



# Early selection for resistance to *Heterobasidion parviporum* in Norway spruce is not likely to adversely affect growth and wood quality traits in late-age performance

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## Abstract

Infections with *Heterobasidion parviporum* devalue the Norway spruce timber as the decayed wood does not meet the necessary quality requirements for sawing. To evaluate the incorporation of disease resistance in the Norway spruce breeding strategy, an inoculation experiment with *H. parviporum* on 2-year-old progenies of 466 open-pollinated families was conducted under greenhouse (nursery) conditions. Lesion length in the phloem (LL), fungal growth in sapwood (FG) and growth (D) were measured on an average of 10 seedlings for each family. The genetic variation and genetic correlations between both LL, FG and growth in the nursery trial and wood quality traits measured previously from 21-year old trees in two progeny trials, including solid-wood quality traits (wood density, and modulus of elasticity) and fiber properties traits (radial fiber width, tangential fiber width, fiber wall thickness, fiber coarseness, microfibril angle and fiber length). For both LL and FG, large coefficients of phenotypic variation (> 26%) and genetic variation (> 46%) were detected. Heritabilities of LL and FG were 0.33 and 0.42, respectively. We found no significant correlations between wood quality traits and growth in the field progeny trials with neither LL nor FG in the nursery trial. Our data suggest that the genetic gains may reach 41 and 52% from mass selection by LL and FG, respectively. Early selection for resistance to *H. parviporum* based on assessments of fungal spread in the sapwood in nursery material, FG, will not adversely affect growth and wood quality traits in late-age performance.

**Keywords** Pathogen resistance · *Heterobasidion annosum* · Forest tree breeding · *Picea abies* · Root rot · Heritability genetic correlation

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Zhi-Qiang Chen and Karl Lundén contributed equally to the manuscript.

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## Introduction

Norway spruce [*Picea abies* (L.) Karst.] is one of the most economically important conifer species in Europe. It is widely used for solid-wood products and production of pulp and paper. The timber is mainly utilized for construction and must meet certain quality requirements in terms of stability, strength, and stiffness (Hannrup et al. 2004). Infections with

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*Heterobasidion annosum* [(Fr.) Bref.] sensu lato (Dalman et al. 2010; Niemelä and Korhonen 1998) reduce the growth of the trees and devalue the Norway spruce logs since the decayed wood does not meet the necessary quality requirements for sawn timber. Infection is also problematic for the pulp and paper industry as the wood is rotted (representing a biomass loss) and discolored. This has made *H. annosum s.l.* the most severe wood-rotting fungus in economic terms (Bendz-Hellgren and Stenlid 1997). *H. annosum s.l.* is a species complex, with three members native in Europe, of which *H. parviporum* (Niemelä and Korhonen) has Norway spruce as its main host (Dalman et al. 2010; Niemelä and Korhonen 1998). In the mid-1980s, the average incidence of *H. annosum s.l.* infections was estimated to be 15% in Swedish Norway spruce trees (Stenlid and Wästerlund 1986). The disease incidence was projected to increase by 23% per decade in managed forests (Thor et al. 2005). Such projections where the model is linked to the temperature are associated with the climate change scenario for northern Europe that prolongs the season of *H. annosum s.l.* spores spread, thus providing a case for implementation of *H. annosum s.l.* resistance in the breeding programmes. It is well established that Norway spruce susceptibility to *H. parviporum* has a genetic component (Arnerup et al. 2010; Skrøppa et al. 2015a, b; Steffenrem et al. 2016), but it has been debated whether the genetic component is significant enough for resistance breeding.

It has been suggested that there may be constraints to the genetic and economic gains of breeding efforts aiming to increase growth, as growth and wood quality traits may be adversely correlated in conifers (Baltunis et al. 2007; Chen et al. 2016; Hong et al. 2014; Lenz et al. 2011; Steffenrem et al. 2009; Wu et al. 2008). Loehle and Namkoong (1987) hypothesized that there will be a trade-off between resistance traits in trees and selection for large volumetric growth. The growth-differentiation balance hypothesis (GDBH; Herms and Mattson 1992; Koricheva et al. 1998) provides a theoretical frame work for examination of trade-offs between growth and resistance (Villari et al. 2014). GDBH considers factors that limit growth and differentiation (such as investments in defensive structures and compounds). The trade-off under GDBH, with the hierarchical process level in the plant's metabolic organization (Koricheva et al. 1998), occurs between growth and constitutive defence at the whole-plant level (Herms and Mattson 1992). If resistance to *H. parviporum* in Norway spruce indeed is restricted by allocational trade-offs, as predicted by the GDBH, with wood quality or growth traits we would expect to find specific correlations between these traits and *Heterobasidion* resistance traits. Dealing with unwanted correlations between traits in breeding is a significant challenge (Hallingbäck et al. 2014). Until now few studies have addressed potential interactions between *Heterobasidion* resistance and growth traits (stem

