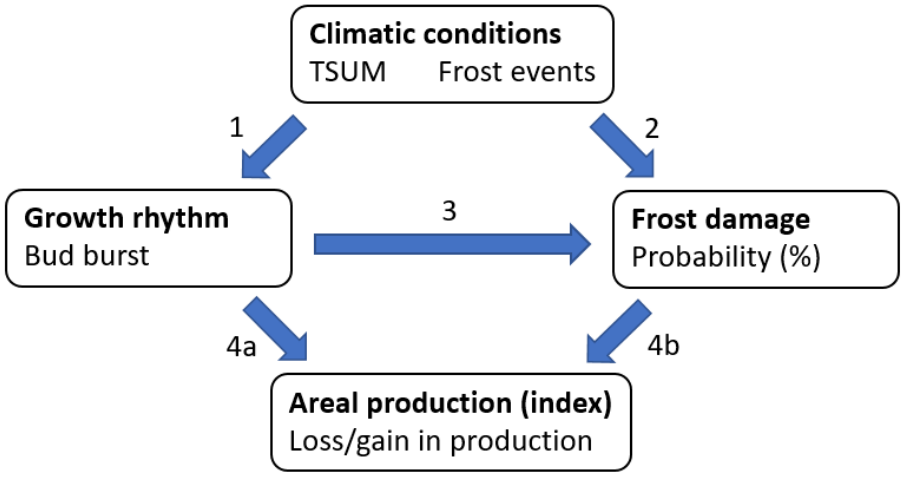


Figure 3 : Schematic overview of the different parts in developing a model to include growth rhythm in a performance index.

Ideally, we would have been able to develop models that would be able to predict the effect on (areal) production given different phenology characteristics and probability of frost damage (4a & 4b in Figure 3). However, with the current knowledge and data available it is not possible to explicitly apply the previously described phenology-frost risk relationship into a performance index. The knowledge attained may still be sufficient to enable the presentation of the distribution and/or risk of each factor as auxiliary charts separated from the performance model. Such descriptions can also be enhanced by detailing of how the distribution of these risk factors are affected by variable climatic conditions.

3.1.3 A memory of the reproductive environment affecting adaptive traits - "epigenetic effects"

In the late 1960s, clones were moved from northern and high-altitude locations to seed orchards further south and at lower altitude for better seed production, but the resulting progeny did not behave as expected according to their northern genetic origin. They displayed a delayed growth phenology, as if they originated from a location with warmer climate (Bjørnstad 1981; Edvardsen et al. 1996; Johnsen 1989a; 1989b, Johnsen et al. 2009). This change in phenology, without any known genetic change, was earlier termed as "the after effect of the maternal reproductive environment" and has been explained by an epigenetic memory developed during embryogenesis and seed maturation (Johnsen et al. 2005) (further discussed in MS25). By comparing genetically identical individuals generated through somatic embryogenesis under different temperature treatments (18 and 28 degrees), Kvaalen & Johnsen (2008) showed that the bud set of the resulting progenies can be delayed by 14 days, similar to a provenance separation of 4-6 latitudes. This change in one of the most heritable adaptive trait occurred without any known change to the genome. It is possible that the strong clinal provenance variation we observe for adaptive traits in traditional provenance trials (e.g. Dæhlen et al. 1995) is inflated by this epigenetic memory since the seed are sampled in the forest and environment of the mother trees origin (Johnsen et al. 2009; Yakovlev et al. 2012).

Variation in phenology have also been observed between materials produced in the same populations but under the different temperatures of warm and cool seed years in seed orchards (Dæhlen et al. 1995; Kohmann & Johnsen 1994) and a large number of natural seed stands (Solvin & Steffenrem 2019). By studying progenies from a heterogenous sample of natural stands, Solvin and Steffenrem, showed that the changes in phenology can be modelled and predicted as a function of the temperature sum during seed maturation and other terms related to the origin of the materials. However, the general pattern was that the temperature sums of the specific seed year showed stronger explanatory power than geographic variables related to the origin of the material. These models can be used to improve decision support by incorporating seed year specific temperature data in addition to the general climatic variables of the provenance origins. Since data from provenance trials with information about seed year is rather scarce, and since epigenetic effects on growth and survival are likely indirect, the most feasible way to implement epigenetic effects in decision support seems to be through the frost risk as a function of the altered phenology.

Four decades of research on the effect of the maternal reproductive environment in Norway spruce has important practical implications for regenerations other than the ones mentioned above. We are now aware of the direct effect that the seed orchard environment has on the progenies produced. Further, in clonal reproduction by tissue cultures, large changes to the adaptive performance can be induced by altering the temperature during somatic embryogenesis.

3.1.4 Genetic diversity and attached tradeoffs

Apart from the task of integrating multiple traits, some of which are connected to climate changes, risks of damage, pests, and diseases we also need to account for unknown risks that cannot be known or predicted aforehand. This is especially important for long-rotation Norway spruce (50-120 years) in the Nordic region as certain risk cannot be reliably quantified over such long frames of time. As such threats obviously cannot be addressed by deploying FRM having any explicit phenotypic character, one

needs to resort to general risk management principles where genetic diversity and variation *per se* act as a safeguard against potential calamities.

First, it should be noted that both breeding and FRM deployment of Norway spruce take provenance choice and adaptation into account necessitating the development of multiple breeding populations and multiple recommended areas of use (seed zones). Among these breeding and deployment units, genetic relationship is necessarily low since they are all developed to be adapted to their respective geographic areas including a certain overlap with neighboring areas. For instance, Sweden has got 9 seed zones and 22 breeding populations for Norway spruce (Danell 1993) and both Norway and Finland have developed similar structures. Such a structure constitutes *per se* a general safeguard for genetic diversity at the national level.

However, for the stand-level deployment of Norway spruce FRM in the Nordic region, genetic diversity *within* seed zones is traditionally done by monitoring and regulating how many clones are established in seed orchards and to what degrees these clones are represented. For deployment purposes it has usually been considered relevant to estimate the effective population size (N_e) or status number (N_S) of a specific seed harvest from a specific seed orchard as this would be an appropriate descriptor of the genetic diversity of an FRM deployed at the stand level. Currently, the required genetic diversity of any FRM, is not strictly regulated by law beyond general formulations that genetic diversity should be *sufficient*. Some studies have been conducted regarding the appropriate number of clones for Norway spruce and Scots pine seed orchards (e.g. Lindgren & Prescher 2005). All Nordic countries thus have some general recommendations where the Norwegian recommendations are somewhat stricter (at least 40 clones) than the corresponding Finnish (at least 25 clones) or Swedish (at least 16 clones) counterparts. In practice, larger numbers of clones are often used to compensate for expected diversity loss due to uneven clonal distribution and uneven flowering. On the other hand, there are also examples of seed orchards having fewer clones if it is expected that the seed will not be widely used in the landscape. For instance, seed from such orchards may only cover specific niches with respect to specific adaption to certain climates or to specific industrial end-uses. For clonal mass propagation, rules and recommendations are less developed since clonal propagation itself has, so far, very seldomly been applied in industrial large scale.

Parameters such as N_e or N_S are simple to calculate in theory but are complicated to assess when considering the practice in seed orchards. For such a parameter to be informative not only the effective number of clones needs to be known but their genetic inter-relationships, their relative reproductive success and the amount of outside pollen (*pollen contamination*) that contribute to fertilization events thus influencing the genetic makeup of the FRM. In several countries advanced software tools have been developed that seeks to optimize the tradeoff in genetic gains (for a trait or any given production index) given a constraint on N_e or N_S (e.g. Brisbane & Gibson 1995; Stoehr et al. 2008; Ahlinder et al. 2014). For the purpose of establishing Norway spruce seed orchards it is common to use optimization softwares such as PIDS and OPSEL (Mullin 2017, Yamashita et al. 2018).

