Sensitivity of *Picea abies* to Butt Rot in Pure Stands and in Mixed Stands with *Pinus sylvestris* in Southern Sweden

Magnus Lindén and Gudmund Vollbrecht

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Repeatedly sampled data from permanent experimental plots in southern Sweden were used to model butt rot development in Norway spruce growing in pure stands and in mixed stands with Scots pine. The data come from 29 sites with pure spruce, altogether 100 plots, and from 15 sites of mixed spruce and pine, altogether 22 plots. A logistic model provided the best fit to the data. The study material revealed that in mixed stands the proportion of spruce trees with butt rot is lower than in pure Norway spruce stands. The difference in the incidence of butt rot cannot be explained by silviculture or windthrow since both factors are accounted for in the study. The most significant effect on butt rot development in Norway spruce by an admixture of Scots pine, was found when the Scots pine admixture was 50%. In order to reduce the incidence of butt rot in Norway spruce, the study material indicate that there is little to be gained by increasing the Scots pine admixture to much more than 50%.

Key words butt rot, *Heterobasidion annosum*, Norway spruce, *Picea abies*, logistic regression, mixed forest, *Pinus sylvestris*
Authors address Southern Swedish Forest Research Centre c/o Asa Experimental Forest, SLU, S-360 30 Lammhult, Sweden **E-mail** magnus.linden@ess.slu.se
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1 Introduction

Root and butt rot cause severe economic losses to the forestry sector throughout the temperate regions of the Northern Hemisphere (Hodges 1969, Bendz-Hellgren et al. 1998, Fiodorov 1998). Many fungal species may cause root and butt rot in conifers. The most important species in northern Europe are *Heterobasidion annosum* (Fr.) Bref. and *Armillaria* spp., of which the former is the most common and causes the most serious damage (Peace 1938, Yde-Andersen 1958, Holmsgaard et al. 1968, Huse et al. 1994). Basidiospores of *H. annosum* infect newly exposed wood, such as stump surfaces created by thinning operations (Rishbeth 1951a, Yde-Andersen 1982). Below ground there is a vegetative spreading of the mycelia to healthy trees by root contacts with infected tissue (Rishbeth 1951b, Paludan 1966).

Measures to control damage by *H. annosum* are, e.g., choice of less susceptible tree species (Petersen 1989, Korhonen et al. 1998), thinning during low risk seasons (Morrison and Johnson 1970, Brandtberg et al. 1996) and stump treatment (Kuhlman et al. 1976, Brandtberg et al. 1996). Mixing tree species has often been proposed as a measure to prevent or reduce the growth of *H. annosum* in a stand (Gayer 1886, Zimmermann 1908, König 1923, Rennerfelt 1946, Korhonen et al. 1998). The positive effect of mixed stands is mainly thought to be a consequence of the wider spacing between susceptible individuals (Heybroek 1980).

In Sweden, Norway spruce (*Picea abies* (L.) Karst.) is the dominant tree species used in forestry. In pure stands of Norway spruce, root and butt rot caused by *H. annosum* are frequently found. However mixed stands of Norway spruce and Scots pine (*Pinus sylvestris* (L.)) cover approximately 15 percent of the forested area (Skogsdata… 1999), and it has been proposed that Norway spruce is healthier in mixtures with Scots pine than in pure stands (Rennerfelt 1945, Piri et al. 1990). Scots pine is also attacked by *H. annosum*. The worst attacks usually occur on dry, sandy soils or soils with high pH (Rishbeth 1951b, Rennerfelt 1952), but on the dominating soil type in Sweden, i.e. soils of sandy loamy till with the soil moisture class mesic (Hägglund and Lundmark 1977), Scots pine generally exhibits low levels of butt rot caused by *H. annosum* (Rennerfelt 1946, Vollbrecht et al. 1995).

On many sites the yield from mixed stands of Norway spruce and Scots pine is of the same magnitude as the yield from pure Norway spruce stands (Agestam 1985). In mixed stands of non-compatible tree species, complicated logging operations can cause damage to residual trees that will result in increased spore infection (Chou 1981), whereas mixed stands of Norway spruce and Scots pine are considered easy to manage due to compatible growth rhythms and similar silvicultural treatments. Consequently mixed stands with Scots pine and Norway spruce are considered as an interesting alternative to pure spruce stands.