diameter), Swedjemark and Karlsson (2004) found positive correlations between tree size and FG while others report no correlations (Steffenrem et al. 2016; Swedjemark et al. 1997).

To further explore the genetic relationships between *Heterobasidion* resistance traits and both growth and wood quality traits in Norway spruce, we focused on a material of half-sib progenies from unrelated families in the Swedish Norway spruce breeding programme which previously had been characterized for growth, several solid-wood quality and fiber properties traits (Chen et al. 2014, 2016). The aim of this study was to: (1) characterize the additive genetic variation in a Norway spruce breeding population for susceptibility to *H. parviporum* after artificial inoculation; (2) estimate the genetic correlations between susceptibility and growth, solid-wood quality, and fiber-dimension traits; and finally (3) to estimate and discuss the response from selection for implementation of resistance breeding.

## Materials and methods

### Measurements of solid-wood quality traits and fiber properties traits in the field progeny materials

Two open-pollinated field progeny trials, S21F9021146 (F1146) and S21F9021147 (F1147), were established in 1990 in southern Sweden (Chen et al. 2014). Increment cores were sampled at age 21 years from 12 trees for each of 524 families. The material was analyzed with a SilviScan instrument (Evans 1994, 2006) at Innventia, Stockholm, for radial variations from pith to bark of wood quality traits. The traits measured were wood density (WD), microfibril angle (MFA), modulus of elasticity (MOE), radial fiber width (RFW), tangential fiber width (TFW), fiber wall thickness (FWT), and fiber coarseness (FC; Chen et al. 2014). Fiber length (FL) was measured with a laboratory fiber analyzer, the Kajaani FiberLab at SLU, Umeå (Table 1; Chen et al. 2016).

### Phenotyping for *H. parviporum* resistance in the nursery progeny materials

#### Plant material

Open-pollinated families from 500 mother trees (genotypes) in the Swedish Norway spruce breeding program with an origin from south to central Sweden were sown in 2015. Of these, 243 families were in common with the progenies in the two field trials, S21F9021146 (F1146) and S21F9021147 (F1147). After the first growth season, the seedlings of 446 families with 6–12 progenies were randomized into a complete block design with three replications, where each family

**Table 1** Summary of growth, disease resistance- and wood quality traits

	Acron.	Year	Unit	<i>N</i>	Mean	Min	Max	<i>N</i> families
<i>Nursery trial</i>								
Diameter at point of inoculation	D	2	mm	4628	4.02	1	9	446
Lesion Length	LL	2	mm	4547	7.61	1	104	446
Fungal growth	FG	2	mm	4554	32.54	0	85	446
Vitality	Vitality	2	classes	4376	1.89	1	3	446
<i>Field progeny trials</i>								
Diameter at breast height	DBH <sub>12</sub> <sup>a</sup>	12	mm	5712	67.15	6	146	524
Diameter at breast height	DBH <sub>21</sub> <sup>a</sup>	21	mm	5693	113.10	21	241	524
Height	Ht <sub>7</sub> <sup>a</sup>	7	cm	5711	222.40	15	475	524
Density	Density	21	Kg/m <sup>3</sup>	5497	429.80	298.20	429.8	524
Microfibril angle	MFA	21		5497	14.16	4.60	32.83	524
Modulus of elasticity	MOE	21	GPa	5497	12.28	5.08	2069	524
Radial fiber width	RFW	21	um	5497	29.43	22.67	35.42	524
Tangential fiber width	TFW	21	um	5497	27.45	22.48	35.31	524
Fiber wall thickness	FWT	21	um	5497	2.16	1.51	3.43	524
Fiber coarseness	FC	21	ug/m	5497	330.60	229.00	506.4	524
Fiber length	FL	21	mm	3008	2.45	1.59	3.42	524