Recently, successive improvements in molecular marker technology have raised the possibilities to estimate, monitor and compare N_e and other relevant genetic diversity parameters by genotyping of seed samples produced by seed orchards at affordable cost (e.g. Sønstebø et al. 2018). Since DNA-based genotyping approaches offers the possibility to directly observe the impacts of uneven paternal contribution and pollen contamination on the genetic diversity, it is less reliant on the rather lofty

assumptions made in this regard when N_e or N_S are estimated solely by clonal distributions and pedigree data. It is also relevant to mention that there is an increasing potential for clonal mass-propagation of Norway spruce by large-scale cutting schemes or by somatic embryogenesis. In such cases, monitoring and regulating genetic diversity in the deployed material would become an even more important aspect in the long-term risk management of FRM.

3.1.5 Summary for Norway spruce

In summary, model development in Norway spruce has so far mainly comprised growth, survival and adaptation to specific climate conditions by establishing reaction norms and developing classical URF-models. This also corresponds to the chief stakeholder criterion of high areal biomass production over rotation age. Our results indicate this to be successful for growth traits and the impact of climate and adaptation on establishment survival was found to be limited.

But aside from this, there are also expectations of safeguarding the general health of Norway spruce forests and to manage risks, especially in the light of climate change. Therefore, serious efforts have been taken, both within and outside the B4EST framework to develop FRM characterization models that would account for the trade-off between growth, phenology and risk of frost events (especially spring frost) and consequences thereof. In this regard it has been shown that both genetic and epigenetic factors can be influential. Also, the overall genetic diversity of an FRM is considered as general factor of resilience against unspecified biotic and abiotic threats and is therefore taken into account.

Finally, there are a number of additional potentially interesting traits that, for different reasons, are not a part yet of the platform. Foremost of these are wood quality traits, drought tolerance and resistance to root rot (*Heterobasidion spp*) and bark beetles. For most of these traits the general shortcoming is that there is a lack of data to the extent that meaningful models cannot be developed although there is ongoing research in the area. Therefore, Norway spruce FRM cannot be characterized with respect to the trait and potential trade-offs cannot be properly assessed even though stakeholder may have an interest in such characteristics. One exception to this pattern is wood quality traits for which some relationships actually have been established at least for breeding materials (e.g. Högberg et al. 2014, Chen et al. 2014, 2016). In the case of wood quality traits it is rather a lack of criteria formulated as desirable by stakeholders that prevent further integration efforts. This is also not very surprising as it is notoriously difficult to know what kind of material characteristics would be considered desirable by a wide variety of stakeholders 60-100 years in the future for a long-rotation species such as Norway spruce.

3.2 Poplars (*Populus spp.*)

In several European countries poplar cultivation has contributed for decades to the development of important economic and productive sectors such as those of paper, wood-based panels and furniture, by providing high-quality raw material. Poplar clones are also widely used in monoculture systems due to their fast growth, wood quality and high biomass production. In addition, lands where poplar trees are planted could enhance ecosystem services including the storage of carbon, soil protection, biodiversity and landscape conservation and phytoremediation (Bergante et al. 2015)

3.2.1 Adaptation of Populus Spp. FRM based on hybrid clones

The intensification of international exchanges of reproductive materials has contributed in many countries to the development of interspecific hybridization programmes of key species provenances (*P. deltoides, P. trichocarpa, P. maximowiczii, P. nigra, P. tremula, P. tremuloides*) beyond their natural range. Hybrid vigor has been one of the main characteristics considered in poplar breeding since times and their high productivity is generally related to a longer vegetation period, compared with the parental species (Yu et al. 2001). Moreover, hybrid clones have usually been found to be more resilient over a range of environments than clones of pure species.

So interspecific hybridization has been the main breeding approach in programs using genetic materials collected at latitudes higher than 25°N-32°N (Stanton et al. 2014). The hybridization of species originating and adapted to different geographic areas has produced a large clinal variability in the bud set time and abiotic stresses, strongly regulated at the genetic and epigenetic level (Vanden Broeck et al. 2018) Germplasm collections of P. nigra and P. deltoides are used both within the B4EST project and for the breeding programs conducted in Italy at CREA-FL. These genetic materials are the object of studies both for genotyping and phenotyping of characters such as bud set time and frost resistance. The provenances from higher latitude undergo dormancy induction under the influence of a relatively longer photoperiod (Farmer 1993, Hall et al. 2007). Hybrids derived from them have not always performed well at lower latitudes, possibly because their annual growth cycle concludes too early to take advantage of the full growing season. The stunted growth is affected by a complex of environmental factors, among which the increased photoperiod might delay the growth if the clone is moved northward from the region of the genotype origin (Lazdiņa et al. 2016; Ingvarsson et al. 2006; Kalcsits et al. 2009). Clones which are not acclimatized to the environmental conditions of the growing site could also be heavily damaged by early frost or low temperature (Sykes et al. 1996). Frost damages have negative effects on the stem quality, e.g. deformed stem straightness, stem cracks, loss of apical dominance (Verwijst et al. 1996; Christersson 2006) with negative consequences for wood production. Frequent frost damages have been observed on *Populus deltoides* clones originating from 33°N and 36°N parallel of United States when cultivated out of the 43°N - 45°N parallel (Cellerino 1976).

In northern Europe (e.g. Sweden), the severe frost damage of the introduced poplar clones has been reported several times (Ferm et al. 1989; Ilstedt 1996; Christersson 1996; 2006; Telenius 1999; Karačić et al. 2003; Pliura et al. 2014), resulting in reduced vitality and mortality of plants (Xiang et al. 1991; Diamandis & Koukos 1992; Pliura et al. 2014). In Scandinavia *Populus tremula* is the only indigenous poplar species (native aspen) so the attention has mainly focused on introduced species like hybrid aspen (*P. tremula* × *P. tremuloides*) and other poplars as *P. trichocarpa*, *P. balsamifera* and *P. maximowiczii* (Stener & Westin 2017). In contrast *P.* ×*generosa* (*P. deltoides* × *P. trichocarpa*), clones have not always performed well in Southern and Central regions of Sweden (stem canker and frost damage) owing to a maladaptation of *P. trichocarpa* provenances from Oregon and Washington (Christersson 1996); a major adaptability to Swedish planting site was observed in the reproductive materials originating from a *P. trichocarpa* parental sources collection from British Columbia (Christersson 2006).

In specialized or mixed stands, commercial hybrid clones obtained from interspecific crosses have been generally used in many European countries (Figure 4). *P.* ×*generosa* (*P. deltoides* × *P. trichocarpa*) and hybrid aspen clones (*P. tremula* × *P. tremuloides*) developed for cooler regions of North-Western Europe (Belgium, France, Germany, Finland, Sweden) perform well also at higher elevation (Western Austria); *Populus* ×*canadensis* (*P. deltoides* × *P. nigra*) in the warmer regions of the Mediterranean

areas (Spain, Southern France, Western Hungary, Northern Italy, Eastern Austria) (Stanton et al. 2014). Germplasm collections of *P. nigra* and *P. deltoides* are used both within the B4EST project and for the breeding programs conducted in Italy at CREA-FL and in France in a consortium INRAE/FCBA/ONF. These genetic materials are the object of study both for genotyping and phenotyping of characters such as aphid and rust resistance.