The effect of mixing tree species on the development of *H. annosum* in Norway spruce has been challenged in several studies (Falck 1930, Peace 1938, Kangas 1952, Kató 1967, Werner 1971 and 1973, Huse 1983, Siepmann 1984). The aim of this study was to estimate the importance of Scots pine admixture to the incidence of butt rot in Norway spruce by modelling data from permanent sample plots.

2 Materials and Methods

2.1 The Data Material

The data used for the analyses come from 100 pure stands and 22 mixed stands that are permanent sample plots (Table 1). The plots are located at 44 experimental sites in southern Sweden (Fig. 1, Fig. 2). The previous land-use is coniferous forest. The site index of the plots, i.e. the dominant height at 100 years of stand age (Hägglund 1973), varies between 22.6 and 38.6 m for spruce. On all sites the soil water class is mesic (Hägglund and Lundmark 1977). The altitude is 40–320 meters above sea-level (Table 1). The pure stands are planted whereas the mixed stands are naturally regenerated. All stands are even aged and single storied and in the mixed stands the species are evenly dispersed.

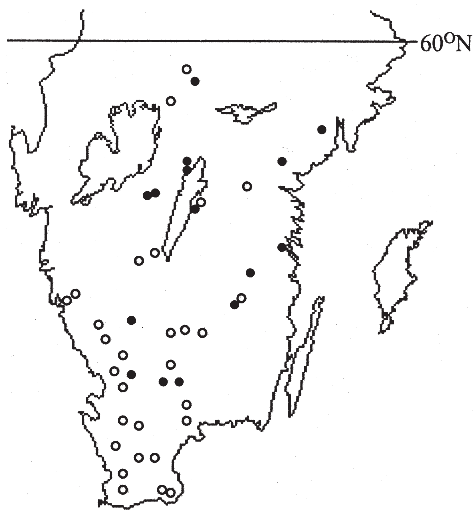

Fig. 1. Location of the experimental sites in southern Sweden; open circles, sites with pure spruce plots; filled circles, sites with mixed plots.

Table 1. Description of the study material.

Stand	No.plots	No.occ.	No.obs.	Sample	SI, m	Age, yrs	Bacc, m^2	Mixbac, p/t	No. thin
Pure	100	265	165	37±24	32.3±3.2	50±15	25.4±18.9	0±0	5±5
Mixed	22	51	29	22±25	30.5±4.4	78±19	12.9± 7.9	0.62±0.23	7±2
Total	122	316	194	35±25	32.1±3.5	54±19	23.6±18.3		6±5

No.plots, number of plots; No.occ., number of butt rot sampling occasions at thinnings; No.obs., number of observations for regression (=No.occ. – No.plots); Sample, number of felled trees on the sampling occasions; SI, site index spruce (Hägglund 1973); Age, total stand age; Bacc, accumulated thinned basal area present felling excluded; Mixbac, mean proportion of Scots pine of total basal area; No.thin., number of thinnings. Means ± Standard deviation.

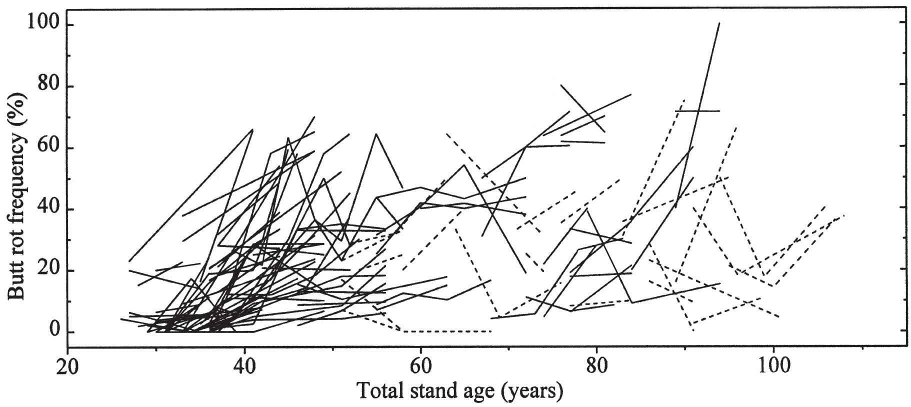

Fig. 2. Development of butt rot frequency between consecutive thinnings on the study plots, dashed lines: mixed plots with spruce and pine, solid lines: pure spruce plots.

