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Modelling the incidence of *Heterobasidion annosum* butt rots and related economic losses in alpine mixed naturally-regenerated forests of northern Italy

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Summary

2,257 recently felled stumps were sampled from 22 mixed naturally-regenerated forest stands in the Aosta Valley, western Italian Alps, and examined for *Heterobasidion annosum* butt rots. Disease incidence ranged from 6% to 71% depending on sites, and *H. annosum* accounted for 92% of the total number of diseased stumps. *H. annosum* incidence was significantly higher (χ^2 multiple comparison tests, p<0.05) on Norway spruce (44%) than on the other tree species (silver fir = 18%; larch = 12%, Scots pine = 6%). Based on information on the airborne inoculum composition of the fungus, all the three European species of *H. annosum* were present, with a variable frequency, depending on site. A Partial Least Squares Regression (PLSR) analysis showed that the relative abundance of Norway spruce and four variables describing the size of trees were the best predictors for the incidence of *H. annosum* butt rots. A model having these variables as predictors was developed ($r^2 = 0.75$; p<0.001) and successfully validated on 5 additional forest stands. An estimate of the losses in yield and value of timber associated with the disease, i.e. direct losses, was also

carried out in the forests included in the survey. The percentage of direct financial losses were either comparable or lower than the average level of disease incidence.

1 Introduction

Root and butt rots of conifers lead to severe economic losses to forestry worldwide. Although several fungal species can cause root and butt rot of conifers, *Heterobasidion annosum* (Fr.) Bref. *sensu lato* (*s.l.*), hereafter referred as *H. annosum*, is by far the most widespread and destructive (ASIEGBU et al. 2005). Financial losses caused by *H. annosum* in the European Union were estimated at 790 million Euros (€) per year (WOODWARD et al. 1998).

In this work we examined naturally-regenerated coniferous forests of the Aosta Valley, in the northwest corner of Italy. The presence of *H. annosum* in this area has been previously reported both in mountain and subalpine stands (GONTHIER et al. 2001; GONTHIER et al. 2003). Forests in the Aosta Valley have been harvested for centuries (NICCO 1997), but nowadays timber yields are generally insufficient to cover logging costs, and thus most of them are being under-exploited or abandoned. From a forestry perspective, Aosta Valley shares common traits with neighboring alpine areas of Italy, France and Switzerland, including tree species composition, steep slopes, and silvicultural history. Thus, we believe outcomes of this research could be extended to a wider area, comprising western and central Alps, as well as other mountain areas of Europe.

The goals of this research were i) to assess and compare the susceptibility to *H. annosum* butt rots of native alpine tree species, ii) to analyze factors associated with occurrence and incidence of *H. annosum* butt rots in pure and mixed coniferous forests, iii) to develop and validate a stand-level model to predict the incidence of *H. annosum* butt rots, and iv) to estimate their direct financial losses and to explore the relationship between disease incidence and direct financial losses.

Several papers relating the damages caused by *H. annosum* to environmental factors have been published (VOLLBRECHT and AGESTAM 1995; PUDDU et al. 2003; THOR et al. 2005; MATTILA and

NUUTINEN 2007). Of these several have led to the development of empirical models enabling the prediction of disease severity based on tree, site or stand variables. These studies, however, referred either to Norway spruce (*Picea abies* (L.) Karsten) and pine stands of northern Europe or to silver fir (*Abies alba* Miller) forest of southern Europe. Furthermore, most of them were conducted in pure stands or artificial plantations. Very little is known about factors affecting disease incidence in mixed and naturally-regenerated alpine forests comprising all the three main hosts of *H. annosum*: pines, Norway spruce and silver fir (KORHONEN and STENLID 1998).

The assessment of economic losses caused by *H. annosum* is a major challenge, and is complicated by both methodological aspects and difficulties in gathering data variables. Therefore, economic losses have been investigated sporadically and with different analytical approaches (PRATT 1998). Estimates of direct losses are generally obtained by assessing the reduction in yield and value of timber due to the rejection of decayed wood. Such estimates have been performed in plantations of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (PRATT 1979), Norway spruce (FEDOROV and POLESHCHUK 1977) and Scots pine (*Pinus sylvestris* L.) (RYKOWSKI and SIEROTA 1984), but they have rarely been conducted in naturally-regenerated or mixed forests.

Models can be useful tools for forest managers as they provide information on the risk of pathogen presence in stands, and consequently they may aid in defining appropriate control measures. This issue is of crucial importance especially for root and butt rots since they are poorly symptomatic diseases. Although comprehensive mechanistic models for simulating the spread of *H. annosum* were developed (WOODWARD et al. 2003; PUKKALA et al. 2005), their application in the Alps is complicated since they currently lack modules simulating the natural regeneration and because there is a general difficulty in collecting data necessary to run the models. There are two further constraints in using the above simulation models in the Alps. First, alpine forests harbour all the three European species included in the *H. annosum* complex, namely *H. abietinum* Niemelä & Korhonen, *H. parviporum* Niemelä & Korhonen and *H. annosum sensu stricto* (*s.s.*) (CAPRETTI 1998; GONTHIER 2010), while these models were tested only for the last two species. Second, the

complex dynamics of disease spread in alpine stands, i.e. infection across root contacts among different tree species and of different age, may lead to distorted simulations. Thus, in this work we constructed a deterministic model rather than a simulation model to be used as a practical tool by forest managers for predicting the disease.

2 Materials and methods

2.1 Study sites, samplings and laboratory observations

The research was carried out in the summers of 2000 and 2001 in 22 naturally-regenerated coniferous forests of Aosta Valley, in the western Italian Alps. Forests were randomly selected among those thinned up to 6 month before samplings. They were located between 1290 and 1975 m a.s.l. and they comprise one or more of the following tree species: Norway spruce, silver fir, larch (*Larix decidua* Miller), Scots pine and Swiss stone pine (*Pinus cembra* L.). The degree of admixture was variable and so was the forest structure, ranging from coetaneous to uneven-aged. The main features of stands are summarized in Table 1.