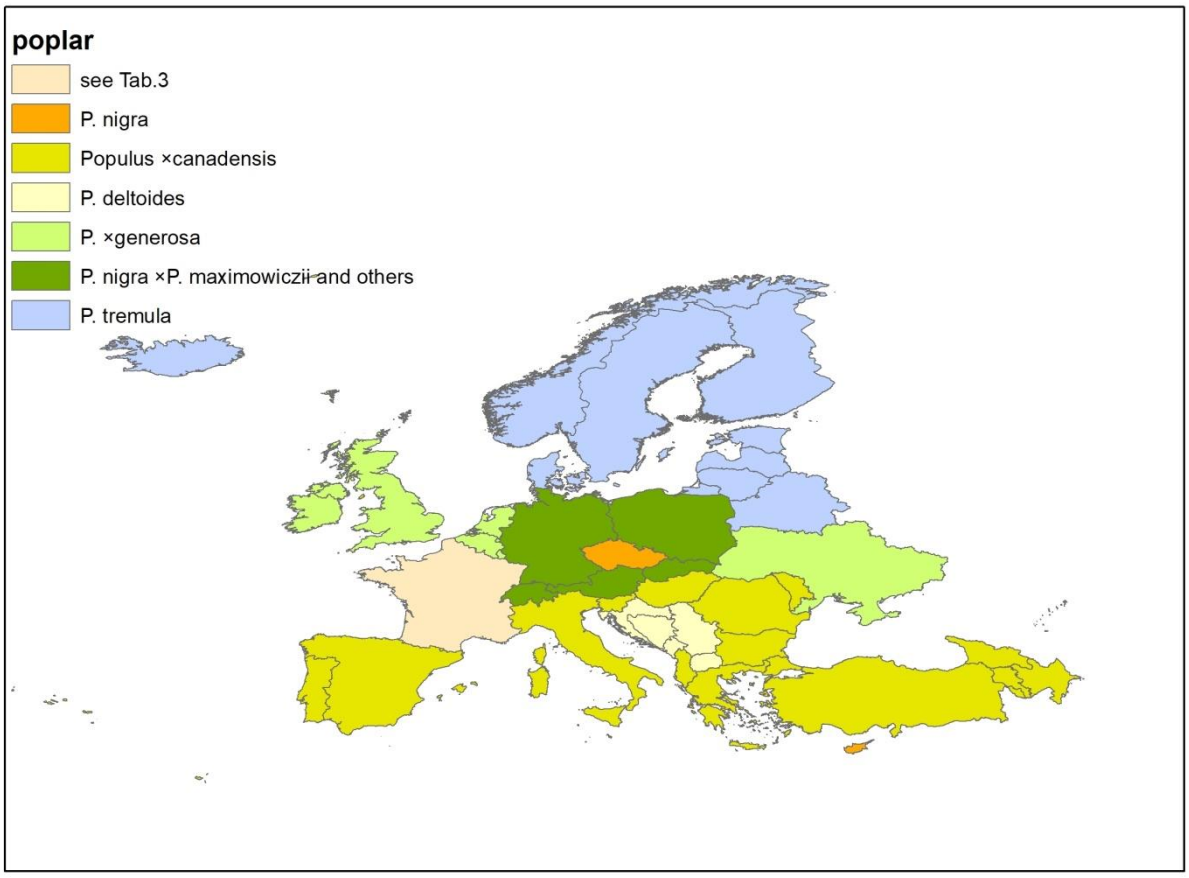


Figure 4: Distribution of poplar hybrids and species in Europe.

3.2.2 Stakeholder interests and selection traits

The main selection traits generally adopted in breeding programs are growth rate, rooting ability wood quality, tolerance or resistance to abiotic and biotic stresses, climatic and soil adaptation. From a biomass and pulp production perspective, resprouting ability and cellulose and lignin content are also of great interest (Rosso et al. 2013). Stem shape and wood properties (wood density, mechanical characteristics) are of fundamental importance (along with proper silvicultural practices), even if the quality of the wood (Table 1) is related to the different uses (pulp for paper, lightweight or structural panels for plywood or packaging). Usually the fast growth of hybrid clones is generally associated with quite low wood density (Beaudoin et al. 2007; Hernandez et al. 1998) even if in the case of new clones recently selected in Italy for plywood production the wood density is not strictly correlated to the growth (Figure 5). Many of these characters have high-to-moderate heritability so they can be improved by a wise parental selection in breeding programs.

Table 1 : Wood quality of several poplar clones useful for different uses.

Clone	Density	Modulus of elasticity		Bending strength	
		Long.	Trasv	Long.	Trasv
	kg/m³	N/mm²	N/mm²	N/mm²	N/mm²
I214	401	3634	2292	35	27
San Martino	415	4489	2497	43	32
Ghoy	459	5327	3071	51	38
Koster	438	5031	3006	55	33
Lena	436	5383	2887	49	34
Neva	428	5301	2971	44	33
Dvina	433	4748	2442	46	28
Oglio	474	**5816**	**2860**	**55**	**37**
Taro	465	5694	3107	50	36
Mella	470	4809	2783	46	33
Soligo	495	5622	3311	46	42
Timavo	451	**5719**	**3330**	**54**	**39**
Sesia	437	5586	2681	50	34
Brenta	457	**6233**	**3183**	**55**	**38**

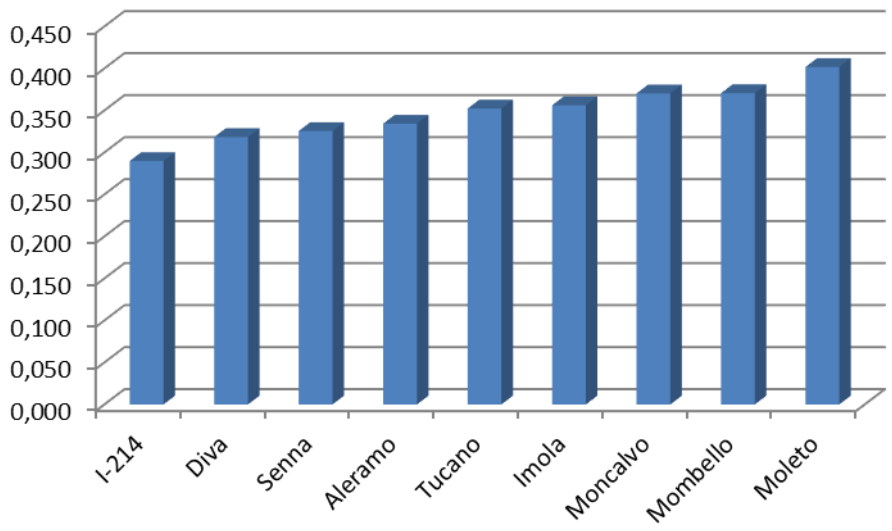


Figure 5 : Wood basal density (g / cm³) of 8 new poplar clones selected in Italy compared with I-214.

Several poplar clones have been selected for pest and diseases resistance, wood quality and made available for different climatic conditions and industrial and energy uses throughout all European countries. Nevertheless, in the past decades only a handful of *P.* ×*generosa* and *P.* ×*canadensis* F1 clones have dominated in plantations used mainly in sawing and peeling industries. In many countries most poplar stands are managed with cultivation practices similar to those of agricultural crops (Stanturf & Van Osten 2014), as the objective is maximizing wood production. Such stands are monoclonal, intensively managed, with a very short harvest cycle (ranging from 10 to 20 years). The low genetic diversity together with the intensive cultural management make poplar plantations exposed to devastating diseases and pest outbreak (Charles et al. 2014; Ostry et al. 2014). The intensification of cultural practices adopted in monoclonal stands together with the narrow genetic basis of the cultivated clones have been the predisposing factor for outbreaks bacterial cancer

(*Xanthomonas campestris*), epidemics of the poplar rusts (*Melampsora* spp.) and Woolly Poplar Aphid (*Phloeomyzus passerinii*) (Ostry & McNabb 1983; Liu et al. 2018).