Within the permanent sample plots, the number of healthy trees and the number of trees with butt rot have been assessed from visual evidence of decay at stump height immediately after at least two thinnings (Table 1). No attempts have been made to distinguish between different decay-causing fungi. All thinnings have been carried out manually during spring, summer or autumn when the risk of spore infection is high (Yde-Andersen 1962, Brandtberg et al. 1996). Logs have been extracted manually or by winch to avoid damage to residual trees. The thinning interval has been two to eight years. In connection with the thinnings, data have been collected to determine the volume and basal area of the remaining and the removed trees.

The number of felled trees on each occasion, i.e. the sample size, varied from 3 to 110 trees (Table 1). It was assumed that the selection of thinned trees with reference to butt rot was random because it is very difficult to identify standing trees with butt rot from external signs (Vollbrecht and Agestam 1995a), and there is little or no difference in the incidence of butt rot in different tree classes (Low and Gladman 1960, Werner 1971, Bruchwald 1984). Accordingly, the butt rot frequency at stump height of the thinned trees can be regarded as representative of the butt rot frequency of the residual stand (Holmsgaard et al. 1968, Bryndum 1969, Vollbrecht and Agestam 1995a). The mean incidence of butt rot among Scots pine trees was 1.0%. Trees that were dead, dying, windthrown or that had external visible damage were excluded from the calculations of the proportion of trees with butt rot.

2.2 Building the Model

A conceptual model was constructed at the initial stage assuming that the development of root and butt rot depends on three main factors: site attributes, stand conditions and silvicultural treatments. Variable describing the site: site index.

Table 2. Tested variables calculated from the data of the study plots. Group indicate variables with similar type of influence.

Group	Name	Description	Unit
Site	SISPRUCE	Site index of spruce	m
Stand density	DENS	Mean density of spruce	n/ha
	DENT	Mean total density	n/ha
Composition	MIXVAC	Mean admixture of pine of total volume	%
	MIXVP	Admixture of pine of total volume after the previous thinning	%
	MIXBAC	Mean admixture of pine of total basal area	%
	MIXBAP	Admixture of pine of total basal area after the previous thinning	%
Thinned b.a.	BAMAX	Thinned basal area of spruce at the heaviest thinning	m^2/ha
	BAFIRST	Thinned basal area of spruce at the first thinning	m^2/ha
	BAPREV	Thinned basal area of spruce at the previous thinning	m^2/ha
	BACC	Accumulated thinned basal area of spruce, present thinning excl.	m^2/ha
Thinned trees	STFIRST	Number of thinned spruce trees at the first thinning	n/ha
	STPREV	No. of thinned spruce trees at the previous thinning	n/ha
	STACC	No. of accumulated thinned spruce trees	n/ha
	NTHIN	No. of thinnings, present thinning excluded	
Miscellaneous	TIMETHP	Time between the two latest thinnings	years
	TIMERP	Time between the observed and predicted levels of butt rot	years
	TIMETH.1	Time from the first thinning to the point in time of the prediction	years
	FORROT	Butt rot incidence at the latest observation before the prediction	%

Variables describing the stand: i) stand age, ii) stand density, iii) butt rot incidence in the previous thinning and iv) admixture of pine. Variables describing the silvicultural treatments: I) stand age at the time for first and subsequent thinnings, II) number of trees thinned, III) number of thinnings and IV) thinned basal area.

For the mathematical model two requirements were stipulated. The first was that the model should always forecast levels of butt rot that were within the 0.0 to 1.0 interval, assuming an S-shaped development pattern of the fungi asymptotically approaching the 1.0 proportion of trees with butt rot. The second requirement was that the algorithms of the model should account for the large variation in sample size, i.e. the number of felled trees (Table 1), ascribing observations where few trees were sampled less weight than observations based on larger sample sizes. The tested models were logistic models, (Allison 1999), and general linear models of multiplicative and additive types (SAS/STAT USER´S GUIDE... 1988).

A set of 19 variables was calculated from the measurements made within the plots (Table 2). The variables were classified into six groups based on their presumed type of influence on the development of butt rot. For the subsequent fitting of the model it was decided that not more than one variable from each group should be represented in the final model. Regression analysis was carried out, where the incidence of butt rot at a given point in time was the dependent variable and the above mentioned variables were independent variables. After testing each variable separately, the variables were put together in various combinations to find the best fit to the data. The available data material was considered too small to be divided into two separate groups. For this reason the model was not validated using separate data. Validation and verification was carried out through behaviour and sensitivity analysis.