The detection of butt rots in standing trees usually requires the extraction of wood cores. Such approach is time-consuming and may be ineffective when asymmetric decay is present in the tree. Furthermore, it rarely allows the measurement of the decay extent inside the tree. Thus, recently felled stumps, rather than trees, were inspected and sampled in this study. In each forest, approximately 100 stumps were randomly chosen (Table 1), irrespective of species and size. As thinning intensity was similar across species in the same forest, the relative frequency of selected stumps of either species did not differ from the relative abundance of tree species in the stand (χ^2 tests and contingency tables, p always > 0.12). It was assumed that the selection of thinned trees with reference to butt rot had been random (VOLLBRECHT and AGESTAM 1995). Selected stumps were at least 15 m one from another. A 2-3 cm thick disk was taken 15-20 cm below the top surface of each stump, corresponding to a stump height of about 50 cm. The mean diameter of disks was measured, and the presence of incipient or advanced decay was assessed by visual examination.

In the laboratory the bark was removed from each disk. In order to assess whether decay was caused by *H. annosum*, disks were incubated at 20° C for at least 10 days in plastic bags containing moist paper towels. A dissecting microscope (20x magnification) was used to identify colonies of the pathogen in its anamorphous form (NICOLOTTI et al. 1999). Visible decay associated with the presence of *H. annosum* as well as other colonized areas of disks were measured with a planimeter as previously described (NICOLOTTI et al. 1999). In the absence of visible decay, disks showing *H. annosum* colonies exclusively at their peripheral areas were scored as negative, because we deemed these infections could have originated from airborne spores landed on stumps (NICOLOTTI et al. 1999). A random sample of colonies was isolated as described by GONTHIER et al. (2003) to ensure they truly belonged to *H. annosum*.

2.2 Identification of *Heterobasidion annosum* species

In order to determine which *Heterobasidion annosum* species were present in the stands and to estimate their relative abundance, we investigated the natural airborne inoculum of the fungus through the wood disc exposure method (RISHBETH 1959). With the exception of two sites (i.e., Jovençan A, Valsavarenche), 18 wood discs per forest (11-13 cm diameter and 1 cm-thick) were exposed for 24 h at the beginning of September 2002 according to the experimental design described by GONTHIER et al. (2001). The month of September was preferred for samplings because, in the area, the airborne inoculum concentration of the pathogen consistently peaks in that period (GONTHIER et al. 2005). After one week of incubation at about 24° C, discs were examined for colonies of *H. annosum* as previously described. To obtain information about the pathogen's airspora composition, up to 121 putative single-spore colonies per site were isolated and identified at the species level by the PCR-based assay described by GONTHIER et al. (2003).

2.3 Data collection for modelling

Survey methods adopted in this study were determined by the practical constraints of day-to-day forest management, and had to be limited to collecting data that are generally available to forest managers or are easy and cheap to collect in the field. Thus, possible independent variables were selected (Table 2).

During samplings, stumps were carefully inspected for the presence of *H. annosum* basidiomata and wounds. These data, as well as the species of the stumps, their diameters and geographical positions were recorded in the field by using a GeoExplorer 3 Global Positioning System (GPS) (Trimble). With the exception of elevation, remaining stand variables were gathered from the silvicultural plans (*Piani Economici dei Beni Silvopastorali, Regione Autonoma Valle d'Aosta*). The mean elevation of sampled stumps, based on stump position recorded through GPS, rather than the stand elevation reported in the silvicultural plans was used as an independent variable because the former set of data was deemed to be more precise.

2.4 Data interpretation, statistics, model construction and validation

We assumed disease incidence as a measure of the susceptibility of trees to the disease. The incidence of *H. annosum* butt rots was expressed as the percentage of infected stumps on the total number of stumps examined. Incidence was calculated overall, for each tree species and for each of the following diameter classes: < 20 cm, 21-30 cm, 31-40 cm, > 40 cm.

χ^2 tests and contingency tables, with 5% cut-offs, were used to compare incidence of *H. annosum* butt rots among the different tree species. In order to fulfill the χ^2 assumptions on the minimal number of expected frequencies, data from Scots pine and from Swiss stone pine were pooled together. χ^2 or Fisher exact multiple comparison tests were performed by using Bonferroni's correction. Such analysis was conducted both on the complete dataset and on data of mixed forests.

The analysis of variance (ANOVA) and the Tukey's honestly significant difference (HSD) for unequal N (SPJOTVOLL and STOLINE 1973) were used to compare butt rot incidence among different diameter classes. The normality and the homogeneity of variances were tested by using the Shapiro-Wilk and the Levene's tests, respectively.

Relationship between the percentage of decayed or colonized areas of stumps and the mean diameter of stumps was assessed through the Pearson product-moment correlation test.

A Partial Least Squares Regression (PLSR) was used to determine which independent variables (predictors) and groups of variables (factors) would better describe and predict the incidence of *H. annosum* butt rots (response variable). Predictors examined were the elevation, the exposure, the stump diameter and the diameter at breast height of all species and of a given species, the relative species abundance, the stand volume, the stand density, the harvested volume, the frequency of basidiomata and the frequency of wounds (Table 2). The cases were the 22 forest stands (Table 1). The PLSR achieves the two goals of description and prediction, combining the principal component analysis and the multiple linear regression. The use of PLSR is appropriate in presence of a large set of independent variables showing collinearity (CARRASCAL et al. 2009). In the PLSR, orthogonal factors are extracted from predictors in order to maximize the explained variance of the response variable (CARRASCAL et al. 2009). Each successive factor extracted accounts for a lower proportion of the response variable variance whose sum provides the cumulative variance explained by the model (r^2) (CARRASCAL et al. 2009). PLSR coefficients are calculated for the independent variables in order to predict the response variable (WOLD et al. 2001) using the following formula:

$$\hat{y}_i = \sum_k b_k x_{ik} + b_0$$

where *i* is the index of a case represented by a specific forest, *k* is the index of predictors, x_k are the predictors, b_k are the PLSR coefficients, b_0 is a constant, $\hat{y}_i$ is the predicted response variable.