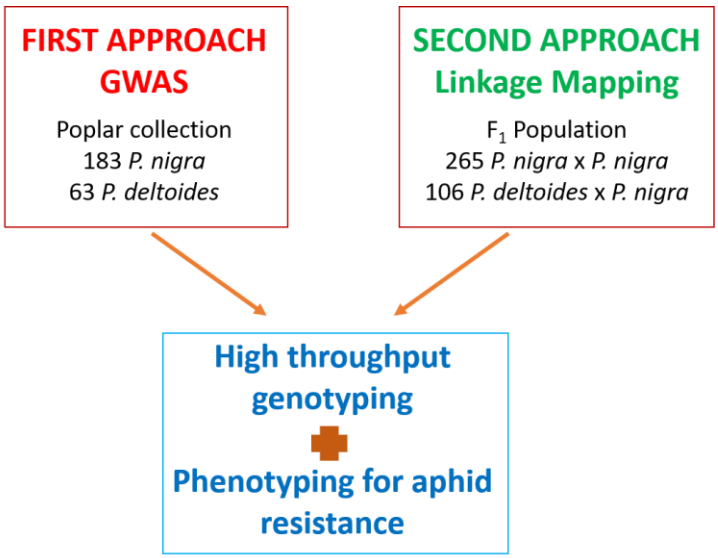
3.2.3 Poplar resistance to aphids (Phloeomyzus passerinii)

Even if no damages have been reported in natural forests, this aphid can cause massive mortality of adult trees in artificial plantations of susceptible poplar clones (Charles et al. 2014; Sallé & Battisti 2016), causing up to 10% of potential production in the infestation area (Carletti et al. 2016; Pointeau et al. 2020). In the context of climate change, worrying damages due to the pest have occurred extending from Southern to Northern France since the end of 1990s (Sallé et al. 2017). In this case the plantation of resistant clonal varieties was regarded as the best long-term strategy. Nonetheless, even if the resistance behaviors of cultivated poplar clones are well described (Arru & Lapietra 1979; Allegro & Cagelli 1996; Sadeghi et al. 2001), the mechanisms and genetic bases of poplar resistance are poorly understood. Thus, the identification of new sources of resistance is pivotal to combat this disease. To date only three QTLs (one major and two minor) for resistance to the Woolly Poplar Aphid (Wpa) have been identified in poplar (Carletti et al. 2016).

Nowadays, the finding of loci regulating specific traits in plants is mainly based on the use of high throughput genotyping based on Next Generation Sequencing (NGS) or hybridization array techniques which allow to genotype up to thousands of individuals at large scale with thousands of Single Nucleotide Polymorphism (SNP) molecular markers in a fast, cost and highly accurate way (Wu et al. 2000; Portis et al. 2014; Wei et al. 2014; Barabaschi et al. 2016).

To find out new Wpa resistance loci, two different approaches based on high throughput genotyping (Figure 6) are in progress within the B4EST project at CREA-FL (Casale Monferrato, Italy) in collaboration with CREA-GB (Fiorenzuola d'Arda, Italy).

Figure 6 : Schematic representation of the two different approaches in progress, within the B4EST project, at CREA to identify the loci implicated in Wpa resistance.



The first approach consists in the application of a Genome Wide Association Scan (GWAS) that will be conducted using a collection including 183 *P. nigra* and 63 *P. deltoides* individuals. The second approach is based on two linkage mapping experiments using two different F1 mapping populations. The phenotyping for aphid resistance of the whole collection revealed a higher resistance for the *P. nigra* sub-population with respect to the *P. deltoides* one. A high genotypic effect for both sub-populations and the whole collection was recorded (indicating that aphid resistance is a suitable trait to be used for GWAS. Further details regarding this work can be found in section 2.2 in Milestone 25.

Along with GWAS and linkage mapping, genomic prediction models have been developed to sustain poplar breeding and clone development. Many economically important traits of relevance in poplar such as the degree of resistance/susceptibility to biotic stresses, are collected as categorical data varying on discrete scales. In B4EST, aphid resistance in the aforementioned populations of *P. nigra*, *P. deltoides*, and F_1 offspring of *P. nigra* x *P. nigra* and *P. nigra* x *P. deltoides*, was evaluated using a discrete scale varying from 1 to 5. For developing genomic prediction models using these ordinal categorical data, B4EST has fitted and cross-validated several threshold genomic predictions models (Montesinos-López et al. 2015), particularly, threshold genomic prediction models that incorporate genotype per environment interaction and additive x additive x environment interactions. These genomic prediction models will be using to select poplar clones that can cope with disease stresses.

The two approaches described here are aimed exclusively at the study of the genetic basis and investigations of the molecular aspects of the resistance to the woolly poplar aphid. Different is the case of breeding programs carried out in order to select poplar clones with useful characteristics (fast growing, biotic and abiotic stress resistance, wood quality) for the cultivation and production of poplar wood as described in subsection 3.2.5.

3.2.4 Poplar resistance to rusts (Melampsora spp)

Poplar rusts are foliar pathogens that causes photosynthesis loss (Eberl et al. 2018) and defoliation causing significant growth reduction in poplar stands (up to 50%; Lemaire et al. 1998); https://ohioline.osu.edu/factsheet/plpath-tree-8). The main causal agent in Europe is *Melampsora larici populina* (*Mlp*). During the 1980s and 1990s the deployment of cultivars with qualitative resistance mainly *P.* ×*generosa* selections caused a major breakdown of this clonal resistance, used in large areas of north-western Europe, Belgium and France in particular. For example, in Northern France during the 90s almost the 80% of the plantations were planted with the 'Beaupré' clone (Pinon et al. 1998). This clone became susceptible due to the differentiation of a new factor of virulence. Rust defoliations can be followed by infections with weakness parasites such as *Discosporium populeum* and *Cytospora chrysosperma* that caused plant death and high economic loss (de Kam 1983). This failure further shifted reliance to the *P.* ×*canadensis* taxon (*Populus deltoides x P. nigra*) which shows a major tolerance to rust infection inherited from *P. nigra* parent; since good level of genetic variability have been found both in pure species and in interpecific hybrids (Pinon et al. 2011; Benetka et al. 2011). Currently, the main priority in the breeding program is to select for quantitative (horizontal) resistance rather than for qualitative (vertical) resistance which means smaller uredinia, longer latent period and less infections.

The risks of monoclonal poplar plantations can be mitigated by clonal diversification. Such and alternative can be useful to avoid the problems deriving from climatic changes and biotic and abiotic stress. In order to increase the genetic diversity in plantation, planting model based on clonal mixture

or a mosaic of monoclonal plots with a group of different clones was already proposed in the past (Heybroek 1982). Currently, a harvested multi-clonal material is perceived by some industry sectors as more cumbersome to work with due to its heterogeneous properties. But even if no benefits of clonal mixtures have been evidenced in terms of wood production (Bisoffi 1992; DeBell & Harrington 1997; Miot et al. 1999), the epidemiological risks are inversely proportional to the genetic variability of the cultivated material. So in plantation it is extremely important to maintain a considerable genetic variability using select clones with a diversified genetic background.

In connection to the multiclonal deployment mixtures, and as a perspective, it is important to note here that the topic of clonal group selection is central to the research in Task 2.3 of B4EST. Group selection here, briefly, is the optimal selection of a group given the synergetic interactions among its members. Interactions could be derived as those related to competition, or absence of it, or those leading to complementarity for pest resistances. Qualitative and quantitative resistance to *Mlp* has been shown to be highly specific in *P.* ×*generosa* but also in *P. nigra*, and depending on diversity of *Mlp* strains (Dowkiw & Bastien, 2004; Bastien comm. Pers.). In *Populus nigra*, we quantified (Task 1.3/Task 2.3) the genotype × strain interaction in order to identify a group of interactive genotypes having complementary behavior against *Mlp* strains representatives of the diversity of the pathogen in France. These results are presented in the deliverable D2.3.

3.2.5 Clones targeting the needs of different regions, industry and society

Currently a systematic and balanced breeding approach where long-term and short-term breeding strategies are integrated is underway at CREA, in Italy and in the consortium “GIS peuplier” (INRAE/FCBA/ONF) in France. At the CREA - Research Centre for Forestry and Wood in Casale Monferrato poplar breeding was launched to select *Populus deltoides* × *Populus nigra* hybrids since in the F1 hybrids useful traits of both species are combined. Traits, of economic importance as fast growth, wood quality, tolerance/resistance to pathogens and pest (Carletti et al., 2016) are inherited from *P. deltoides* while good rooting ability and resistance to Poplar Mosaic Virus originate from *P. nigra* (Bisoffi & Gullberg 1996). The most promising genetic materials obtained in the initial stages of the 'semi-reciprocal' selection program within the inter-specific crossings (*P. deltoides* × *P. nigra*) have been initiated to the selective process and evaluated in multi-sites nurseries and in plantations established on Italian sites characterized by diversified pedo-climatic conditions. New hybrids selected and tested for production of veneers for plywood panels and other clones to be used in short rotation coppice for biomass and particle board production have been released. These clones, registered in Italy in the National Registry of Base Materials, have recently been included in the list of poplar clones in "Greater Environmental Sustainability" and will allow a more 'sustainable' cultivation (Chiarabaglio et al. 2020) as an alternative to the traditional approach (Table 2). Trial activities also conducted in other countries (i.e. France, Spain) in different pedo-climatic conditions, has allowed to confirm their good level of environmental adaptability, tolerance/resistance to the main poplar adversities. The updated list of poplar clones with different genetic origins, recommended for cultivation in the different departments of France is shown in Table 3.