2.3 Simulations

The adopted model, was used to predict the development of butt rot in four theoretical stands with varying admixture of Scots pine. The stands were generated in a growth simulator to obtain basal area development (Ekö 1985). Input values to the growth model: site index for Norway spruce = 32 meters, four thinnings performed at the stand ages 21, 26, 36 and 46 years, 30% of the

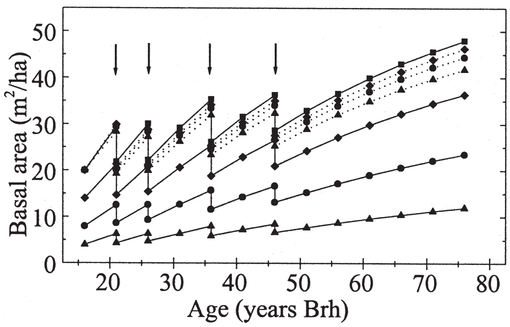

Fig. 3. Basal area development and thinnings of the stands used to model butt rot; Site index spruce = 32 m (Hägglund 1973); Basal area (BA) development according to Ekö (1985); squares, pure spruce stand; diamonds, 25% pine of total BA; circles, 50% pine; triangles, 75% pine; dotted lines, total BA; solid lines, spruce BA. Arrows indicate thinnings.

basal area cut at each thinning, 10% initial butt rot frequency (Fig. 3). The stands have a high volume production and the applied treatment is intensive but these conditions are not rare in southern Sweden and they are in accordance with the study material.

3 Results

3.1 Model Characteristics

A linear model with a logistic link function was found to account for both the variation in sample size and the demand for levels between 0 and 1. The values are transformed with the link function, equation 1, describing how the expected value of the response variable is related to a linear component (Hosmer and Lemeshow 1989). The linear component of additive type, equation 2, provided the best fit to the data. In the equation, $C_1 \ldots C_i$ are the coefficients and X the value of the variable. The response variable is the proportion of infected spruce trees, r/n, and it is denoted

$$\eta = \log(\mu / (1 - \mu)) \quad (1)$$

$$\eta = C_1X_1 + C_2X_2 + C_3X_3 + \ldots + C_iX_i \quad (2)$$

Table 3. Model description. The dependent variable is the proportion of trees with butt rot, μ.

Variable	Unit	Estimate	Std Err (%)	P
Intercept		–2.5863	3.8	0.0001
BACC	m^2	0.0134	17.9	0.0001
MIXBAC	%	–0.0024	36.7	0.0189
FORROT	%	0.0419	6.3	0.0001
TIMERP	years	0.0515	15.1	0.0001

Link function for transformation = log (μ / (1 – μ)) where μ is the proportion of trees with butt rot, N = 194, for symbols see Table 2.

μ in the link function. The number of spruce trees felled, n, is regarded as a weight (Allison 1999). The logistic model was fitted to the data through an iterative fitting process that was repeated until no improvement in model fit was achieved. In this process, the link function is used to relate the dependent variable to the independent variables.

The adopted model includes the following variables (Table 3): accumulated thinned basal area of Norway spruce (present thinning excluded) (BACC), mean admixture of Scots pine as a proportion of total basal area (MIXBAC), time between the latest sampling of butt rot and the point in time for the predicted value (TIMERP) and incidence of butt rot at the latest observation before the prediction (FORROT).

3.2 Verification

The simulated levels of butt rot range from 0.12 to 0.79 (Fig. 6). During sensitivity analysis, proportions of butt rot above 0.85 could be achieved using repeated heavy thinnings and rotations of more than 100 years, but they could not be achieved using normal thinning regimes. The mean of the residuals is zero and they are evenly distributed over the different admixtures of pine (Fig. 4, Fig. 5). Pearson's correlation was studied (SAS/STAT USER´S GUIDE... 1988), and the correlation coefficients were generally less than 0.25 except between the variables BACC and FORROT where the correlation coefficient was 0.42 (Table 4).

