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The effect of fertilization on genetic parameters in *Picea abies* clones in central Sweden and consequences for breeding and deployment

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ABSTRACT

The aim of this study was to analyze the effect of repeated fertilizer application on the genetic parameters of Norway spruce. Genetic and environmental variances of growth and phenological traits were estimated to find differences between fertilized and control treatments in broad sense heritability and accuracy of estimated genotypic value. Furthermore, genotype × environment interactions (GxE) between the two treatments were investigated. Two Norway spruce clonal field trials in central Sweden were subjected to both treatments and were measured at various points in time up to a field age of 15 years, to monitor the effects of fertilization. For growth traits, trees in the fertilized treatment exhibited lower environmental variance than those in the non-fertilized treatment; consequently, fertilization yielded higher heritability and greater accuracy of estimated genotypic value. Furthermore, the GxE increased as the effects of fertilization became more pronounced; the genetic correlation between treatments dropped to around 0.5 in the last measured growth period. For phenological traits, no GxE but a slight increase in heritability of prolepsis on the leader shoot was found. The results from this study show that, for the conditions encountered in central Sweden, Norway spruce clones should be tested and selected under the conditions in which they are to be deployed. If repeated fertilizer application is to be adopted under operational conditions, substantial losses in genetic gain for growth can be expected when using current selected clones due to the induced GxE. While the fertilized treatment yielded a higher heritability and accuracy of estimated genotypic value for growth traits than did the control, the Swedish Norway spruce breeding program will not benefit from fertilizing genetic field trials because the increased accuracy of estimated genotypic value is nullified by the GxE.

1. Introduction

If society is to develop in a sustainable fashion, it will be necessary for forests to fulfil a variety of functions. Amongst other things, they will have important roles to play in carbon sequestration, preserving biodiversity, recreation, reducing fossil fuel emissions, and as a source of raw material for the forest industry. However, there is an inherent contradiction in satisfying all these demands simultaneously, requiring a well-balanced trade-off between different forest uses. One way of addressing this trade-off is to increase production by cultivating forests intensively in certain suitable areas. This would enable other forest areas to be used for alternative purposes, e.g. making it possible to set more forest land aside for conservation. The potential of intensively managed forests is illustrated by the example of plantation forestry, which in 2000 used only 5% of the world's total forest land to produce 35% of its industrial wood supply (FAO, 2000). In Sweden, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) are the two major commercial tree species, accounting for 38% and 42% of the standing volume of 3000 million m^3 and contributing in a similar way to the annual harvested volume of 80 million m^3 (Skogsstyrelsen, 2010). At a Swedish national level, intensive forestry (i.e. silvicultural methods that result in significant yields but have restricted practical application due to e.g. legalities and/or Governmental policies) has the potential to increase biomass production by up to 50% (Larsson et al., 2009). The three methods suggested to have the biggest practical application were: (i) increased use of *Pinus contorta*; (ii) increased use of vegetatively propagated and genetically improved Norway spruce (clonal forestry); and (iii) nutrient optimisation systems (e.g. repeated fertilizer application) (Larsson et al., 2009).

Repeated application of fertilizers to young stands of Norway spruce is a nutrient optimization system that could potentially increase the production of stem wood by 80–300% over that which is typically possible using traditional forest management (Bergh et al., 2005, 2008). Fertilization in young stands does not only increase the production, it also shortens the unproductive phase in

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the beginning of the rotation period (Bergh et al., 2005). Repeated fertilization in young stands of Norway spruce is not currently practiced on an operational scale, but the Swedish national agency of forestry has decided (July 2010) to revise their recommendations regarding this new fertilization method. It has been estimated that in the coming 10 years, 300,000 ha of forest land in Sweden could be suited for repeated fertilizer application (Skogsstyrelsen, 2008).

Another way to improve forest production is to use genetically improved seedlings from seed orchards or to use cuttings. In Swedish forest regenerations, around 80% of the Scots pine seedlings and 50% of the Norway spruce seedlings come from seed orchards (Almqvist et al., 2010). The use of seedlings derived from contemporary Swedish seed orchards generally results in a volume production gain of 10–15% relative to that achieved with unimproved trees; the new seed orchards that are being established are expected to raise this gain to ca. 25% (Rosvall et al., 2001). However, these beneficial genetic effects are approximately 20–25% lower than they could potentially be when using seedlings sourced from conventional seed orchards due to e.g. background pollination (Rosvall et al., 2001). Using vegetative propagation would make it possible to reap the full benefits of the seedlings superior genotypes, including non-additive genetic variation which is lost during recombination in seed orchards. However, vegetative propagation of Scots pines is currently not permitted and the application of clonal forestry in Norway spruce is highly restricted. It has been suggested by Larsson et al. (2009) that clonal forestry (using genetically improved Norway spruce) should be used on a larger scale than is currently allowed. There is a considerable body of knowledge regarding the vegetative propagation of Norway spruce, concerning both currently available systems (e.g. methods for producing rooted cuttings using donor plants) and novel emerging systems such as somatic embryogenesis (see e.g. Högberg, 2003).