Q^2 values obtained by using the leave-one-out cross-validation technique allowed an estimation of the predictive ability of models (WOLD et al. 2001). The model with a number of factors resulting in the highest Q^2 was deemed the best one (WOLD et al. 2001) among models built on up to 6 factors. In order to simplify this model, the PLS-VIP (Partial Least Squares - Variable Importance in the Projection) method was employed to identify the least relevant predictors (CHONG and JUN 2005). All the variables resulting in a VIP score < 0.8 (WOLD 1994) were removed from the model (CHONG and JUN 2005).

A simplified model combining the lowest number of predictors and the highest Q^2 was further validated by comparing the predicted and the observed incidence values through the Spearman rank order correlation test on data of 5 additional stands randomly selected in the Aosta Valley Region. Stands were located in the municipalities of Aymavilles, Jovençan, Courmayeur, Brusson and La Magdeleine, and their main characteristics are reported at the bottom of Table 1. The incidence of *H. annosum* butt rots in these additional stands was determined as described above on at least 35 stumps per stand.

All statistical analyses were performed by using PASW Statistics 18 and Systat 13 softwares.

2.5 Economic investigations and parameters

In order to estimate the direct financial losses, we assessed for each forest the current value of retrievable timber and its theoretical value in the absence of *H. annosum* but rots. We assumed that there were no differences in the cost of management of *H. annosum* infected forests and healthy ones. Direct financial losses were calculated with the following formula:

$$DFL\% = \frac{VT_H - VT_I}{VT_H} \cdot 100$$

where VT_H is the theoretical value of timber in the absence of *H. annosum* butt rots and VT_I is the actual value of timber in the presence of *H. annosum* butt rots.

In order to determine the volumes of trees relating to their stump diameters, the volume tables included in the silvicultural plans were used. These tables were fully available for 21 out of the 22 forest stands. The shape and the height of each tree was determined by applying the general equation of the dendrometric solids (LA MARCA 1999), which allows to predict sequential diameters up the stem, and to calculate the incremental volumes of different lengths of timber.

The height of a column of decay was estimated by multiplying the diameter of decay at stump by a fixed ratio (20.5) as used by PUKKALA et al. (2005). The decay column was assumed to be of conical shape. To include stochasticity, the height of the decay column was multiplied by a tree-specific random number with a standard deviation of 25% (PUKKALA et al. 2005). Trees with diameter at breast height smaller than 12.5 cm were discarded as they are worthless and cannot subsequently influence the financial damage.

Based on local market conditions, three assortments were used to calculate the timber value: beams (diameter > 18 cm, length = multiple of 6 m), saw timber (diameter > 30 cm, length = 4 m) and fuel-wood. The market prices have been estimated for each assortment, according to average prices of late 2009-beginning of 2010. Prices ranged from 60 to 137 € m^{-3} for beams, from 50 to 95 € m^{-3} for saw timber and from 16 to 25 € m^{-3} for fuel-wood, depending on species . To simulate real-world conditions, 15% of randomly chosen trees were assumed to be defective, and they were assigned to the production of fuel wood. Volume losses associated with saw were assumed to account for the 3% of the marketable volume.

Two different scenarios were applied to the estimation of losses in yield and value:

i.   in the first scenario we assumed that trees affected by *H. annosum* were assigned to fuel wood regardless of the size of the decay column. This first scenario is a maximum damage scenario (MAX);

ii. in the second scenario, length of stems containing visible and incipient decay were assumed to be cross-cut and uninfected portions sold ordinarily as long as they were of appropriate size. This second scenario is a minimum damage scenario (MIN). In this

scenario we assumed a reduction of 10% in assortment value because of higher

handlings costs.

For each of the two scenarios, a linear regression equation was fitted to the data of butt rot

incidence and financial losses.

3 Results

3.1 Susceptibility to *H. annosum* butt rots

A total of 2,257 stumps were examined. 815 (36.1%) contained advanced or visible incipient decay,

of which 750 (33.2%) were found by inspection to be caused by *H. annosum*. All fungal colonies

isolated belonged to *H. annosum* based on micromorphological inspection. All forest stands were

infested by the pathogen, with levels of disease incidence ranging from 5.8% to 70.9% (Table 3).

Overall, levels of disease incidence differed significantly among tree species ($\chi^2 = 237.3$, d.f. = 3, p

< 0.0001). According to the χ^2 multiple comparison tests, the incidence of *H. annosum* butt rots was

significantly higher in Norway spruce (44.2%) than in the other tree species. Disease incidence in

silver fir (17.6%) did not differed significantly from disease incidence in larch (12.0%), but it was

significantly higher than that observed on pines (5.6%). The incidence of butt rot caused by *H.

annosum* in larch and in pines was not significantly different (p > 0.05). Within mixed stands,

significant differences in terms of disease incidence when comparing species were also observed

(Table 3). Disease incidence in Norway spruce was significantly higher than in the other tree

species in most forests, including silver fir-dominated stands (i.e., Avise).

