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Incidence and distribution of *Heterobasidion* and *Armillaria* and their influence on canopy gap formation in unmanaged mountain pine forests in the Swiss Alps

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Abstract

Various disturbance factors on different spatial scales can lead to the creation of canopy gaps in forest ecosystems. In this study, we investigated the role of root rot fungi in the formation of canopy gaps in the Swiss National Park in the Central Alps. Dying or recently dead mountain pine (*Pinus mugo* subsp. *uncinata* trees (n = 172) and saplings (n = 192) from 42 canopy gaps were assessed for Armillaria and Annosum root rot. *Heterobasidion annosum* s.str. proved to be the dominant pathogen and was isolated from 49% of the trees and 64% of the saplings. *Armillaria* was found on 13% of the trees and 20% of the saplings. Three *Armillaria* species, *A. borealis*, *A. cepistipes*, and *A. ostoyae*, were identified. *Armillaria ostoyae* was the most frequent species, accounting for 72% of all *Armillaria* isolates. A total of 31 (74%) gaps were associated with *H. annosum*, and six (14%) with *A. ostoyae*. The remaining gaps were either associated with both pathogens (7%) or with other, unknown, factors (5%). Our findings suggest that the two pathogenic fungi, *H. annosum* s.str. and *A. ostoyae*, are the main reason for the large-scale mortality of mountain pines and the creation of canopy gaps in high elevation forests of the Swiss National Park.

Introduction

Canopy gaps are important structural elements in forest ecosystems that influence their dynamics and diversity (e.g., Liu and Hytteborn, 1991). Since a large proportion of the seedlings and saplings in a forest are often found in such openings, canopy gaps can play a fundamental role in tree regeneration. In general, plant pathogens such as root rot fungi can act as destructive agents that reduce plant fitness, cause mortality, and thereby change the structure and composition of plant communities. At the same time, plant pathogens facilitate successional processes or may help to maintain species diversity (Gilbert, 2002; van der Kamp, 1991). One pathogenic fungus that may cause canopy gaps, *Armillaria ostoyae* has even been considered as a 'rejuvenating factor' (Durrieu et al., 1985).

Armillaria species are important components of the mycoflora in many forest ecosystems worldwide (see reviews in Shaw and Kile, 1991). These species behave as primary or secondary pathogens, causing root and butt rot on a large number of coniferous and broadleaved tree species. All *Armillaria* species can survive saprotrophically on woody substrates, and they produce rhizomorphs. As a saprotroph, *Armillaria* degrades all wood components causing white rot. Several *Armillaria* species act as primary pathogens and can cause significant economic losses by damaging timber.

In forest ecosystems, *Heterobasidion* spp. included in the *Heterobasidion annosum* species complex are also widespread pathogenic fungi (Woodward et al., 1998). These species attack conifers in the temperate and boreal regions of the Northern Hemisphere.

Armillaria predominantly spreads vegetatively via root contacts between healthy and infected roots and via rhizomorphs in the soil, while dispersal by spores is less common (Shaw and Kile, 1991). *Heterobasidion* spreads by both root contact and spore infections (Woodward et al., 1998). As a consequence, *Heterobasidion* mostly forms numerous small genets, whereas *Armillaria* is found to build fewer, but larger genets (e.g., Ferguson et al., 2003; Garbelotto et al., 1999). Through vegetative spread, *Heterobasidion* and pathogenic *Armillaria* species can infect and kill nearby trees, which often results in expanding disease centres (Hodges, 1969; Kile et al., 1991). These disease centres may be limited to a few trees or encompass several hectares (e.g., Garbelotto et al., 1999; Korhonen, 1978; Worrall, 1994). Besides having a high incidence of root rot, canopy gaps caused by root rot fungi are generally characterized by the presence of dead trees that have died at different times, symptomatic trees in various stages of decline, and fallen trees that show evidence of stem or root failure, typically lying with the stems pointing in different directions. The inoculum potential of root rot fungi is typically highest at the margin of these disease centres (e.g., Peet et al., 1996).

The mountain pine (*Pinus mugo* subsp. *uncinata*) is a subalpine pioneer conifer species that occurs in the mountains of western Europe from the Pyrenees to the Central Alps (Dengler, 1992). The tree typically grows on unfavourable or disturbed sites, and has a far-reaching and shallow root system. Some mortality of mountain pines in the Swiss National Park in the Grisons was ascribed to pathogenic fungi. As early as 1932, Gäumann and Campell claimed that *Armillaria* was the reason for the dying of the mountain pines they observed. Relatively high tree mortality, often occurring in clusters, was also reported by Brang (1988) and Hauenstein (1998). Although the exact causes of the mortality were not examined in these studies, Armillaria root rot, bark beetles, and competition have been suspected as possible agents. Only recently, *H. annosum* has been identified as an important cause of tree mortality in this area (Cherubini et al., 2002; Dobbertin et al., 2001). Both pathogens, *Armillaria* and *H. annosum*, were isolated from recently dead mountain pines in a two-hectare study plot in the Swiss National Park. The *Armillaria* species were identified as *A. cepistipes* and *A. borealis* and *Heterobasidion* as *Heterobasidion annosum* sensu stricto (s.str.) (Rigling, 2003). *Armillaria cepistipes* and *A. borealis* are considered to be generally weakly pathogenic (Guillaumin et al., 1993), whereas *H. annosum* s.str. is a serious pathogen, particularly on pine species (Korhonen et al., 1998).