Disease resistance traits were quantified in a nursery trial, and growth and wood quality traits were measured in two field progeny trials

Presenting total number of observations (*N*), grand mean (Mean), minimum (Min), maximum (Max), number of families included in the materials (*N* families). The data on wood and fiber traits are presented as averages for cross-sections

<sup>a</sup>Subscripts of diameter at breast height (DBH) at 1.3 m and height (Ht) represent the tree ages when they were measured

was planted in 4-tree row-plots in plastic trays consisting of 24 individual 0.124 L plastic pots. The seedlings were grown for another season in Skogforsk's experimental forest tree nursery at Ekebo (55°56'53.1"N 13°6'52.2"E) following ordinary watering and fertilization routines. No fungicides were used during cultivation.

### Inoculation experiment

To prepare the inoculum, the heterokaryotic *H. parviporum* Rb175 (Stenlid 1987) grown on Hagem medium (Stenlid 1985) was allowed to colonize 6 mm diameter wood dowels for 6 weeks prior to the inoculation experiment.

At the day of inoculation, the vitality of the seedlings was measured according to the following score: (1) fully vital; (2) some loss of vitality (Fig. S1a) and (3) pronounced loss of vitality (Fig. S1b). To allow the fungus to enter the plant, bark was removed with a 6 mm diameter cork borer at 10 cm from the base of the seedling. A wooden dowel colonized by *H. parviporum* was fixated at the wound with Parafilm<sup>®</sup>. The plants were kept under ambient light and temperature in the forest tree nursery and 21 days post-inoculation the seedlings were harvested.

At harvest the diameter at the point of inoculation (D) was measured and the induced defence responses in the phloem were estimated by measuring the lesion length (LL) spread

upwards and downwards from the edge of the inoculation point on the inside of the bark. Fungal growth (FG) was measured according to the established protocols (Arnerup et al. 2010; Stenlid and Swedjemark 1988). The inoculated stem was then cut up into 5 mm discs and placed on moist filter papers in Petri dishes. To avoid contamination, the stem was cut from the top towards the point of inoculation and then from the bottom and towards the point of inoculation. After approximately 1 weeks' incubation under humid conditions, the presence of *H. parviporum* on the discs was determined by observation under the stereo-microscope (Arnerup et al. 2010; Stenlid and Swedjemark 1988). Samples with no conidia detected on the inoculation plug and a total lesion length of 2 mm or shorter were removed from the analysis as the inoculation was deemed as non-successful (Lind et al. 2014).

### Statistical analyses

Due to the deviation from normal distribution of the lesion length data, a natural logarithm was used to transform the data to an approximation of a normal distribution (Steffenrem et al. 2016). Variance and covariance components for genetic analyses were estimated using ASReml4.1 (Gilmour et al. 2015) and the following linear mixed model for nursery data analysis was fitted:

$$y_{ijklm} = \mu + B_j + V_i + P_k + D_{ijklm} + F_{l(k)} + e_{ijklm}$$

where  $y_{ijklm}$  is the observation on the  $m$ th tree from the  $l$ th family within the  $k$ th provenance in the  $j$ th block and belongs to the  $i$ th vitality class ( $V_i$ ),  $\mu$  is the general mean,  $B_j$ ,  $V_i$ , and  $P_k$  are the fixed effects of the  $j$ th block, the  $i$ th vitality and the  $k$ th provenance, respectively. The variable  $F_{l(k)}$  is the random effect of the  $l$ th family within the  $k$ th provenance, and  $e_{ijklm}$  is the random residual effect.  $D_{ijklm}$  is a covariate for diameter at inoculation point. Significance of the fixed effects was tested by Wald  $F$ -test. Non-significant fixed effects were dropped from the model after preliminary analysis. Estimates of heritability were obtained for each trait using variance components from the univariate analysis. Standard errors were estimated using the Taylor series expansion method (Gilmour et al. 2015).

