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Genetic evaluation of damage caused by ash dieback with emphasis on selection stability over time

Lars-Göran Stener

The Forestry Research Institute of Sweden, Ekebo 2250, 268 90 Svalöv, Sweden

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ABSTRACT

Damage caused by *Hymenoscyphus fraxineus*, the causal agent of ash dieback, was genetically evaluated based on scorings made on five occasions during the years 2006–2016 at two seed orchards of ash (*Fraxinus excelsior* L.) established in southern Sweden in 1992 and 1995, respectively. The studied population included grafts originating from 106 plus-tree clones selected from 27 stands in southern Sweden.

The study verified previous results of (1) high genetic control of damage traits, (2) high genotypic variation in disease susceptibility and (3) that only a small proportion of the natural population are at least partly resistant. The clonal response for dieback damage was stable over the 10-year period, i.e. the least susceptible clones selected in 2006 still belong to the healthiest ones after several years of heavy infection pressure.

There were no clear trends in the development of damage over time for trees being alive at each assessment. However, the proportion of trees that died was substantial (7–8% per year), but this estimation was influenced by other factors than the disease, such as wild game and sanitary cuttings.

Altogether, the results are promising for initiating breeding programs to improve the dieback resistance. However, this is a heavy and costly task, since only a very small proportion of the ash trees are partially resistant to the dieback disease. Thus, a joint breeding program involving all the northern European countries is justified.

1. Introduction

Common ash, *Fraxinus excelsior* L., henceforth called ash, is today severely damaged all over Europe due to a newly identified pathogenic fungus *Hymenoscyphus fraxineus* (Timmerman et al., 2011; Gross et al., 2013; Baral et al., 2014; Queloz et al., 2010). *H. fraxineus* originates from East Asia where it has co-evolved with native ash species (*F. mandshurica*), without any negative effects on growth and health (Gross et al., 2014; Cleary et al., 2016). Most likely *H. fraxineus* has been transferred to Europe by imports of plant material, and has undergone a host jump to a similar, yet native host (*F. excelsior*). The resulting effect has been devastating.

Both young and old trees are affected and whole stands have been devastated. The first observations of ash dieback were made in Lithuania (Juodvalkis and Vasiliauskas, 2002) and eastern Poland (Przybyl, 2002) in the middle of the 1990s. Since then, Lithuania has lost more than 50% of the forest stands where ash was a dominant species (Pliura et al., 2017).

The infections primarily take place through the leaves of ash by the pathogens' ascospores. From there it can spread to branches and stem where phloem and xylem are infected, reducing water and nutrient transportation, which ultimately kills the tree (Timmerman et al., 2011). The main symptoms are wilting of shoots, necrosis on leaves, bark and stem, discoloration of wood and crown dieback (Bakys et al., 2009; Kowalski and Holdenrieder, 2009). In addition, the dieback of branches often results in production of epicormic shoots giving a bushy appearance of the tree (e.g. Kirisits and Freinschlag, 2012).

In Sweden, the disease was first observed in the southernmost regions in 2001 and had within some few years spread across the entire Swedish ash population (Barklund, 2005, 2006; Johansson et al., 2009). By the year 2010, the population had declined so much that the species was added to the Red List that provides information about endangered species in Sweden (Artdatabanken, Swedish Species Information Centre, www.artdata.slu.se). In 2015 ash was downgraded on the Red list from "vulnerable" to "critically endangered". Thus, it is considered to be at high risk of extinction.

Ash in Sweden often grows in mixed stands together with other broad-leaved species and it is a minor commercial species on a national level. The total growing stock of ash on forest land is around 6 million m^3. This can be compared with 41 million m^3 of oak, *Quercus robur* L., the most frequent noble broad-leaved species in Sweden and 1425 million m^3 of Norway spruce, *Picea abies* (L.) H. Karst, the main species in Sweden (Anon, 2016; Cleary et al., 2017). Still, ash is of economic importance for quite many private owners in southern Sweden and it is

E-mail address: lars-goran.stener@skogforsk.se.

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Table 1
Description of traits. “X” denotes the year of observation, i.e. X = 06 represents 2006 and X = 16 represents 2016.

Trait	Explanation
Surv_X	Survival. Classified as 0 = dead or 1 = alive
Dia_X	Diameter in mm at 13 dm above ground
Vit_X	Overall vitality based on the entire tree. Scored in 5 classes in years 2006 and 2007 from 1 = bad … to 5 = very good and in 9 classes years 2010, 2011 and 2016 from 1 = bad to 9 = very good
Dam_06	Dieback damage. In year 2006 the scoring of dieback damage was based on the entire crown and also included damages on the stem, in 10 classes, from 0 = no damage … to 9 = very serious damage
Dam_07, Dam_10, Dam_11	Dieback damage. In years 2007, 2010 and 2011 the scoring of dieback damage was based on the entire crown but divided into (a) annual shoots, (b) second year shoots and (c) remaining crown as well as damages on the stem. In this study only damage according to (c) was considered, using 10 scoring classes, where 0 = none, 1 = very little … to 9 = very serious damage
Dam_16	Dieback damage. In year 2016 scoring of dieback damage was based on the entire crown and scored in 10 classes, from 0 = none, 1 = very little … to 9 = very serious damage
StCa_16	Stem canker. In year 2016, observations of canker on stems were classified in 10 classes, where 0 = none … and 9 = severe
BrCa_16	Branch canker. In year 2016, observations of canker on branches were classified in 10 classes, where 0 = none … and 9 = severe
Bush_16	Bushiness. In year 2016, observations of bushiness as a result from resprouting of new shoots, were classified for trees clearly deviating from the site mean, in 10 classes, where 0 = none … 5 = average “bushiness” … and 9 = very severe bushiness
Ram_16	Ramicorns. In year 2016, the number of severe ramicorns and forks were registered