Data of butt rot incidence were normally distributed ($W = 0.9770$, p = 0.1610) and variances were

homogeneous ($F = 2.6450$, p = 0.0550). Considering all tree species together, butt rot incidence was

similar in each of the four diameter classes ($F = 0.0515$, p = 0.9845). Within Norway spruce or

silver fir, incidence was higher in larger trees, although differences were not significant ($F =

1.6702$, p = 0.1804; $F = 0.5060$, p = 0.6988, respectively). In the case of larch, more small trees

were affected than large trees ($F = 3.8978$, p = 0.0122).

The percentage of decayed or colonized areas of stumps was significantly, but only weakly correlated with the mean diameter of stumps (r = 0.0139, p = 0.0045).

3.2 Species of *Heterobasidion annosum* present

Putative single-spore colonies of all the three species of *H. annosum* were identified in 12 forests (Table 4). Three forests and five forests harboured two and a single species of the pathogen, respectively. *Heterobasidion abietinum* was the most frequent species in the two sites where silver fir was significantly present (i.e., Avise, Pré St. Didier). In all the remaining sites the airspora was dominated by *H. parviporum*, including in stands where the most common tree species was the larch (i.e., Quart, Valgrisenche) and the Scots pine (i.e., St. Nicolas).

3.3 Modelling *H. annosum* incidence

During surveys, only 10 basidiomata were found, and visible wounds were observed on only 2% of sampled stumps. Thus, due to their low frequency, basidiomata and wounds were discarded as possible predictors.

A PLSR model with two factors and a r^2 of 0.7614 resulted in the highest Q^2 value ($Q^2 = 0.4300$) (Table 5, model 1). Nine predictors showed a VIP score < 0.8 and were removed, resulting in a model with 12 predictors (EL, MSD, SDNS, SDL, SDSF, MDBH, DBHNS, DBHL, DBHSF, RSANS, RSAL, DEN) (Table 5, model 2). Subsequent predictors removed were: EL, SDSF, DBHSF, RSAL, DEN (Table 5, model 3), SDL (Table 5, model 4), MDBH (Table 5, model 5). Model 5 was built with MSD, SDNS, DBHNS, DBHL, RSANS as predictors, and showed the highest Q^2 value (0.5970) among the tested models. Model 5 r^2 was 0.7520.

The incidence of *H. annosum* butt rots in stands selected for the validation of the model ranged from 15% of Brusson B to 90% of Aymavilles. The disease incidence was 35%, 40% and 50% in the sites of La Magdeleine, Jovençan B and Courmayeur B, respectively. By running model 5 on

data of the 5 additional forest stands, observed and predicted incidence values were significantly correlated (Spearman R = 0.9000, p = 0.0374).

3.4 Economic losses

1,995 of the 2,257 stumps were from trees with DBH greater than 12.5 cm, and thus saleable. Of these, 66% were Norway spruce, 22% larch and 12% other species.

The marketable volume of all these trees was 1,274 m^3, of which 35% would be sold for beams, 10.3% for saw-timber and 54.7% for fuel wood. The average price for this assortment would have been 58.3 € m^{-3} but the presence of decay depressed the value of this timber to 47.9 € m^{-3} and 38.7 € m^{-3} in the first (MIN) and second (MAX) scenarios, respectively. Thus, the average direct financial losses (DFL%) were 18% and 34% in the MIN and MAX scenarios, respectively.

The relationship between disease incidence and direct financial losses for each of the two scenarios are showed in Fig. 1. Except for the MAX damage scenario in a few sites, the direct financial losses % are lower than the *H. annosum* butt rot incidence. The difference in terms of financial losses between the two scenarios increases with the increase of the *H. annosum* incidence.

4 Discussion

The incidence of root and butt rots has been studied extensively in artificial plantations both in northern and southern Europe, while it has received little attention in mixed naturally-regenerated forests. Our investigation is one of the first and most extensive conducted in such stands in the alpine region.

Heterobasidion annosum has long been regarded as one of the most widespread and pervasive pathogens in alpine forests (BENDEL et al. 2006). *Heterobasidion annosum* was detected as the causal organism in 92% of the 815 trees found to contain butt-rot. Other species known to be implicated as butt rot agents in alpine coniferous stands include *Climacocystis borealis*, *Armillaria* spp. and *Stereum sanguinolentum* (BUTIN 1995; RIGLING et al. 2005).

We found one third of the sampled stumps to be infected by *H. annosum* with disease incidence varying from 5.8% to 70.9% depending on site. These levels are comparable to those reported from the eastern Alps using similar experimental approaches (LA PORTA and PEDRON 2008), suggesting that *H. annosum* is significantly widespread in the whole alpine region.

Comparable information on relative susceptibility of host species can be obtained when observations are made on sites with different tree species on a limited area (DELATOUR et al. 1998), and our sites were ideal for this work. The results clearly indicate that Norway spruce is the most susceptible tree species in the northwestern Italy. This was true not only in spruce-dominated stands, but also in stands comprising or dominated by other species, including silver fir and larch. Our data on the airspora composition suggest that even in these last stands, butt rots on Norway spruce are likely to be caused by the Norway spruce associated species *H. parviporum*.

The second most attacked host was silver fir, confirming observations made in the alpine region by ANSELMI and MINERBI (1989). All these data combined suggest that the susceptibility of fir may be lower in the Alps than in southern Italy, where the fungus has been locally reported from more than 50% of trees (PUDDU et al. 2003). It should be noted that the observed levels of disease incidence on silver fir in our study sites were not the results of a lack of *H. abietinum*, i.e. the *H. annosum*

species specialized on silver fir (CAPRETTI et al. 1990), since that fungal species was significantly present in stands comprising silver fir trees.