As there is a good genetic connection between nursery trial and the two field progeny trials (243 common parents), the following linear mixed model for joint nursery and progeny data was fitted:

$$y_{hijklmn} = \mu + S_i + B_{j(i)} + V_h + P_{l(k)} + D_{hijklmn} + F_{m(l(k))} + e_{hijklmn}$$

where  $y_{hijklmn}$  is the observation on the  $n$ th tree from the  $m$ th family within the  $l$ th provenance in the  $j$ th block within the  $i$ th trial belongs to  $h$ th vitality ( $V_h$ ),  $\mu$  is the general mean,  $S_i$ ,  $B_{j(i)}$ ,  $V_h$ , and  $P_{l(k)}$ , are the fixed effects of the  $i$ th trial, the  $j$ th block within the  $i$ th trial, the  $h$ th vitality and the  $l$ th provenance within the  $k$ th materials (including two types of data, from nursery and progeny), respectively.  $D_{hijklmn}$  is the covariate for diameter at inoculation point. The variable  $F_{m(l(k))}$  is the random effect of the  $m$ th family within the  $l$ th provenance within the  $k$ th materials and  $e_{hijklmn}$  is the random residual effect. The random  $F_{m(l(k))}$  is assumed to be normally distributed with the expectation value at zero and structured as:  $\text{var}(F_{m(l(k))}) = \begin{bmatrix} \sigma_{aP}^2 & \sigma_{aPN} \\ \sigma_{aPN} & \sigma_{aN}^2 \end{bmatrix} \otimes I$ , where  $\sigma_{aP}^2$ ,  $\sigma_{aN}^2$ ,  $\sigma_{aPN}$

are the additive variance for progeny data, additive variance for nursery data, and covariance for progeny and nursery data, respectively. The random  $e_{hijklmn}$  is assumed to be normally distributed with the expectation value at zero and structured as:  $\text{var}(e) = I \otimes \begin{bmatrix} \sigma_{eP1}^2 & 0 & 0 \\ 0 & \sigma_{eP2}^2 & 0 \\ 0 & 0 & \sigma_{eN}^2 \end{bmatrix}$ , where  $\sigma_{eP1}^2$ ,

$\sigma_{eP2}^2$  and  $\sigma_{eN}^2$  are the residual variances for progeny trials F1146, F1147, and nursery data, respectively. Preliminary analyses indicated that there was no significant provenance by site effect for all traits and also no any provenance effect for lesion length and sapwood fungal growth. Therefore, these effects were removed in the final model. A two-tailed likelihood ratio test (LRT) against the null hypothesis of genetic correlation of zero was used to check the significance of genetic correlations between disease traits in the nursery and wood quality traits in the progeny trials.

The individual-tree narrow-sense heritability for each trait was estimated by

$$\hat{h}_i^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_p^2} = \frac{4 \times \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_e^2}$$

assuming half-sib relationship and where  $h_i^2$ ,  $\hat{\sigma}_a^2$ ,  $\hat{\sigma}_f^2$ ,  $\hat{\sigma}_e^2$ , and  $\hat{\sigma}_p^2$  were narrow-sense heritability and additive genetic, family within provenance, residual, and phenotypic variance components, respectively. Phenotypic and genetic correlations between traits were calculated as:

$$r = \frac{\widehat{\text{Cov}}(x, y)}{\sqrt{\hat{\sigma}_{(x)}^2 \times \hat{\sigma}_{(y)}^2}}$$

where  $\hat{\sigma}_{(x)}^2$  and  $\hat{\sigma}_{(y)}^2$  are the estimated phenotypic or genetic variances for traits  $x$  and  $y$  or the same trait variances at two different ages, respectively, and  $\widehat{\text{Cov}}(x, y)$  is the estimated phenotypic or genetic covariance between traits  $x$  and  $y$ .

Coefficients of additive variation ( $CV_a$ ) and phenotypic variation ( $CV_p$ ) were calculated by dividing square root of additive and phenotypic variances by mean value of that trait, respectively.

Genetic gain ( $G$ ) was calculated using a selection intensity of 1% ( $i = 2.67$ ):

$$G = i \times CV_p \times h_i^2$$

where  $CV_p$  is coefficient of variation of phenotypic effect (calculated as the phenotypic standard deviation divided by the mean of a specific trait) and  $h_i^2$  is individual narrow-sense heritability.

To study the impact of early selection of disease resistance at late-age performance of tree growth and wood quality traits, the correlated response (CR) expressed as the percentage of the mean for those traits ( $y$ ) in field progeny trials to early selection based on nursery resistance traits ( $x$ ) is calculated as:

$$CR_y = \frac{ih_x h_y r_a \sigma_{p_y}}{M_y} \times 100$$

where  $h_x$  and  $h_y$  are the square roots of individual narrow-sense heritability for early selection trait  $x$  and correlated late-age trait  $y$ ,  $r_a$  is the genetic correlation between traits  $x$  and  $y$ , and  $\sigma_{p_y}$  is the phenotypic standard deviation for trait  $y$ ,  $M_y$  is the mean value of trait  $y$  (Falconer and Mackay 1996).