Table 2: Characteristics of poplar clones mainly cultivated in Italy.

	CLONE	SPRING LEAF AND SHOOT BLIGHT	LEAF RUSTS	MARSSONINA LEAF SPOT	WOOLLY APHID	GENETIC ORIGIN
	I-214	*****	***	**	**	*Populus ×canadensis*
1	AF8	*****	****	*****	****	*Populus ×generosa × Populus trichocarpa*
2	ALERAMO	****	*****	*****	****	*Populus ×canadensis*
3	BRENTA	*****	***	*****	*****	*Populus ×canadensis*
4	DIVA	****	*****	*****	*****	*Populus ×canadensis*
5	DVINA	*****	****	*****	****	*Populus deltoides*
6	ERIDANO	*****	*****	*****	*****	*Populus deltoides × Populus maximowiczii*
7	HARVARD	*****	****	*****	****	*Populus deltoides*
8	KOSTER	*****	****	***	*****	*Populus ×canadensis*
9	LAMBRO	*****	***	*****	*****	*Populus ×canadensis*
10	LENA	*****	****	*****	****	*Populus deltoides*
11	LUX	*****	****	*****	*****	*Populus deltoides*
12	MELLA	*****	***	*****	****	*Populus ×canadensis*
13	MOLETO	****	*****	*****	*****	*Populus ×canadensis*
14	MOMBELLO	****	****	*****	*****	*Populus ×canadensis*
15	MONCALVO	****	*****	*****	*****	*Populus ×canadensis*
16	OGLIO	****	*****	*****	*****	*Populus deltoides*
17	ONDA	*****	****	*****	****	*Populus deltoides*
18	SAN MARTINO	*****	****	****	****	*Populus ×canadensis*
19	SENNA	****	*****	****	*****	*Populus ×canadensis*
20	SILE	****	*****	*****	*****	*Populus deltoides × Populus ciliata*
21	SOLIGO	*****	*****	*****	****	*Populus ×canadensis*
22	STURA	****	*****	*****	*****	*Populus ×canadensis*
23	TARO	*****	****	*****	*****	*Populus ×canadensis × Populus ×generosa*
24	TUCANO	****	*****	*****	*****	*Populus ×canadensis*
25	VILLAFRANCA	*****	*****	*****	*****	*Populus alba*

LEGEND

*	highly susceptible
**	susceptible
***	tolerant
****	resistant
*****	highly resistant

Table 3: Poplar clones recommended for cultivation in different territories in France

RECOMMENDED POPLAR CLONES	South-East			South-West		North-West					North	Noth-East	
	Auvergne-Rhône-Alpes	PACA	Corse	Occitanie	Nouvelle Aquitaine	Pays-de-la-Loire	Bretagne	Normandie	Centre-Val-de-Loire	Île de France	Hauts-de-France	Grand-Est	Bourgone-Franche-Compté
Populus euramericana													
ALBELO													
ALERAMO													
BLAC DI POITOU													
BRENTA													
DANO													
DIVA													
DORSKAMP													
FLEVO													
GARO													
KOSTER													
I-45/51													
LAMBRO													
LUDO													
MOLETO													
MONCALVO													
MUUR													
OUDENBERG													
POLARGO													
RONA													
SOLIGO													
TARO													
TUCANO													
VESTEN													
Populus interamericana													
RASPALJE													
Populus trichocarpa													
FRITZI-PAULEY													
TRICHOBEL													
Populus deltoides													
ALCINDE													
DELGAS													
DELLINOIS													
DELVIGNAC													
DVINA													
LENA													
OGLIO													
hybrids *trichocarpa* x *maximowiczii*													
BAKAN													
SKADO													

Eligible

Not eligible

In France, in the Consortium "GIS peuplier", the same *P. deltoides* × *P. nigra* scheme (Figure 7) is also used, including intraspecific recombination step, for developing cultivars for vigor and resistance to pathogens. Other species are also subject of selection for diversified purposes with the aim at diversifying the catalog of cultivars: (i) pure *P. deltoides* for South of France; (ii) pure *P. trichocarpa* and *P. trichocarpa* × P. maximowiczii hybrids for Northern France and Europe; (iii) backcrossing *P.* ×*generosa* × *P. deltoides* to improve resistance to *Mlp*.

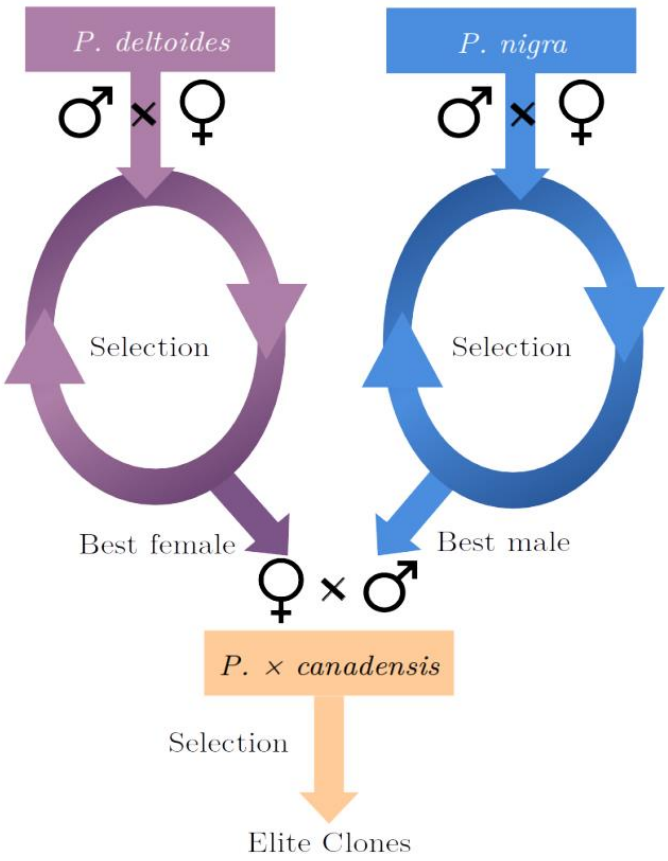


Figure 7 : Breeding scheme for recombination inside P. deltoides and *P. nigra species to select the best parents for P. ×canadensis hybrids*

The commercial material of hybrid aspen and poplar available for regeneration in Sweden and Denmark is scarce and has a narrow genetic base. Today only 15 clones of hybrid aspen and 16 clones of Balsam poplar have been selected and tested for commercial use in southern Sweden and there is no such material available at all in central and northern Sweden. Here 'OP42 (*P. maximowiczii* × *P. trichocarpa*) is the most commonly clone cultivated, In Denmark is the only one hybrid poplar clone utilized. With the aim to use fast growing poplars as a part of a sustainable high-productive forest system in Scandinavia region a broaden genetic base in poplar materials is needed (Stener & Westin 2017).

3.2.6 Summary for Poplars

So, the adoption of cultivation models based on the use of poplar clones with greater environmental sustainability, as envisaged by the Rural Development Plans, allows to pursue the strategic objectives set out in the European Rural Development Plan. In addition to providing the poplar growers with numerous advantages of productive, economic and environmental nature, allows to apply to the sustainable forest management standards required by the Forest Stewardship Council certification scheme (Forest Stewardship Council FSC INTERNATIONAL STANDARD) and the Forest Endorsement Program (Technical documentation - PEFC - Programme for the Endorsement of Forest Certification). In perspective the adoption of cultivation models more environment-friendly and less-energy consuming, besides the selection of clonal varieties well adapted to climate change are a priority objective of many public institutions and private companies of the forest sector. The Sustainable Forest Management will have a key role in reaching the European Green Deal objectives by year 2050 and

poplar cultivation offer great opportunities to build a green economy and to face the challenges of climate change and in Europe.