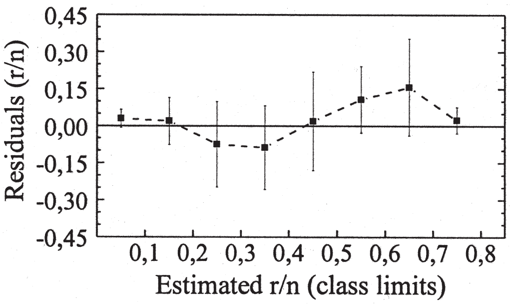

Fig. 4. Verification of the model. Residuals, estimated observed proportion of trees with butt rot; r/n, proportion of spruce trees with butt rot; square with bar indicate mean residual ± standard deviation within class.

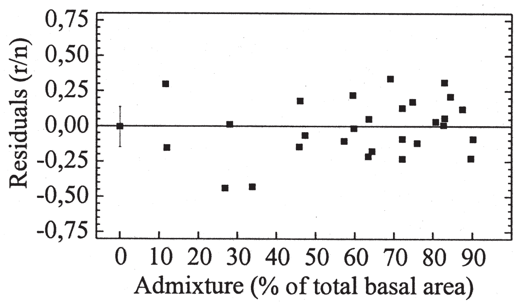

Fig. 5. Residual analysis. Residuals, estimated observed proportion of trees with butt rot; r/n, proportion of spruce trees with butt rot; square with bar indicate mean residual ± standard deviation within class.

Table 4. Correlation coefficients of the model variables, for symbols see Table 2.

Variable	BACC	MIXBAC	FORROT	TIME
BACC	1.00	–0.24	0.42	–0.19
MIXBAC	–	1.00	0.06	0.14
FORROT	–	–	1.00	–0.08
TIME	–	–	–	1.00

3.3 The Predictions

The proportion of spruce trees with butt rot was lower in the mixed stands than in the pure stands (Fig. 6). The difference was enhanced with an increasing admixture of pine. The greatest effect on the incidence of butt rot in Norway spruce was achieved with 50% admixture of Scots pine. The difference between the incidence of butt rot in the four studied cases increased with age. The isolated effect of admixture was described in a partial analysis (Fig. 7). In this case the difference between treatments is lower because of increased growth of butt rot in the mixed stands.

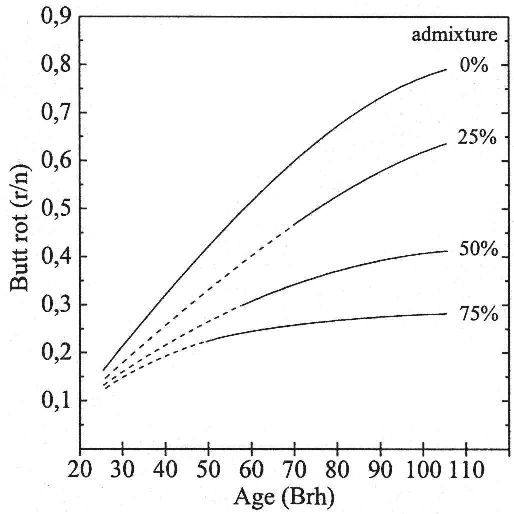

Fig. 6. Predicted development of the proportion of spruce trees with butt rot; r/n, (number of spruce trees with butt rot) / (total number of felled spruce trees); admixture, proportion of pine of total basal area; age Brh, age at breast height, dashed sections indicate extrapolations of the study material.

4 Discussion

The results indicate that there is a lower incidence of butt rot in Norway spruce stands with an admixture of Scots pine than in pure Norway spruce stands. This difference cannot be explained by differences in thinning intensity alone since this variable is accounted for in the model (Table 3, Fig. 7). Neither can it be explained by differences in logging season since all the plots have been thinned during spring, summer or autumn when the risk of spore infection is high. Adding the thinning intensity factor (BACC), the effect of mixture is enhanced (Fig. 6). This is probably

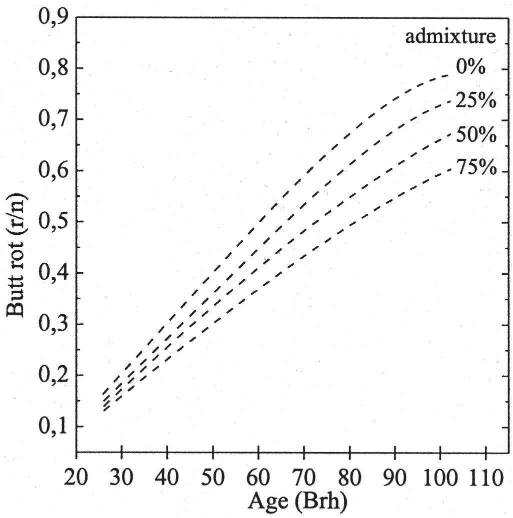

Fig. 7. Partial effect of Scots pine admixture. Simulated butt rot development with uniformly thinned basal area applied; admixture, proportion of pine of total basal area; age Brh, age at breast height.