## Results

### Selection for the most disease resistant seedlings could lead to significant genetic gains

The seedlings at the nursery had an average diameter of 4.02 mm at the point of inoculation (D) at the harvest. The mean LL 3 weeks after inoculation with *H. parviporum* was 7.61 mm long with a minimum of one mm to the maximum of 104 mm. FG was on average 32.54 mm with variation from 0 to 85 mm (Table 1). Summary statistics of 11 growth and wood quality traits from two field progeny trials that have 46% common families with the nursery trial is shown in Table 1. In the two field progeny trials, each was scored in 524 families; diameter at breast height (DBH) increased from 67.15 mm at tree age 12–113.10 mm at tree age 21. Height mean was 222.4 cm at age seven. The means for density, MFA, MOE, RFW, TFW, FWT, FC, and FL at trees age 21 were 429 kg/m<sup>3</sup>, 14.16°, 12.28 Gpa, 29.43, 27.45, 2.16 um, 333.60 ug/m, and 2.45 mm, respectively. These mean values are based on cross-sectional averages, calculated by weighting data using areas of growth rings

Variance components, heritabilities, and coefficients of variation (CV) are presented in Table 2 for the nursery trial. Heritabilities of D and disease resistance traits were all significant and varied from 0.26 for D to 0.42 for FG. CV<sub>a</sub> varied from 16.4% for D to 30.3% for FG, and CV<sub>p</sub> were all more than 32.3%, with the highest value of 47.0% for LL. It was estimated that genetic gains could be 22.4%, 41.4%, 52.5% for D, LL, and FG, respectively, if the best 1% seedlings were selected.

### Fungal growth in sapwood correlates with lesion length and tree growth in the nursery trial but not in the two field progeny trials

As expected, there were moderate phenotypic (0.48) and genetic (0.47) correlations between LL and FG in the nursery trial (Table 3). LL had no correlation with D (0.03). However, FG had moderate positive genetic correlation with D (0.48). However, when disease-resistant traits data from the nursery experiment were matched with data on growth and wood quality traits for the same families

**Table 3** Genetic (above diagonal) and phenotypic (below diagonal) correlations between traits in nursery trial

	LL	FG	D
LL		0.47 (0.07)	0.03 (0.08)
FG	0.48 (0.01)		0.48 (0.06)
D	0.05 (0.02)	0.27 (0.02)	

Standard errors are shown in the parenthesis

LL lesion length, FG fungal growth, D diameter at point of inoculation

scored from the two field progeny tests at age 21, only weak and non-significant genetic correlations were found (Table 4). The genetic correlation between LL and growth and wood quality traits ranged from –0.22 to 0.11. Similarly, the genetic correlations between FG and both growth and wood quality traits ranged from –0.23 to 0.16. LL had the highest negative, but non-significant genetic correlation with MFA (–0.22), while the FG had the highest negative and non-significant genetic correlation with FL (–0.23). LL and FG also showed negligible genetic correlations with Ht<sub>7</sub>, DBH<sub>12</sub>, and DBH<sub>21</sub> in the field trial (–0.02 –0.15).

### Expected responses for late-age growth and wood quality traits from early selection for disease resistances

Early selection for resistance to *Heterobasidion* (lower values of LL and FG) had negligible effect on growth with the expected response for all growth traits less than –1.17% with selection intensity of 1% (Table 5). For solid-wood quality traits, early selection for resistance to *Heterobasidion* had no negative effect, but had small negative impact on MFA and MOE if selection based on LL (5.08% for MFA and -4.17% for MOE). For fiber properties traits, early selection for resistance to *Heterobasidion* had negligible effect on traits RFW, TFW, and FC, but small negative effect on FWT (–6.89%) if selection is based on LL and positive effect on FL (5.78 and 29.98% based on LL and FG, respectively).