3.3 Douglas fir (*Pseudotsuga menziesii*)

Douglas-fir is one of the most important timber species in its native North America, thanks mainly to the favorable combination of good wood quality, fast growth and absence of major pest and diseases throughout the natural range. Introduced in Europe almost two centuries ago, it has become an essential reforestation species notably in central and western countries. Of the 824,000 ha of Douglas fir in Europe, more than half is to be found in France, where it is the second most widely planted conifer after Maritime pine. The species tolerate a wide range of soil types, although deep, well-drained and moist soils provide generally the best growing conditions. Best performances are usually found at mid-elevations (900 m at most) and with annual rainfalls of at least 800 mm (further details and references in Bastien et al. 2013).

Although many countries across Europe established field experiments for guiding the choice of seed origins and initiated first breeding initiatives, mostly back in the 60's and 70's, only French public institutions still conduct a large-scale recurrent breeding program with a seed-orchard scheme and extensive field-testing network. Such a network could be a sounding support for multi-trait and multi-criteria performance modeling with direct impacts on FRM deployment. For that reason, most of the subsequent report on the species relates to that country and discusses on the perspectives to setup such a modeling framework.

3.3.1 Desired traits and stakeholder criteria for Douglas fir

In a joint effort by three French public institutions (INRAE, FCBA and ONF), funded by the Ministry of Agriculture, Agri-Food and Forestry (2015-2020), a multi-criteria evaluation modeling has been set to produce the current generation of the Douglas fir breeding program in France. Such a multi-criteria model combined all the available measurements collected in the field-testing network, involving multiple site assessments on growth, tree architecture, wood density and phenology, totaling over 240 000 individuals and 1 800 000 observations. Previous surveys (Chaumet 2017) collecting French stakeholders' expectations stressed the importance of wood quality aspects over growth, through improvement of architectural and wood density assessments, and monitoring adaptation. Such choices were approximately fulfilled given the available genetic variation and nature of assessments. For instance, architecture (branching habits) were given high weightings, while phenological and wood density were constrained to remain at intermediate values. The approach used an optimization algorithm with given desired levels or thresholds of gain. Unlike the kind of modeling reported in this deliverable for Norway spruce providing overall performance functions across an environmental gradient, the one used for Douglas fir produces individual-based breeding performances, once environmental adjustments have taken place. In both cases, however, the kind of data that is required can be very similar, genetically structured and obtained across multiple testing sites.

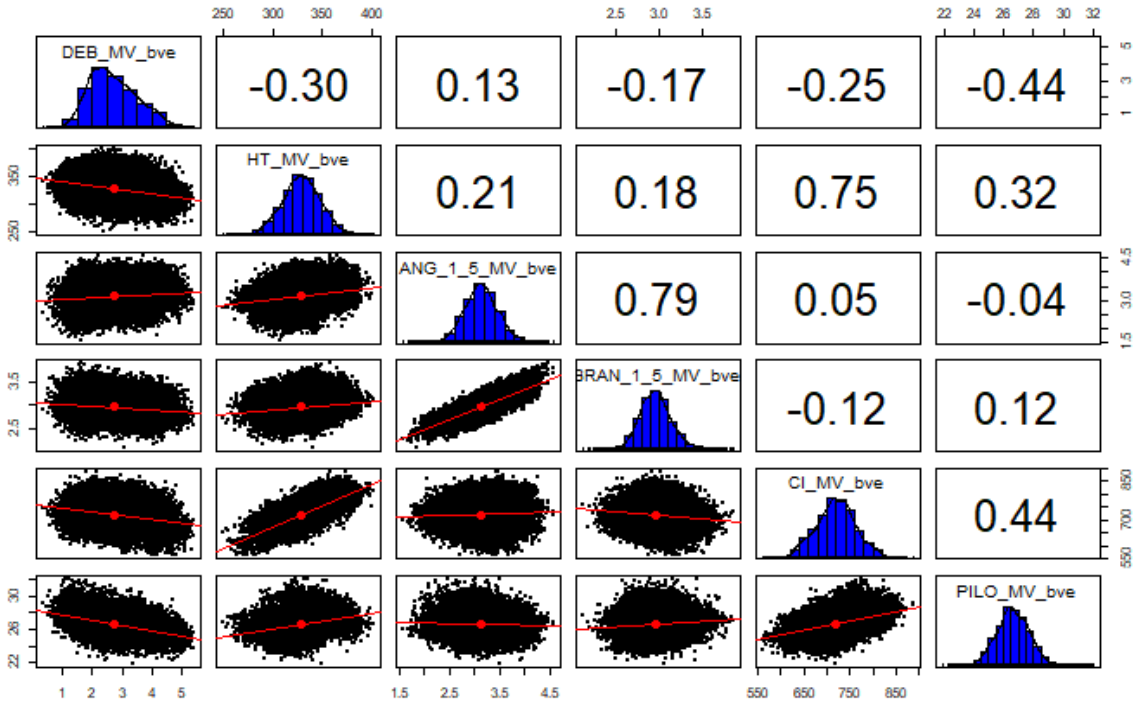


Figure 8 : Genetic relationships between some of the selected traits in a subset of the French breeding program genetic evaluation. Traits from left to right are: bud flush ("DEB_MV_bve"), height ("HT_..."), branch insertion angle ("ANG_..."), branch thickness and numbers ("BRAN_..."), circumference ("CI_...") and penetrometer ("PILO_..."). Diagonal histograms represent the distribution of breeding values, upper right panels contain Pearson correlations, and lower left panels contain scatterplots between traits with a linear relationship (red line).

It is difficult to define multivariate performance without being too simplistic. For breeding, for instance, the selection decision of previous French project implied a delicate compromise involving 7 traits, with some combinations bearing unfavorable genetic correlations impairing multivariate genetic gain (see Figure 8 for six of those traits, unpublished results). Wood density, typically an important trait related to mechanical properties and to tolerance to water stress, resulted in unfavorably correlated values to height, diameter and lateness of bud flush, where height and diameter constitute two of the bases of wood production, and lateness of bud flush is a favorable feature to avoid frost damage. In such a constrained multidimensional scenario, there might be still many favorable combinations guaranteeing acceptable levels for each trait, with the final choice depending ultimately on a set of arbitrary weights reflecting breeders' preferences or market demands. The selected set is then one possible realization among many solutions, chosen by the genetic potential for gain but with no specific assumptions regarding the deployment environment. According to the testing sites where selection took place and recent past growing conditions, genotype-by-environment interactions were generally negligible for most traits, justifying the application of a single breeding (and seed) zone. However, such a simple scenario might not hold any longer according to global change.

3.3.2 Available Douglas fir seed orchards and resulting FRM for deployment

A new series of seed orchards resulting from current selections has already started to be established in 2020 with a rolling out scheme of 20 new ha every 5 years and a final target of 140 ha. The evolution of their genetic composition and the deployment guidelines will be based both on assessments of

existing and recently installed clonal tests. In the meanwhile, seed needs at French level are covered at 95% by mature seed orchards from the previous first-generation. These relatively aged orchards, listed and briefly characterized in the following Table 4, have been the object of an extensive multiple site testing experiment aimed at gauging performance and plasticity over very contrasting environments.