explained by the fact that, in the pure spruce forest more wood susceptible to infection is exposed compared to the mixed forest. Most of the effect of an admixture of Scots pine on the incidence of butt rot in Norway spruce is achieved when the admixture is 50%. In order to decrease the incidence of butt rot in Norway spruce by an admixture of Scots pine, the effect of increasing the admixture to much more than 50% appears to be small. After four thinnings at 70 years stand age, the forecasted proportion of Norway spruce with butt rot is 0.35 in the stand with 50% Scots pine admixture. At the same age the proportion is 70% higher in the pure Norway spruce stand.

The lower incidence of butt rot in Norway spruce in admixture with Scots pine is probably because in mixed stands there is a wider spacing between susceptible trees, in this case Norway spruce, which will delay the spread between those individuals (Heybroek 1980). Additionally in mixed stands there are probably fewer root contacts between the Norway spruce trees. Root grafts between individuals of different tree species have been found to be less abundant than between individuals of the same species (Epstein 1978). Since the spread of *H. annosum* below ground depends on root contact with infected tissue (Peace 1938, Rishbeth 1951b, Paludan 1966, Stenlid 1985), this would probably contribute to slower spread. Moreover the number and the basal area of Norway spruce stumps is smaller in the mixed stands than in the pure Norway spruce stands, which will decrease the extent and the number of potential spore infections from which *H. annosum* can spread to adjacent trees. A fourth factor, that might influence the development of butt rot, is the presence of antagonistic fungi. It has been proposed that a mixture of tree species could lead to an increased presence of antagonistic fungi that restrict the spread of *H. annosum* (Johansson and Marklund 1980, Fedorov and Poleschuk 1981). There are several fungi, that may be more abundant in mixed forests, that are strong competitors to *H. annosum* (Kirby et al. 1990, Holmer and Stenlid 1993, Holmer and Stenlid 1997).

The low magnitude of the variable describing Scots pine admixture (MIXBAC) compared to the variable describing thinned basal area (BACC) indicates that the effect of thinning intensity is more important to the development of butt rot than the effect of Scots pine admixture alone. In this context it should be noted that Scots pine may act as a spreading agent for the P-type intersterility group of *H. annosum* in Norway spruce. The P-type intersterility group has been found to attack both Norway spruce and Scots pine while the S-type intersterility group mainly has been found to attack Norway spruce (Korhonen 1978). The mixed plots in this study are slightly more northerly located than the pure plots and there is evidence that the P-type intersterility group of *H. annosum* is more common in the south of the studied region compared to the north where the S-type is dominating (Stenlid 1987, Karlsson 1993). Thus, in mixed stands of Scots pine and Norway spruce where only the S-type intersterility group is present, it is more likely that the admixture of Scots pine would reduce the incidence of *H. annosum* than if the P-type intersterility group is present. Consequently, it is possible that the effect of the Scots pine admixture is smaller than found in this study in areas where the P-type intersterility group of *H. annosum* is present. However, the distribution of intersterility groups could not be investigated since there was no record of it.

4.1 The Study Material

It has been proposed that naturally regenerated stands are less vulnerable to attack by fungi causing root and butt rot than planted stands (Kuhlman et al. 1976, Graber 1994). This could be important since the mixed stands were naturally regenerated and the pure stands were planted. In naturally regenerated stands, slower growth, higher wood density and occurrence of non-susceptible tree species would slow down the development of butt rot. However, naturally regenerated stands are generally more dense than planted stands (Due 1960), and butt rot has been found to be positively correlated with planting density (Venn and Solheim 1994, Johansson 1997). In either case, the magnitude of the difference in the incidence of butt rot in planted and naturally regenerated stands is generally found to be small (Flury 1907, Kuhlman et al. 1976). Furthermore the difference in butt rot proportions between stands of different admixtures can not be explained by any such effect of regeneration method. A seperate analysis of planted plots and plots with natural regeneration did not reveal any difference in the frequency of butt rot between the two types of establishment.