**Table 2** Variance components, heritabilities, coefficients of genetic (CV<sub>a</sub>) and phenotypic variations (CV<sub>p</sub>), and genetic gains (G) for diameter at point of inoculation (D), lesion length (LL), and fungal growth (FG) in the nursery trial

Trait	$\sigma_a^2$	$\sigma_e^2$	$\sigma_p^2$	$h_i^2$	CV <sub>a</sub> (%)	CV <sub>p</sub> (%)	G (%)
D	0.44	0.48	1.70	0.26 (0.02)	16.40	32.29	22.42
LL	0.20	0.56	0.61	0.33 (0.04)	26.97	46.96	41.38
FG	96.99	207.71	231.95	0.42 (0.05)	30.26	46.80	52.49



**Table 4** Genetic correlations estimated between nursery traits and field progeny traits

	H <sub>t</sub>	DBH <sub>12</sub>	DBH <sub>21</sub>	Density	MFA	MOE	RFW	TFW	FWT	FC	FL
LL	-0.02 (0.14)	0.07 (0.13)	0.05 (0.14)	-0.01 (0.14)	-0.22 (0.17)	0.14 (0.16)	0.06 (0.13)	0.06 (0.15)	0.05 (0.14)	0.11 (0.15)	-0.05 (0.17)
FG	0.07 (0.13)	0.15 (0.13)	0.12 (0.13)	-0.07 (0.13)	-0.11 (0.16)	0.02 (0.15)	0.16 (0.13)	0.04 (0.14)	-0.02 (0.11)	0.11 (0.15)	-0.23 (0.16)

No significant parameter was found at  $p$  value  $< 0.05$  using likelihood ratio test (LRT). Standard errors are shown in the parenthesis

## Discussion

The results presented in this work were based on an extensive resistance phenotyping work: on average ten two-year-old progenies from each of 446 open-pollinated families were phenotyped for the resistance to *H. parviporum* by artificial inoculation. The scale of this study allowed us to use a larger phenotyped data set compared to most previous studies to estimate additive genetic variation for the resistance to *H. parviporum* in Norway spruce. This study found the largest narrow-sense heritability (LL with 0.33 and FG with 0.42) hitherto reported. In fact, with the low standard errors estimated in this study, the estimated narrow-sense heritability are comparable with previously reported broad-sense heritabilities of LL ( $\leq 0.35$ ) and FG ( $\leq 0.27$ ) for *Heterobasidion spp.* resistance (Skrøppa et al. 2015a; Swedjemark et al. 1997). Steffenrem et al. (2016) used parent–offspring regression to estimate the narrow-sense heritability and obtained a relatively weak value of 0.16 for LL. In their two progeny trials, the narrow-sense heritabilities for LL varied from 0.14 to 0.26 for two single-site analyses and a joint-site analysis, and with high standard errors. Skrøppa et al. (2015a) showed a weak value of 0.21 for LL for the broad-sense heritability in Norway spruce (Skrøppa et al. 2015a). The narrow-sense heritabilities of LL and FG obtained in this study were higher than that of growth traits in the two field long-term progeny trials (Chen et al. 2015), but similar to most wood quality traits (0.33–0.50; Chen 2016). The size of genetic variation in a population is an important factor for breeding selection. We found strong coefficients of additive genetic ( $CV_a > 26\%$ ) and phenotypic ( $CV_p > 46\%$ ) variation for *H. parviporum* resistance traits. Steffenrem et al. (2016) used the LL as a measure of resistance to *H. parviporum*. The additive and phenotypic genetic variation for active defense in the phloem thus allows for a direct comparison between studies.  $CV_a$  and  $CV_p$  for *H. parviporum* resistance is higher in the present study. Furthermore, both studies find higher genetic and phenotypic variation than those that were previously reported for growth traits and wood properties by Chen et al. (2016). It is possible that the additive genetic variation for resistance to *H. parviporum* in Norway spruce has been underestimated in previous studies and it may well be in the range where meaningful improvements can be made by breeding selection within a large breeding population. In fact our estimations suggest that the genetic gain could be up to 52.49% for control of fungal spread in the sapwood, if the best 1% seedlings in terms of that trait were selected.