Table 4: List of current seed orchards in production in France (source Bastien et al. 2021)

SEED ORCHARD NAME	PLANTATION	CLONES	SURFACE (HA)	ORIGIN
DARRINGTON	1978	70	13.7	USA (Washington)
LUZETTE	1980	226	38.9	USA (Washington, Oregon)
WASHINGTON	1984	289	7.6	USA (Washington)
WASHINGTON 2	1983	135	8.5	USA (Washington)
FRANCE 1	1989	110	6.5	France (Limousin region)
FRANCE 2	1989	116	5.1	France (Ariège region)
FRANCE 3	1989	129	9.9	France (Vosges)
CALIFORNIE	1985	116	5.5	USA (California)
TOTAL		**1191**	**95.7**	

Such an extensive multiple site testing experiment involves 43 tests sites over a total of 39 ha across the French geography, with each site harboring between 60 and 100 representative descendants per seed orchard. Four different typologies of sites have been selected to cover a wide range of environments, including optimal as well as suboptimal sites for the species. Within the typology of optimal sites, 16 tests cover environments for which the optimality is expected to be preserved at least during a full rotation time (50 to 70 years for the species), altitudinally (120 to 800 meters), climatically and pedologically speaking. A second typology involves sites (15 tests) that, while being optimal at current conditions, are expected to become suboptimal or even unsuitable within the rotation time due to foreseen climatic shifts. The third typology covers sites (6 tests) that are currently suboptimal for growing Douglas-fir, mimicking at the present extreme climates that could be encountered by the species within rotation times. The fourth typology of sites (6 tests) involve high altitude environments within the range of 1000 to 1300 m, too high for what is considered to be suitable for the species. All these typologies and sites will offer a wide range of environments to fit conveniently performance functions for each of the seed orchards, allowing a guidance in the choice of suitable seeds according to sites and climatic perspectives, following the example of Norway spruce.

3.3.3 Research and development of Douglas fir performance model

First results based on early (5 years) assessments for survival, growth and phenology (bud flush) suggest already the presence of contrasting behaviors amongst the different genetic pools. Firstly, bud flush gave indications of substantial discrimination between some seed orchards, notably California (early flushing) *versus* Washington origins (late flushing). Tree height showed very important variation across the different site typologies, although the ranking of seed orchards for the trait remained basically unchanged through the gradient, with Californian origins showing the weakest performance and Washington counterparts the best outputs. Finally, survival was high (at least 80%) across sites, with negligible differences between gene pools. These preliminary results are the object of a publication (Bastien et al. 2021).

Further analyses need to be carried out, accounting for the new campaign of measurements (8 years from plantation) and with a finer characterization for each testing site. These analyses will be carried out in the framework of B4EST in 2021.The perspectives for these analyses will be along the following lines:

- Identify the past environmental factors (climate variables, pedological descriptors) with significant effects on the performances of the different seed orchards for the measured traits, together with those factors that might explain the differences in behavior between the seed orchards. Machine learning techniques will be used for the ranking and selection of factors and their interactions. The raw climatic variables will be collected from the B4EST datasets made available in WP1, and according to the positions of the 43 sites. Some elaborate indexes will also be tested, notably those corresponding to the climatic compatibility model IKSMAP (further information, exclusively in French, at https://climessences.fr/modele-iks/presentation/presentation-du-modele-iks), recently developed at the R&D department of French ONF (French Forest Service).
- Use selected variables and elaborated indexes identified previously on a prediction model fully or partially calibrated on the experimental network of 43 sites for each of the traits. Derive the functions describing the per-trait-performance across selected environmental variables.

Such an analytical approach remains a preliminary step before the development of a truly performance model, like the one for Norway spruce, mostly due to the fact that available assessments still cover an earlier stage of development for the trees, not necessarily well correlated to final stages of production. Also, although extensive, the testing network is still limited in terms of genetic representation of each seed orchard and covers only the first generation of production populations. Moreover, predicting trait functions would still require an additional step involving trait specific weightings in order to derive a global performance index, and such weighting step is not fully matured yet. In any case, such an exercise is an essential training before the new generation of seed orchards enter into commercial production.

3.3.4 Summary for Douglas fir

As a summary, we reported some actions in the context of the French breeding program of relevance for devising a global performance based on multiple traits of economic and adaptive importance. We stressed the difficulties in accommodating biological constraints from antagonistic correlations and stakeholders' expectations, when doing selection for breeding. Although the knowledge gained at that step is of relevance when devising a performance criterion for deployment, the resulting evaluation cannot be used directly as a guidance for the deployment stage. A new testing network involving progenies from all seed orchards in production is briefly described and the analytical objectives in the framework of B4EST detailed. Some new insights are expected concerning the importance of the genotype by environment interactions across such new testing network, which covers some extreme environments mimicking future climate change scenarios.

4 Conclusions

4.1 Platform for multi-trait and multi-criteria based deployment

Within this work, we found that the situation for each species varied considerably and depended both on fundamental biological, industrial and societal conditions in such a way that the development of a multi-trait and multi-criteria platform that fit all species would not be straightforward. This was aptly

illustrated by the variety of ways the traits of FRM can or cannot be properly characterized for different species and differences in which criteria are formulated by stakeholders and how they are formulated.

Despite the considerable structural differences between species, we here propose a platform in the form of a generalized flowchart approach that would determine key variables and trade-off situations that would require consideration within species-specific deployment tools (Figure 9). The tree age at full rotation was found to be a key variable determining the nature of such a platform.

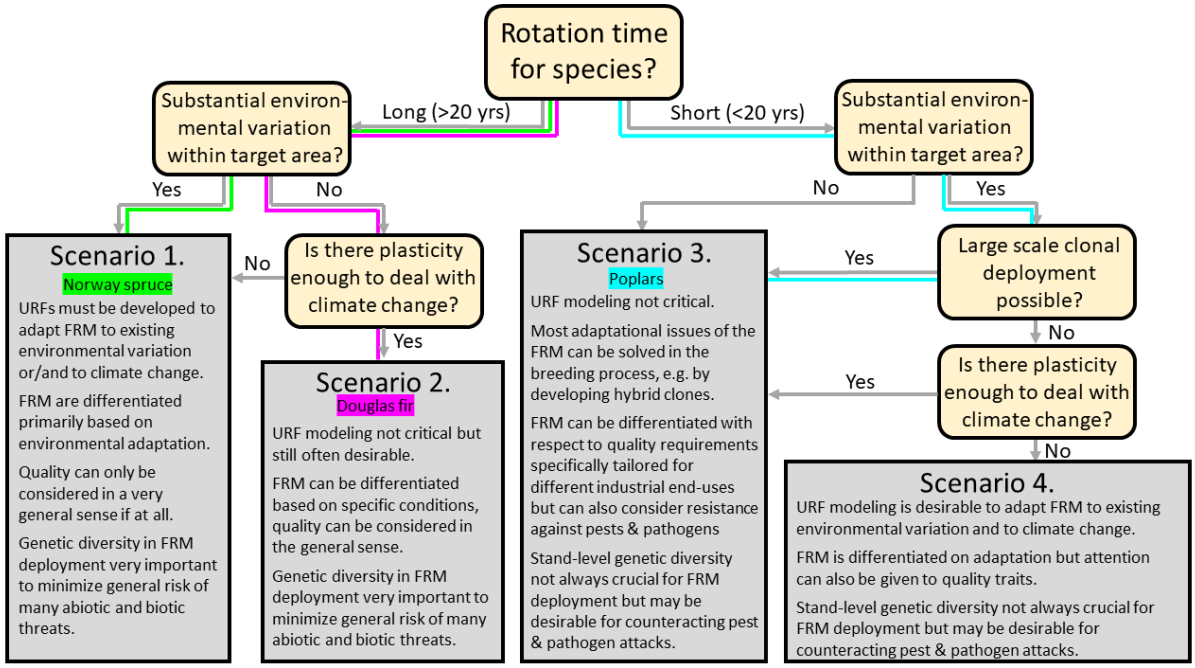


Figure 9: Flowchart representation of a multi-trait and multi-criteria FRM deployment platform in which key characteristics of the tree species will lead to different scenarios suggesting specific models and trade-offs important to that type of species. As an illustration, the decision paths of the example species included in this deliverable are shown in different colors (Norway spruce – green, Douglas fir – magenta, Poplar species - cyan; URF : Universal Response Function).