The objectives of this study were: (i) to determine the large-scale occurrence of Armillaria and Heterobasidion root rot in the mountain pine forests of the Swiss National Park, and (ii) to assess the importance of these root rot fungi as driving forces in the formation of canopy gaps.

Materials and methods

Study site

The study area included the almost pure mountain pine forests west of the Ofen Pass in the Swiss National Park (lat. 46°39′N, long. 10°13′E). These forests are found mainly on southern slopes, and extend over an area of approx. 10 km^2 at an altitude between 1800 and 2200 m a.s.l. Other tree species that are admixed in the forests include Swiss stone pine (*Pinus cembra*) and occasionally European Larch (*Larix decidua*) and Norway spruce (*Picea abies*) (e.g., Risch et al., 2004).

The climate in the Swiss National Park is characterized by an annual mean precipitation of 902 mm and an annual mean temperature of −0.1 °C (MeteoSchweiz, measured at the weather station Buffalora situated on the edge of the Park at 1970 m a.s.l.). Since the foundation of the Park in 1914, management activities ceased.

In the mountain pine forests of the Swiss National Park, canopy gaps with a minimum size of 900 m^2 and a maximum of 20% tree cover were previously delineated on aerial photographs (Guthapfel, 2002). A total of 95 canopy gaps were defined, and their areas calculated in ArcMap™ 8.3 (© ESRI Inc. 1999–2002). Among the 95 gaps, 42 were selected for the present study. Permanent openings, in which the rocky substrate conditions

restrict tree growth, were excluded. Gaps smaller than 900 m^2 were not considered in this study because their delineation in the open type of forest found in the Swiss National Park becomes increasingly arbitrary.

Field sampling

In the field, between May and October 2003, the gap edges were defined according to Runkle (1982) by connecting the locations of the stems of living, non-symptomatic trees that had a crown transparency of less than 50%. Crown transparency was estimated by comparing the trees at the edges of each gap with local reference trees that had the maximum amount of foliage under local growing conditions. Crown transparency is expressed as the % reduction in local crown density.

Where present, five trees with stems ≥12 cm dbh (diameter at 130 cm) and five saplings with stems < 110 cm height that were symptomatic but still living (≥50% brown needles) or recently dead were selected within or at the edge of each canopy gap. For each tree, the dbh was recorded, while for the saplings their height was measured. Trees and saplings were examined for the presence of *H. annosum* and *Armillaria* fruiting bodies. Three main roots were excavated from each tree, and one wood core sample was taken from each root at a distance of approx. 20 cm from the stem using an increment borer. The increment borer was sterilized in 70% ethanol and dried with paper towels after each sampling. In most saplings, the whole root system was dug out. In a few larger saplings, three roots were sampled by taking root cores at a distance of approx. 5–10 cm from the stem, as described above for the trees. Wood core samples and excavated root systems were placed in sterile plastic tubes and bags and kept cool until isolation. All samples were processed within 4 days after sampling.

Fungal isolation and identification

Three pieces (about 1-cm long) from each root core sample were surface-sterilized in sodium hypochlorite (active chlorine = 7%) for 30 sec and rinsed twice in sterile, demineralised water for at least 15 sec. The roots of the saplings were thoroughly washed with tap water and three to four discs (5–10 mm thick) were cut from the main roots. After removing the bark, one piece (10×10 mm) was cut from each disc and surface-sterilized as described above. The pieces were dried using paper towels and placed on agar plates (20 g l^{-1} malt extract, 15 g l^{-1} Bacto Agar, 230 mg l^{-1} thiabendazole (added in 1 ml concentrated lactic acid, 85–90%), 100 mg l^{-1} streptomycin, 50 mg l^{-1} polymyxin sulphate, 100 mg l^{-1} sodic benzylpenicillin) modified from Legrand and Guillaumin (1993). This semi-selective medium allows good mycelial growth for both *Armillaria* and *H. annosum* (D. Rigling, M. Bendel, unpublished data). All plates were incubated in the dark at room temperature. After 2–4 weeks, colonies were transferred to malt extract agar (20 g l^{-1} Bacto Agar, 20 g l^{-1} diamalt).