The trade-off between growth, resistance, and fiber properties could be viewed as a result of whole-plant level allocation of energy at higher hierarchical process level

**Table 5** Expected response (%) for growth and wood quality traits in field progeny trial when early selection for disease resistance (lower score of LL and FG) at nursery is conducted with selection intensity of 1% ( $i=2.67$ )

	Ht <sub>7</sub>	DBH <sub>12</sub>	DBH <sub>21</sub>	Density	MFA	MOE	RFW	TFW	FWT	FC	FL
LL	0.04	-0.48	-0.18	0.01	5.08	-4.17	-0.53	-0.43	-6.89	-0.09	5.78
FG	-0.15	-1.17	-0.48	0.06	2.86	-0.67	-1.58	-0.33	3.11	-0.10	29.98

in the plant's metabolic organization (Herms and Mattson 1992; Koricheva et al. 1998). The only study, until now, examining genetic correlations between wood quality traits and resistance in Norway spruce indicates a moderate negative genetic correlation of resistance (LL) to *H. parviporum* with spiral grain (Steffenrem et al. 2016) suggesting a potential trade-off. Given that more than half of the mothers in the nursery trial also were part of previous progeny trials focused on growth, solid-wood quality and fiber property traits (Chen et al. 2014, 2016), we were able to use this overlap to analyze the correlations between those traits and *H. parviporum* resistance. We found no significant correlations between any wood quality traits and either LL or FG. There were no significant phenotypic and genotypic correlations between LL and growth traits in either the nursery phenotyping experiment (D) or the field progeny trials. These results seem to be in line with previous studies. Swedjemark and Karlsson (2004) reported a significant phenotypic correlation between growth and LL but no significant genetic correlation and several other studies report no significant correlations between growth and LL (Swedjemark et al. 1997, 2001). Generally, there appear to be no interaction between FG and growth, except in one study (Swedjemark and Karlsson 2004). The non-significant genetic correlation between the disease resistance, growth, and wood quality traits is favorable in designing multiple-traits breeding strategy for improvement of Norway spruce. In this study, we found that selections of FG or LL alone will cause a negligible effect on growth, density, and most of fiber properties traits. For MFA, MOE and FWT, the responses were small, but for FL a large positive effect was seen. Current breeding target in Norway spruce is mainly for growth and adaptation, with progressive incorporation of solid-wood quality traits (Rosvall et al. 2011). If we select for resistance to *Heterobasidion* at nursery based on FG, the selected stocks will not adversely affect growth and wood quality traits. Therefore, incorporation of disease resistance to existing breeding strategy of Norway spruce targeted for the tree growth and solid-wood quality can be achieved relatively easily through independent culling or an index selection approach.

In line with these results, a weak and significant phenotypic correlation (0.27) and a significant moderate genetic correlation (0.47) were found between FG and larger stem

diameter (D) in the nursery experiment. Thus, we see signs of a trade-off between growth and defense in young seedlings, as the bigger the FG or LL values are the more susceptible the seedling is. Genetic constraints between early plant growth potential, about the same growth phase as our nursery grown plants, and constitutive defensive investment have been found in Maritime pine (*P. pinaster*), but only under nutrient-limited conditions (Moreira et al. 2015). If there are allocational trade-offs operating between growth, wood and fiber property traits and resistance to necrotrophic pathogens on a more general scale, then our set up based on material of different age and under different environmental conditions may not be appropriate to detect them as the genetic trade-offs between growth and defense may be strongly modulated by environmental conditions (Moreira et al. 2015). Nevertheless, these results further strengthen the arguments for including disease resistance in the Swedish Norway spruce breeding strategy.

A moderate additive genetic correlation between FG and LL for *H. parviporum* was found in this study, compared with a significantly higher genotypic correlation ( $r=0.72$ ) for *H. annosum s.l.* in a clonal trial (Swedjemark et al. 1997). This, and previously reported positive phenotypic correlations between FG and LL (Swedjemark and Karlsson 2004; Swedjemark and Stenlid 1997; Swedjemark et al. 1997, 2001), suggests that the measured traits together are relevant for estimating the relative susceptibility of Norway spruce to *H.annosum s.l.* or *H. parviporum* (Arnerup et al. 2010). Resistance to *H. parviporum* is a quantitative trait under polygenic control and the two traits FG and LL for Norway spruce are controlled by different areas of the genome (Lind et al. 2014). Lind et al. (2014) report two and four non-overlapping QTL regions, respectively, for LL and FG in a classical QTL study of one full-sib family of Norway spruce. One marker for one of the QTLs from that study has been validated and is available for deployment in breeding and selection (Nemesio-Gorrioz et al. 2016).

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