also of great value for cultural, ecological and biodiversity reasons. For instance, the number of species depending on ash has been estimated to 483, out of which 123 are threatened (Hultberg et al., in prep.).

The declining health condition of ash trees is alarming. However, there are several reports showing considerable genetic variation in susceptibility, indicating a high potential to improve resistance to the dieback damage by selection and breeding (McKinney et al., 2011; Pliura et al., 2011, 2014; Kjaer et al., 2012). This was also previously verified by Stener (2013), where clonal resistance against the ash dieback was studied in two seed orchards of *F. excelsior* in southern Sweden during the years 2006–2011. In that study, the results showed that ash dieback is strongly genotypically controlled and that the genotypic variation among individuals is considerable. As a practical result of that study, the best five of the 106 tested clones were selected to be used in cooperation with other European countries for further breeding. One question that emerges, is whether the selection still is valid after another 5 years of growth. Differences in, for instance, climate, pathogen strains and infection pressure may have changed the clonal resistance over time, which if that is the case, make selection and breeding more complicated.

The main aim of this study was to make a final genetic evaluation of the material in the two ash seed orchards in southern Sweden with specific emphasis on the clonal stability over time for traits related to ash dieback symptoms. Such information will be essential for future resistance breeding of ash.

2. Materials and methods

2.1. Material

The study is based on the same test material as in Stener (2013) where results from inventories during the period 2006–2011 were reported. This new study includes an additional inventory in 2016.

The material consists of plus-tree clones selected from natural populations in southern Sweden in 1991–1992, i.e. well before ash dieback was observed in Sweden. Vigorous growth, stem quality and vitality were selection criterions. Thus, the selected population may be slightly biased compared to a representative sample of the ash population in southern Sweden.

A total of 106 plus-tree clones were selected from 27 different stands, ranging from latitudes 55°41′N and 58°02′N (Stener and Werner, 1997), for establishment of two seed orchards on former agricultural land. All selected trees were vegetatively propagated by grafting. A total of 100 clones, with 40–60 ramets each, were randomly planted out in 1992 at Snogeholm (55°32′N, 13°32′E, 50 m), covering an area of 7.4 ha. An additional plantation was established at Trolleholm (55°57′N, 13°12′E, 100 m) in 1995, including the same clones as in Snogeholm and 6 additional clones. A maximum of 10 grafts per clone were planted at Trolleholm, totally covering an area of 1.0 ha. A spacing of 3.5 × 3.5 m was used at both sites.

The analyses for Trolleholm were based on tree observations in the entire seed orchard area, while the analyses for Snogeholm only refers to approximately 2/3 of the originally planted area. This was due to a high mortality in the excluded parts, which was mainly caused by vegetation competition, voles and drought in the years immediately following planting.

2.2. Data collection

The first inventory at Snogeholm was carried out in September 2006, i.e. 15 years after the establishment of the seed orchard. Three additional assessments were performed in the middle of August in 2007, 2010 and 2011. At Trolleholm, two inventories were performed in the middle of August in 2010 and 2011, i.e. 16 and 17 years after planting. The data from previous inventories was used in this study, together with new observations from the middle of August 2016.

Dead trees were registered but all observations (Table 1) refer to trees alive at the time of inventory. All traits beside diameter, were scored. The resistance to the ash dieback was based on classifications of dieback damage sustained to the crown (leaf defoliation) and the stem (discoloration, canker), that most likely were related to natural infections of *H. fraxineus*. However, trait definitions have changed during the years (Table 1). Damage classification in 2006 was based on the entire tree (crown and stem), while in 2007–2011 separate scores were assigned to different parts of the tree, as a way to improve the resolution of the analyses. In year 2016, the plan was to use the same scoring system as for 2007–2011, but since, after a first field check, there were no signs of damages on the annual shoots, such as necrotic spots or wilting, the 2016 inventory refers to the entire crown (see Table 1). Some new traits were also included, such as canker on stems and branches, bushy appearance which is related to the development of epicormic shoots, as well as number of severe ramicorns and forks. “Bushiness” (Bush_16) was normally quite frequent for all trees and since it was difficult (time consuming) to make a relevant scoring, it was decided only to score trees that severely differed from a standard, set to a score of 5. Furthermore, the number of classes used for scoring vitality, i.e. an overall subjectively scored health status of the tree, was changed from five scoring classes in 2006 and 2007 to ten in the following years.

Trees that were severely damaged by deer or exhibited very poor growth, i.e. having a diameter less than 10 mm, were excluded from the analyses. In total, 30% of the material in Snogeholm was excluded,