On average, larch was 3-4 times less susceptible than Norway spruce. Our results are consistent with those of a previous study conducted in the Alps (BARZANTI and CAPRETTI 1997), but contrast with previous reports from Great Britain (GREIG et al. 2001) and southern Sweden (VOLLBRECHT et al. 1995), showing higher *H. annosum* incidence on larch than on Norway spruce. Interestingly, these reports refer to sites heavily infested by *H. annosum s.s.* Although we did not identify isolates from butt rots in this study, previously published data (GONTHIER 2010) suggest that the large majority of larch trees in the Alps is affected by *H. parviporum* rather than *H. annosum s.s.*, and this is especially true in mixed spruce stands heavily infested by the pathogen. In this study, this observation is further supported by the fact that in several stands characterized by high levels of disease incidence on larch (i.e., Doues, Etroubles, Gignod, Gressoney) the airborne inoculum of *H. annosum s.s.* was either absent or present at very low levels, and the overwhelming majority of spores belonged to *H. parviporum*. Therefore, the different relative susceptibility patterns between the Alps and Great Britain or southern Sweden could be either ascribed to the concomitant presence of a susceptible host (i.e., spruce) and of a well documented specialized pathogen (i.e., *H. parviporum*) in the Alps, or to a lower susceptibility of larch trees to *H. parviporum* than to *H. annosum s.s.* It should be noted that these two hypothesis are not mutually exclusive. Besides, several other factors may account for the lower susceptibility of larch with respect to Norway spruce in the Alps, including its lower growth rate (PETITCOLAS et al. 1997) which has been reported to affect the rate of spread (RISHBETH 1957), and differences in the architecture of the root system between the two host species.

Although the sampling intensity was too low to draw conclusions on the susceptibility of Swiss stone pine, evidence of a low susceptibility of Scots pine to *H. annosum* is presented in this study. This is in agreement with previous reports indicating that Scots pine is only marginally threatened by *H. annosum* in the Alps, at least in naturally-regenerated forests (BARZANTI and CAPRETTI

1997). However, while these reports referred to the most frequent root rot disease leading to tree mortality, in this study we show that Scots pine may be also susceptible of heart and butt rot in the western Alps, which was previously reported as a rare and local phenomenon in UK (GREIG 1995). Overall, the incidence of butt rots was similar in the different tree diameter classes. However, this was the result of contrasting patterns among the different tree species. In silver fir and especially in Norway spruce larger trees were the most attacked. In larch, the opposite was true: an unexpected result since in forest plantations the incidence of butt rot tends to increase with increasing tree age and diameter (THOR et al. 2005).

We did not find any clear relationship between the diameter of stumps and the extent decayed or colonized wood within stumps. The amount of decay within a tree is likely to depend upon several factors, including the host resistance, the virulence of pathogen genotypes, and especially the time elapsed from infection. In uneven-aged forests managed by selective thinning, infection by *H. annosum* may occur continuously through time, and this may explain the lack of relationship described above.

In the PLSR analysis, the relative abundance of Norway spruce (RSANS) and few variables describing the size of trees (DBHNS, DBHL, SDNS, MSD) were the best predictors for the incidence of *H. annosum* butt rots. The tree size is included in several models aimed at predicting the incidence of *H. annosum* at the stand level (THOR et al. 2005; MATTILA and NUUTINEN 2007), and such a trait is consistent with disease dynamics (THOR et al. 2005). It should be noted that the predictors we identified are generally available to forest managers or are easy and cheap to collect in the forest. The best model was successfully validated in the field. However, all the other models we developed were also internally cross-validated, resulting in a good predictive power,

The stand elevation was identified as a relevant predictor for disease incidence only in the first two models (models 1 and 2), suggesting its role might be of limited importance. It should be noted that the relationship between the incidence of *H. annosum* and site elevation has been investigated by several authors, with contrasting results. One group obtained evidence of a decrease of damage with

increasing elevation (MATTILA and NUUTINEN 2007), while the other found positive relationship between the two variables (BENIZRY et al. 1988; THOR et al. 2005).

During field samplings, a few basidiomata of *H. annosum* were found, in spite of the high levels of disease incidence. This observation suggests that estimation of disease incidence based on the frequency of basidiomata, although largely used elsewhere, may not be appropriate in the alpine ecosystem.

We did not find evidence that felling done in the last 25 years played a role in determining current levels of disease incidence, as might have been expected given the knowledge on the infection biology of *H. annosum*. However, in most coniferous forests of the western Alps, the fungus has probably been present for hundred of years permitting tree-to-tree spread across root contacts to dominate over the infection of stumps by basidiospores as the main means by which the fungus spreads in these old forests. This hypothesis is in agreement with recent findings from northern Europe (OLIVA et al. 2010), indicating that it takes a long time for spore infections to transfer into increased rot incidence in forests that also have old infections.

Other factors, such as site history (i.e., forest soil vs former agricultural soil) and soil type (i.e., peat soil vs mineral soil) have been shown to affect the incidence of *H. annosum* (PUDDU et al. 2003; THOR et al. 2005). We believe these factors could significantly account for disease expression also in alpine forests. However, since systematic data regarding site history and soil type are still rarely available and they cannot be derived from most stand record databases in the western Alps, we decided to exclude these parameters from the models.

Average direct financial losses accounted for 18 to 34% depending on assortment criteria. Since the criteria for dealing with butt rot are inconsistent and vary from one logging operation to another (for example by discarding whole trees as opposed to discarding only decayed portions of trees), the average losses sustained in practice probably fall between the two criteria adopted for this study. These differences probably account for the fact that the financial losses we estimated in our minimal damage criteria are comparable to those reported by PRATT (1979) in Sitka spruce

plantations of Great Britain, while our maximum is about twice that value. It has been shown that *H. annosum* is responsible for other losses, by causing for instance a reduction of tree growth (BENDZ-HELLEGREN and STENLID 1997) and a reduction in resistance of stands to storm damages (DIMITRI and TOMICZEK 1998).