However, little is known about the effects of combining repeated applications of fertilizer with clonal forestry as described above. In particular, a considerable genotype × environment interaction (GxE) could reduce the possible gain from combining the two methods. A large GxE could cause genotypes that perform well in one environment to exhibit average or poor performance in another. An understanding of the GxE relating to the application of intensive fertilization in forests of genetically-improved Norway spruce clones will be required if the two methods are to be employed on an operational scale in Sweden.

For Norway spruce, GxE in growth traits has generally been found to be small or moderate in field trials in southern and central Sweden, with the exception of trials susceptible to late spring frost (summary in Karlsson, 2000). However, it can be argued that the repeated application of fertilizer would cause a radical change in the environment and could thus affect estimates of genetic parameters and/or induce a considerable GxE. Greenhouse studies on the reactions of seedlings/cuttings with different genotypes to various nutrient regimes have been performed for several coniferous species. Significant genotype × nutrient interaction was observed in e.g. *Picea mariana* (Mill.) B.S.P. (Mullin, 1985), *Picea sitchensis* (Mari et al., 2002), *Pinus taeda* (Li et al., 1991), *Pinus elliottii* (Dewald et al., 1992), *Pinus pinaster* (Zas and Fernandez-Lopez, 2005) and *Pinus sylvestris* (Jonsson et al., 1997). In a greenhouse study of 30 open pollinated families of Norway spruce, Mari et al. (2003a) found weak genotype by nutrition interaction for height growth but significant interaction for biomass traits. Furthermore, the heritabilites and coefficients of additive variation were higher in fertilized treatments for all growth traits. Strong interactions in growth traits between genotypes and nutrition levels in Norway spruce were also found by Fober (2004), who studied 20 provenances and 50 open pollinated families of Polish origin under greenhouse conditions.

Although studies under greenhouse conditions indicate that different genotypes respond differently to specific nutrient regimes, the connection between greenhouse results and performance in field tests has generally been weak (e.g. Jansson et al., 1998; Karlsson et al., 2003; Mari et al., 2002). Field trials examining the impact of fertilizer treatment (sometimes in combination with other treatments) on genotype performance and genetic parameters are therefore crucial for breeding and deployment purposes. A number of studies of this kind examining various coniferous species have been performed, yielding a wide range of conclusions; in some cases, a small or negligible GxE was observed while others identified large GxE that caused rank changes which would in turn affect breeding and deployment strategies (Table 1). However, we are not aware of any such studies that focused on Norway spruce.

In a breeding program, good estimates of genetic parameters are needed to accurately select the best genotypes. In particular, the ability to enhance estimates of genetic variation and reduce the magnitude of environmental variation is important. This is achieved by using optimal field trial designs (considering e.g. areal homogeneity and statistical power) and methods for the post-processing of field data (e.g. Dutkowski et al., 2002; Ericsson, 1997). However, it has also been suggested that intensive fertilization could be used in forest tree breeding as a tool for faster and more accurate genetic selection, even for trees to be grown under traditional silvicultural regimes. It is reasonable to assume that fertilized field trials will have a more nutritionally homogeneous environment. In statistical terms, fertilization reduces environmental variance and increases the accuracy of estimated genotypic value (henceforth referred to as accuracy) (e.g. Lopez-Upton et al., 1999; McKeand et al., 2004). However, these potential gains resulting from increases in the accuracy could be nullified if there is a significant GxE and the selected material is going to be planted without fertilization.

The aim of the present study was to analyze the effect of repeated fertilizer application on the genetic parameters of Norway spruce. The genetic and environmental variances of growth and phenological traits were estimated to identify differences between fertilized and control treatments in broad sense heritability and accuracy of estimated genotypic value. Furthermore, the genetic correlations of growth and phenological traits were studied to identify potential genotype × environment interactions between fertilized and control treatments. The paper concludes with an analysis and discussion of the impact of intensive fertilization on both breeding and deployment strategies.

2. Materials and methods

2.1. Field trials

Field trials were conducted in two locations (Ålbrunna and Grangärde) that had originally been selected for use in a clonal forestry project with the objective of selecting optimal clones for cutting propagation and deployment in forest plantations. The trials were established in 1995 with four year old rooted cuttings grown in Jiffy Pot containers in the nursery. The clones were selected from two year old seedlings in nursery beds. The seedlings originated from seeds collected in natural stands in the Vitebsk region of Belorussia. Seedlings with superior early growth and late budburst were selected and propagated as rooted cuttings. Norway spruce material from eastern European stands is currently used in southern and central Sweden since suitable seed orchard material does not cover the demand. Due to its combination of late budburst (avoiding damages from late spring frosts), high growth capacity and intermediated date of growth cessation, Belorussian stand seed is generally considered to have a 10% gain in growth compared to Swedish stand material (e.g. Rosvall et al., 2001). A