Although the previous stand is coniferous forest for both the mixed stands and the pure stands it can not be completely excluded that differences in butt rot frequency in the previous generation has influence the frequency of butt rot in the present rotation. According to our study in cases where the previous stand was a pure spruce stand the frequency of trees with butt rot was probably higher compared to sites where the previous stands were mixed. This may have affected the initial frequency in the present stands since transfer of butt rot have been reported from coniferous stumps to seedlings (Piri 1996). In that case the effect of Scots pine admixture would be delayed but it would not affect the but rot development from one occasion to another. However there is no evidence that this is the case in the used data material and according to Rönnberg (1999) no significant long term correlation between butt rot in the previous rotation and the present have been found.

Advanced stages of decay weaken the stability of standing trees that can result in increased windthrow of trees with butt rot (Greig 1962). As a consequence the exclusion of dead, dying and windthrown trees can result in an underestimate of the actual incidence of butt rot. Norway spruce is generally considered to be more vulnerable to windthrow than Scots pine and it may be speculated that the admixture of Scots pine could have had a stabilising effect on the spruce trees in the mixed stands. In that case the effect would be that because of the exclusion of dead, dying and windthrown trees, the difference in butt rot levels between the treatments has been underestimated. On the other hand the risk of windthrow generally increases as tree crowns expand (Peltola et al. 1999). Since the mixed stands are considerably older than the pure stands (Table 1), this points to a higher vulnerability to windthrow. There was no severe windthrow on the plots.

The fertility of the pure spruce plots is slightly higher compared to the mixed plots (Table 1). The effect of site fertility was tested by Vollbrecht and Agestam (1995b) using partly the same data meterial as in this study and a weak negative correlation was found. There is no consistency in the literature regarding the effect of site fertility on the frequency of butt rot. Sites with high fertility and fertilised sites with nitrogen have in some cases been found to increase growth of *H. annosum* in Norway spruce (Falck 1930, Ennerstvedt and Venn 1979, Dimitri and Schumann 1988, Wahlström and Barklund 1994). However in other studies the highest frequency of butt rot has been found on the poorest sites and nitrogen fertilisation has been found to reduce growth of the butt rot causing fungi (Rohmeder 1937, Kangas 1952, Filip 1994). In yet other studies the highest butt rot frequencies have been found on the poorest and on medium fertile sites (Kallio and Tamminen 1974, Huse et al. 1994) According to Korhonen et al. (1998), attack of *H. annosum* is primarily related to excess (and deficiency) of nitrogen. In this context the variation in site fertility of the data material in this study is small and the mean fertility is higher than in the studies by Kallio and Tamminen (1974) and Huse (1983) (Table 1). In conclusion there is no agreement to support the idea that differences in site index is of any major importance in the present study.

4.2 Verification and Validation

The forecasted levels of butt rot are higher in this study compared to previous work in similar forest types (Rennerfelt 1946, Enerstvedt and Venn 1979, Bruchwald 1984, Rymer-Dudzinska 1986, Piri et al. 1990, Huse et al. 1994). The reason for this may be that all plots have been thinned during spring, summer and autumn, i.e. the time of the year when spore infection by *H. annosum* are common. Thinning during these seasons without stump treatment favours the spreading of *H. annosum*. However site conditions and silvicultural treatments are not accounted for in the previous studies which also may contribute to the variation in the levels of butt rot. In either case the forecasted levels of butt rot in this study are probably overestimated compared to normally managed stands where thinnings are carried out throughout the year.

Generally, the correlation between independent variables was low but could not be avoided completely (Table 3). The correlation between accumulated thinned basal area and previous incidence of butt rot is explained by the fact that both variables increase with age in normally managed stands. Biologically it does not appear to have any significant effect on the results.

In conclusion the present study shows that an admixture of Scots pine may be an effective tool to decrease the incidence of butt rot in Norway spruce. The most significant effect on the butt rot development in Norway spruce is found when the Scots pine admixture is 50%. In order to reduce the incidence of butt rot in Norway spruce, the studied plots show that there is little to be gained by increasing the Scots pine admixture to much more than 50%. The logistic model can be used to produce prognoses of butt rot in Norway spruce in stands established on old forest land.

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