For species with long rotation times (>20 years) adaptation traits will be crucial, both with respect to existing climate gradients or to progressive climate changes. In such conditions the question of FRM adaptation cannot be entirely delegated to breeding operations but must also be combined with the deployment phase. Thus, adaptational issues would play a very important role in the choice of FRM for deployment. For such long rotation species there is a need for a variety of FRM adapted to different climatic conditions to choose from, in particular when faced with a substantial environmental variation in the target area. Each of these FRM units will also need to exhibit a certain level of genetic diversity in order to safeguard against a considerable variety of abiotic and biotic threats whose occurrence are too sudden and unexpected to be solved by breeding based FRM development. Finally, due to the requirement of variation, among and within FRM, dedicated to growth potential, climate adaptation and risk management there is usually limited scope to develop FRM dedicated to any specific end-uses. Moreover, given rapid changes in technology and material use in society, it is difficult to predict the desirability of quality traits over long rotation times. In this regard, quality trait requirements can usually only be formulated in the very general sense and should consider aspects of multi-purpose use.

In contrast, a short rotation age (<20 years) would imply that genetic testing and breeding could to a greater degree solve adaptational issues on its own. With respect to gradual climate changes and to such non-persistent and localized threats (e.g. frosts, droughts, storm and some pests & pathogens) where risks can be modelled or quantified, it should be possible develop FRM accounting for these traits by targeted breeding. In this regard it appears that the need for genetic diversity within an FRM at the stand-level is lesser than that of long-rotation species. Nonetheless, also for short rotation species, genetic diversity in an FRM can be important to counteract threats that are sudden, persistent and not limited to specific local conditions. In particular epidemic-scale attacks from certain pests and pathogens (e.g. rusts in *Populus spp*) would fit this description. Furthermore, given a short rotation age the choice of FRM could to a greater extent, be directed towards specific industrial end uses thus bringing trade-offs between growth and wood quality into greater focus. A trade-off between wood quality and genetic diversity within FRM may also need to be considered because certain industrial stakeholders tend to value material homogeneity and predictability as a desirable features *per se* which could come in conflict with genetic diversity within FRM.

It should be noted that the flowchart approach (Figure 9) still relies on a set of assumptions that we found to be reasonable and common across all studied species.

1. The differentiation of FRM according to divergent requirements and the management of trade-offs are important prerequisites for successful FRM deployment.
2. Genetic diversity and variation are always important factors for breeding and genetic conservation and for deployment considerations at regional/national levels. However, its importance in industrial deployment situations at the stand-level may vary across species and countries.
3. Climate changes will have an impact on FRM deployment decisions in one way or another although the nature of the impact may vary with species. In many situations climate change highlights the value of phenotypic plasticity and vulnerabilities to extreme events within a prospective FRM.
4. Industry sectors relying on forest biomass output will always desire a material that is specifically tailored for their process chain and for the intended end product. Whether such a requirement can be satisfied by the deployment of a specific FRM depends however on the species-specific conditions.

From the flow-chart approach it is thus possible to determine what conceivable criteria formulated by stakeholder that could reasonably be addressed and would also determine the outline and key characteristics of decision-making tools for each species including important trade-off considerations to be made (see also Table 5). It should be noted that the questions regarding rotation time and geography-based environmental variability/gradients were considered as more important factors than the species ability for large-scale clonal propagation. It was found that the advantage of clonal propagation would still not fundamentally alter the considerations required for long rotation species because the long rotation time *per se* would enforce the necessity of climate change adaptation and risk management, both by differentiating the choice of FRM but also by regulating genetic diversity of the deployed FRM in itself.

Table 5: Summary of which key characteristics should be required and what trade-offs should be highlighted in decision-making tools based on species-specific conditions (Scenarios). The species included in the deliverable are categorized within this scheme with colors.

	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Deployment tools for local adaptation (based on URFs or reaction norms)	Advanced tools required	Simple or none required	Simple or none required	Required
Aspects for which genetic diversity within an FRM are important and relevant.	Most abiotic and biotic threats	Most abiotic and biotic threats	Epidemic pest & pathogen attacks	Epidemic pest & pathogen attacks
Criteria for differentiation between FRM	Mostly adaptation	General quality	Industry-specific quality & resistance	Adaptation & quality
Most important trade-offs to be managed	Growth, adaptation & diversity	Growth, quality & diversity	Growth, quality & resistance	Growth, adaptation & quality
The nature of an FRM unit	Seed orchard harvests or clone mixes	Seed orchard harvests or clone mixes	Single clones or clone mixes	Seed orchard harvests
Species example	Norway spruce	Douglas-fir	Poplars	

Because there are few reports about the role of *epigenetic memory effects* for any other species than Norway spruce, it was not included in the decision flowchart or the following toolbox summary (Figure 9 & Table 5) in this deliverable. However, if we assume that epigenetic factors can be modelled, predicted or even regulated for any type of species, we envision that it could potentially be used for the purpose of adapting FRM to local climates and to climate change under all the aforementioned scenarios. In the case large scale free-land seed orchards are used, epigenetic effects would be best utilized by monitoring key climatic variables in combination with epigenetic factors included in predictive models (e.g. integrated components in URF models or reaction norms). However, if small indoor- or greenhouse-based seed orchards are used or if clonal propagation can be made at industrial scale, it is easy to speculate that epigenetic regulation could be directly manipulated e.g. by artificially altering environmental conditions during the development of flowers, seeds, embryos or clonal propagules.

Given the framework flowchart detailed in Figure 9 & Table 5, decision-making tools usable at the stand-level are possible to develop. Within B4EST the development of such tools are indeed pursued in Task 4.5, most explicitly for Poplars (D4.6) but also for Norway spruce and Scots pine (D4.8). Such tools could be web-based (such as *The Planters Guide*) or be presented in an alternative fashion. However, it is also important to point out that the successful launch of a stand-level decision-making tool would be reliant on the outcome of strategic-level discussions among the major stakeholders for the species, country or region, which is a question outside the scope of this deliverable. At landscape, regional and national levels, the platform flowchart presented here and the multi-trait models offered by this deliverable can be used in such a way that a set of desired criteria for FRM could be formulated and consequently establish a definition of performance. At that level methods such as multi-criteria decision analysis (MCDA) could be employed among all concerned stakeholders (Blagojević et al. 2019) to prioritize among desired criteria. Such an approach can be particularly relevant for trade-off relationships between genetic diversity and other traits because there are few methods available to

derive the value of genetic diversity in mechanistic manner. Within B4EST, these higher-level questions are closely associated with the "National events for stakeholders" pursued in D4.9 and WP6. Subsequently, having established a set of desired criteria and/or a definition of performance, the multi-trait models will again constitute an instrumental component for the development of a stand-level decision tool for selecting an appropriate FRM for forest regeneration operations.

4.2 Deliverable dissemination plan

Since the deliverable is public, there is an ambition to reach out primarily to all key players within the B4EST consortium, but also to other interested parties that could use the information for the development of long-term strategies. As a first step we have the ambition to highlight the platform approach as a news piece on the B4EST webpage and social media channels (e.g. blog post) during the spring 2021.

In general, the performance models for the example species and methods/conclusions derived can be seen as a benchmark and guidance for other species in B4EST when similar trade-offs situations are analyzed and combined with knowledge about adapted silvicultural methods and strategies to address uncertainty in future climatic conditions in the last phase of the project. More specifically, results from this deliverable will be directly used in D4.6 "Performance models for poplar clonal FRM and deployment guidelines", D4.8 "Joint Nordic Planter's guide web-decision tool for Scots pine and Norway spruce" and D4.9 "Guidelines for deployment and silvicultural management of improved FRM accounting for climate projections, risks of natural disturbances, and end-user requirements and acceptances" in WP4. In addition, knowledge developed here will also be included in D5.4-5.7 which are reports on benefits, costs and risks related use of improved FRM in different parts of Europe.

Furthermore, in WP6 one task (6.4) focusses on stakeholder exchange and knowledge transfer activities for forest managers, advisors, industry and policy makers. This includes both EU-level and regional/national policy briefs and national stakeholder events, and will disseminate B4EST-project results both in more general terms (as a way to sustainably manage forests in Europe) and more specific decision making and breeding tools. The trade-offs and definition of performance developed in this deliverable, together with risk management due to uncertainty about future climatic conditions (D4.4) will be important parts in these activities.

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