In conclusion, our results show that *H. annosum* is very widespread in coniferous forests of western Alps, causing high levels of butt rot incidence especially on Norway spruce. The relative abundance of Norway spruce and variables associated with tree size (DBH and stump diameter) are the best predictors for modelling. While levels of financial losses are comparable or lower than levels of disease incidence, the latter variable is a good predictor for the estimation of direct financial losses. However, since trees with rot in stem, trunk or main roots are more easily windthrown than healthy trees, the pathogen is likely to cause additional, hidden losses by endangering the long-term stability of the forest (VOLLBRECHT and JORGENSEN 1995). We believe the economic losses associated to *H. annosum* in the Alps to be largely under-estimated, since this estimation only deals with timber production, and we expect hidden losses be particularly high in the western Alps since most forests there are protection forests.

Acknowledgements

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Table 1. Main features of forests examined for the presence of *Heterobasidion annosum* butt rots. Forests with codes 1-22 were used for model construction, while forests with codes 23-27 were used for model validation.

Footnotes of Table 1:

[1] only coniferous tree species.

[2] forests used for model validation.

Table 2. Description of independent variables selected as possible predictors of *H. annosum* butt rots.

Footnotes of Table 2:

[1] elevation was calculated as the mean elevation of sampled stumps, details in the text.

[2] exposure North = EXN, exposure East = EXE, exposure West = EXW, exposure South = reference category.

[3] stump diameter Norway spruce = SDNS, stump diameter larch = SDL, stump diameter silver fir = SDSF, stump diameter pines = SDP.

[4] diameter at breast height Norway spruce = DBHNS, diameter at breast height larch = DBHL, diameter at breast height silver fir = DBHSF, diameter at breast height pines = DBHP.

[5] relative abundance of Norway spruce = RSANS, relative abundance of larch = RSAL, relative abundance of silver fir = RSASF, relative abundance of pines = RSAP.

Table 3. Incidence (%) of *H. annosum* butt rots in 22 forest stands of the western Alps. Butt rot incidence on different tree species was compared through χ^2 or Fisher exact multiple tests; within

each stand, values followed by different letters are significantly different after Bonferroni's correction.

Footnotes of Table 3:

[1] this category includes Scots pines and Swiss stone pines.

[2] statistical analysis not applicable.

Table 4. Relative abundance (%) of putative single-spore colonies of *H. annosum* species isolated in the forest stands.

Footnotes of Table 4:

[1] data not available.

Table 5. Summary of the results of PLSR analysis. The response variable is the incidence of *H. annosum* butt rots. For each model PLSR coefficients, r^2 and Q^2 are reported. For predictors acronyms see table 2.

Fig. 1. Relationship between the direct financial losses and the incidence of *H. annosum* butt rots based on data of 21 forest stands in the Aosta Valley, western Alps (F_{MIN} 62.3, $p < 0.001$; F_{Max} 41.7, $p < 0.001$).

Table 1. Main features of forests examined for the presence of *Heterobasidion annosum* butt rots. Forests with codes 1-22 were used for model construction, while forests with codes 23-27 were used for model validation.

Site code and location	Lat-Long coordinates (UTM WGS84)	Exposure	Altitude (m a.s.l.)	Tree species and composition[1] (%)	Forest structure	Other species	Number of stumps sampled
1 Avise	Lat. 5062599 Long. 353922	NE	1327	*Abies alba* (74%) *Picea abies* (17%) *Larix decidua* (7%) *Pinus sylvestris* (2%)	Uneven-aged	*Populus tremula, Betula pendula, Sorbus aucuparia, Fraxinus excelsior*	102
2 Brusson A	Lat. 5067291 Long. 401493	NE	1307	*Picea abies* (61%) *Larix decidua* (20%) *Pinus sylvestris* (19%)	Uneven-aged by groups	*Alnus* sp., *Salix caprea, Betula pendula, Sorbus* sp., *Acer pseudoplatanus*	105
3 Champorcher	Lat. 5053213 Long. 394516	SSW	1290	*Larix decidua* (90%) *Picea abies* (5%) *Pinus sylvestris* (5%)	Even-aged	*Sorbus* sp., *Betula pendula, Alnus* sp., *Salix caprea*	100
4 Cogne	Lat. 5051133 Long. 372587	N	1823	*Picea abies* (65%) *Larix decidua* (29%) *Pinus cembra* (6%)	Irregular	*Vaccinium mirtillus, Vaccinium vitis-idea*	105
5 Courmayeur A	Lat. 5073199 Long. 342971	W	1426	*Larix decidua* (53%) *Picea abies* (47%)	Even-aged	*Sorbus aucuparia, Sorbus aria, Acer pseudoplatanus, Fraxinus excelsior*	101

6 Doues	Lat. 5076040 Long. 367179	E	1774	*Picea abies* (78%) *Larix decidua* (22%)	Irregular	*Juniperus* sp., *Betula pendula, Populus tremula*	102
7 Etroubles	Lat. 5074242 Long. 363234	NE	1473	*Picea abies* (69%) *Larix decidua* (31%)	Uneven-aged by groups	*Salix caprea, Populus tremula, Sorbus* sp.	105
8 Fenis	Lat. 5062255 Long. 381712	NNE	1806	*Larix decidua* (52%) *Picea abies* (48%)	Uneven-aged by groups	*Populus tremula, Sorbus* sp.	109
9 Gignod	Lat. 5071296 Long. 365647	N	1600	*Picea abies* (65%) *Larix decidua* (35%)	Irregular	*Juniperus* sp.	100
10 Gressoney	Lat. 5068466 Long. 408643	NE	1595	*Larix decidua* (42%) *Picea abies* (25%) *Pinus sylvestris* (20%) *Abies alba* (13%)	Uneven-aged	*Alnus viridis, Sorbus aucuparia, Sorbus aria*	102
11 Introd	Lat. 5060523 Long. 356599	N	1522	*Picea abies* (60%) *Larix decidua* (23%) *Abies alba* (13%) *Pinus sylvetris* (4%)	Irregular	*Populus tremula, Betula pendula, Salix caprea*	100
12 Jovençan A	Lat. 5060523 Long. 366380	N	1803	*Picea abies* (84%) *Larix decidua* (11%) *Pinus cembra* (5%)	Irregular to uneven-aged	*Pinus sylvestris, Betula pendula, Salix caprea*	103
13 La Thuile	Lat. 5063617 Long. 340455	NE	1669	*Picea abies* (80%) *Larix decidua* (20%)	Irregular to uneven-aged by groups	*Sorbus aucuparia, Alnus* sp., *Salix caprea*	105
14 Nus	Lat. 5073261 Long. 384432	NW	1643	*Picea abies* (82%) *Larix decidua* (18%)	Irregular to uneven-aged by	*Salix caprea, Alnus* sp., *Sorbus aucuparia*	103

					groups		
15 Pré St. Didier	Lat. 5068841 Long. 343489	NW	1540	*Abies alba* (54%) *Picea abies* (41%) *Larix decidua* (5%)	Uneven-aged	*Alnus viridis*, *Betula* sp., *Acer pseudoplatanus*, *Fraxinus excelsior*	86
16 Quart	Lat. 5069234 Long. 376760	SW	1616	*Larix decidua* (86%) *Pinus sylvestris* (14%)	Even-aged	-	103
17 Rhêmes St. Georges	Lat. 5057760 Long. 357418	NW	1599	*Picea abies* (59%) *Larix decidua* (40%) *Pinus sylvestris* (1%)	Irregular	*Salix caprea*	107
18 St. Nicolas	Lat. 5063981 Long. 357351	E	1291	*Pinus sylvestris* (67%) *Picea abies* (32%) *Larix decidua* (1%)	Even-aged	*Quecus pubescens*, *Prunus avium*	109
19 St. Vincent	Lat. 5068025 Long. 399086	SW	1754	*Picea abies* (72%) *Pinus sylvestris* (16%) *Larix decidua* (12%)	Irregular	*Sorbus aucuparia*, *Populus tremula*, *Betula alba*	102
20 Torgnon	Lat. 5074381 Long. 387932	SE	1975	*Picea abies* (84%) *Larix decidua* (15%) *Pinus sylvestris* (1%)	Irregular	*Sorbus aucuparia*, *Juniperus* sp.	102
21 Valgrisenche	Lat. 5056346 Long. 350210	W	1917	*Larix decidua* (79%) *Picea abies* (21%)	Irregular	*Salix caprea, Alnus viridis*	106
22 Valsavarenche	Lat. 5047063 Long. 360398	W	1740	*Picea abies* (63%) *Larix decidua* (37%)	Uneven-aged by groups	*Betula pendula, Alnus viridis, Salix caprea*	100

23 Aymavilles[2]	Lat. 5060636 Long. 364942	N	1655	*Picea abies* (80%) *Larix decidua* (15%) *Pinus cembra* (5%)	Uneven-aged by groups	*Populus tremula*, *Sorbus* sp.	40
24 Brusson B[2]	Lat. 5068015 Long. 404430	SE	1868	*Larix decidua* (95%) *Picea abies* (5%)	Even-aged	-	40
25 Courmayeur B[2]	Lat. 5072460 Long. 343121	W	1470	*Picea abies* (60%) *Larix decidua* (40%)	Even-aged	*Sorbus aucuparia*, *Acer pseudoplatanus*, *Fraxinus excelsior*	36
26 Jovençan B[2]	Lat. 5062651 Long. 365744	N	1050	*Abies alba* (80%) *Picea abies* (15%) *Larix decidua* (5%)	Irregular	*Sorbus* sp., *Betula pendula*, *Populus tremula*	35
27 La Magdeleine[2]	Lat. 5073130 Long. 392737	W	1600	*Larix decidua* (55%) *Picea abies* (45%)	Irregular	*Sorbus aucuparia*, *Betula pendula*, *Populus tremula*	40

[1] only coniferous tree species.

[2] forests used for model validation.

Table 2. Description of independent variables selected as possible predictors of *H. annosum* butt rots.

Variable	Acronym	Description	Scale	Source
Elevation	EL	Elevation above sea level	m	Survey[1]
Exposure	EX[2]	Main exposure of the stand	N, E, S, W	Silvicultural plans
Stump diameter	MSD	Mean diameter of stumps at about 50 cm	cm	Survey
Stump diameter, species	SD[3]	Mean diameter of stumps of a given species at about 50 cm	cm	Survey
Diameter at breast height	MDBH	Mean diameter at breast height of all species	cm	Silvicultural plans
Diameter at breast height, species	DBH[4]	Mean diameter at breast height of a given species	cm	Silvicultural plans
Relative species abundance	RSA[5]	Proportion of a given species in the stand	%	Silvicultural plans
Stand volume	SV	Total volume of trees in the stand	m^3 ha^{-1}	Silvicultural plans
Stand density	DEN	Number of trees in the stand	n. trees ha^{-1}	Silvicultural plans
Harvested volume	HV	Volume of timber harvested from the stand in the previous 25 years	m^3 ha^{-1}	Silvicultural plans
Basidiomata (frequency)	BAS	Number of stumps with *H. annosum* basidiomata on the total number of stumps examined	%	Survey

Wounds (frequency)	W	Number of stumps with wounds on the total number of stumps examined	%	Survey

¹ elevation was calculated as the mean elevation of sampled stumps, details in the text.

² exposure North = EXN, exposure East = EXE, exposure West = EXW, exposure South = reference category.

³ stump diameter Norway spruce = SDNS, stump diameter larch = SDL, stump diameter silver fir = SDSF, stump diameter pines = SDP.

⁴ diameter at breast height Norway spruce = DBHNS, diameter at breast height larch = DBHL, diameter at breast height silver fir = DBHSF, diameter at breast height pines = DBHP.

⁵ relative abundance of Norway spruce = RSANS, relative abundance of larch = RSAL, relative abundance of silver fir = RSASF, relative abundance of pines = RSAP.

Table 3. Incidence (%) of *H. annosum* butt rots in 22 forest stands of the western Alps. Butt rot incidence on different tree species was compared through χ^2 or Fisher exact multiple tests; within each stand, values followed by different letters are significantly different after Bonferroni's correction.

Sites	Incidence of *H. annosum* butt rots				
	Mean	Norway spruce	Larch	silver fir	pines[1]
1 Avise	24.0	43.8a	-	20.5b	-
2 Brusson A	30.5	36.5a	7.7a	-	14.3a
3 Champorcher	14.9	18.0a	9.7a	-	0a
4 Cogne	22.2	26.5a	7.1a	-	0a
5 Courmayeur A	55.4	76.6a	18.9b	-	-
6 Doues	45.9	54.1a	20.8b	-	-
7 Etroubles	27.6	34.8a	15.4b	-	-
8 Fenis	27.5	34.8a	15.4b	-	-
9 Gignod	42.0	48.8a	11.1b	-	-
10 Gressoney	14.7	22.6a	2.6b	-	-
11 Introd	48.4	56.9a	22.7b	-	-
12 Jovençan A	70.9	71.3[2]	50.0	-	-
13 La Thuile	31.3	39.5a	4.0b	-	-
14 Nus	31.4	35.6a	6.7b	-	-
15 Pré St. Didier	15.9	30.8a	12.5a	13.4a	-
16 Quart	5.8	0a	0a	-	7.8a
17 Rhêmes St. Georges	14.4	16.9a	11.1a	-	-
18 St. Nicolas	28.0	35.7a	-	-	0b
19 St. Vincent	40.8	54.4a	17.6b	-	0b
20 Torgnon	64.7	67.3[2]	0	-	-
21 Valgrisenche	34.0	50.0a	17.3b	-	-
22 Valsavarenche	40.0	45.3a	7.1b	-	-

[1] this category includes Scots pines and Swiss stone pines.

[2] statistical analysis not applicable.

Table 4. Relative abundance (%) of putative single-spore colonies of *H. annosum* species isolated in the forest stands.

Sites	Number of colonies typed	*H. parviporum*	*H. abietinum*	*H. annosum sensu stricto*
1 Avise	121	43.8	46.3	9.9
2 Brusson A	83	91.6	1.2	7.2
3 Champorcher	3	100.0	0	0
4 Cogne	39	89.7	0	10.3
5 Courmayeur A	67	71.6	25.4	3.0
6 Doues	4	100.0	0	0
7 Etroubles	27	100.0	0	0
8 Fenis	72	90.2	5.6	4.2
9 Gignod	43	97.7	2.3	0
10 Gressoney	9	88.9	0	11.1
11 Introd	53	94.3	1.9	3.8
12 Jovençan A	n.a.[1]	n.a.	n.a.	n.a.
13 La Thuile	28	85.7	10.7	3.6
14 Nus	28	100.0	0	0
15 Pré St. Didier	56	30.4	60.7	8.9
16 Quart	55	70.9	1.8	27.3
17 Rhêmes St. Georges	66	78.8	3.0	18.2
18 St. Nicolas	10	80.0	10.0	10.0
19 St. Vincent	106	92.4	1.9	5.7
20 Torgnon	10	100.0	0	0
21 Valgrisenche	115	82.6	14.8	2.6
22 Valsavarenche	n.a.	n.a.	n.a.	n.a.

[1] data not available.

Table 5. Summary of the results of PLSR analysis. The response variable is the incidence of *H. annosum* butt rots. For each model, PLSR coefficients, r^2 and Q^2 are reported. For predictors acronyms see table 2.

	Model 1	Model 2	Model 3	Model 4	Model 5
b_{EL}	0.007	0.007			
b_{EXN}	1.915				
b_{EXE}	-0.047				
b_{EXW}	-3.680				
b_{MSD}	0.789	0.809	1.536	1.438	1.507
b_{SDNS}	0.290	0.241	0.084	-0.043	-0.020
b_{SDL}	0.135	0.115	-0.120		
b_{SDSF}	-0.244	-0.305			
b_{SDP}	0.076				
b_{MDBH}	0.199	0.110	-0.216	0.042	
b_{DBHNS}	0.228	0.147	-0.104	-0.259	-0.210
b_{DBHL}	0.638	0.710	1.247	1.465	1.429
b_{DBHSF}	-0.254	-0.315			
b_{DBHP}	0.017				
b_{RSANS}	0.094	0.102	0.300	0.282	0.267
b_{RSAL}	-0.073	-0.075			
b_{RSASF}	-0.083				
b_{RSAP}	0.057				
b_{SV}	-0.000				
b_{DEN}	0.010	0.015			
b_{HV}	0.009				
b_0	-43.959	-42.886	-50.706	-55.781	-56.656
r^2	0.761	0.748	0.748	0.751	0.752
p	<0.001	<0.001	<0.001	<0.001	<0.001
Q^2	0.430	0.502	0.390	0.542	0.597

Fig. 1.