The presence of *H. annosum* was assessed under a dissecting microscope by observing its *Spiniger meineckellus* conidial stage (Worrall and Harrington, 1992). To determine the *Heterobasidion* species (or intersterility groups), one *Heterobasidion* isolate was randomly chosen from each canopy gap (total 41 isolates). The *Heterobasidion* isolates were identified to species level using PCR–RFLP analysis. The ITS region of the isolates was amplified using the primers ITS1 and ITS4. The resulting PCR product was digested with the restriction enzyme *Hin*6I (*Hha*I). Based on sequence data (Kasuga et al., 1993), the use of this enzyme allows differentiation of *H. annosum* s.str. from *H. parviporum* and *H. abietinum*.

The *Armillaria* isolates were identified to species level by diploid–haploid pairings according to the method described by Korhonen (1978), using three haploid tester strains for each of the following species, *A. cepistipes*, *A. borealis*, and *A. ostoyae*. The presence of other European *Armillaria* species in the high elevation forests of the study sites is unlikely because they are reported to be restricted to lower elevation areas in Switzerland (Rigling et al., 1997). No attempt was made to identify other decay-causing fungi growing out of the wood samples.

Data interpretation and statistical analysis

A tree was considered infected only if *H. annosum* or *Armillaria* or both fungi could be isolated from at least one root sample. The presence of rhizomorphs was not regarded as evidence of infection, since rhizomorphs can surround tree roots without infecting them (Gregory et al., 1991).

A canopy gap was considered to be associated with a pathogen if at least 50% of the mountain pines sampled (trees and saplings combined) were infected with either *H. annosum* or *Armillaria* (Table 1). If neither fungus reached 50%, but together they were isolated from at least 50% of the trees, the gap was considered to be associated with both fungi. If less than 50% of the trees were infected with *H. annosum* and/or *Armillaria*, other factors were assumed to be involved in the formation and the enlargement of the canopy gap.

The χ^2-test in contingency tables was used to test the hypothesis that the frequency of infection did not differ between saplings and trees. The Wilcoxon rank sum test was applied to test whether (i) infected and non-infected saplings differed in height, (ii) individual mountain pine trees infected with *H. annosum* or *Armillaria* spp. occurred at different elevations, and (iii) gaps created by *H. annosum* and *Armillaria* differed in size. Statistical analysis of data was performed using R for Windows, version 1.9.1 (R Development Core Team, 2004).

Results

A total of 172 trees and 192 saplings from 42 canopy gaps were examined. Overall, 76% of trees and saplings were infected with *Armillaria* and/or *H. annosum* (Table 2). The incidence of infection was significantly higher in mountain pine saplings than in trees (χ^2-test, χ^2 value = 16.7, d.f. = 1, $p = 0.001$). Both trees and saplings were more frequently infected by *H. annosum* than by *Armillaria*. Only a small percentage of trees were infected with both pathogens. Except for one symptomatic sapling, *Armillaria* was isolated only from dead trees and saplings, whereas *H. annosum* was found on more than half of the symptomatic but still living trees and saplings.

Infected saplings were significantly taller than non-infected saplings (Wilcoxon rank sum test, $p = 0.01$). Trees and saplings infected with *Armillaria* were found at higher elevations than those infected with *H. annosum* (Wilcoxon rank sum test, $p = 0.03$). Among the 71 *Armillaria* isolates, *A. ostoyae*, known as a primary pathogen, was the dominant species and accounted for 72% of the isolates (Table 3). The two mainly saprotrophic species, *A. cepistipes* and *A. borealis*, each accounted for 14% of all *Armillaria* isolates. All trees and saplings were infected with only one *Armillaria* species. In the PCR–RFLP analysis, all 41 *Heterobasidion* isolates tested showed the same restriction pattern as expected from the sequence of *H. annosum* s. str. published by Kasuga et al. (1993). Fruiting bodies of *H. annosum* were found on 13 (10.5%) saplings and on six (5.5%) trees. The fruiting bodies were rather small (0.5–3 cm) and were growing at the stem base of the trees, just below the litter surface. No fruiting bodies of *Armillaria* spp. were observed in the study area between May and October 2003.

The majority of the gaps (74%) were associated with *H. annosum* (Table 4, Figure 1 and 2).

Table 1. Criteria for the classification of canopy gaps

Gap associated with	% mountain pines[a] infected with		
	H	A	Sum
H. annosum (H)	≥50	< 50	≥50
Armillaria (A)	< 50	≥50	≥50
H. annosum & *Armillaria*	< 50	< 50	≥50
Other factors	< 50	< 50	< 50

[a]Trees and saplings combined.

Table 2. Incidence of *Heterobasidion annosum* and *Armillaria* in symptomatic and recently dead mountain pine trees and saplings

Mountain pines sampled	*H. annosum*	*Armillaria*	*H. annosum* & *Armillaria*	Other or no fungi	Total
Trees (≥12 cm dbh)					
Symptomatic	10	0	0	6	16
Dead	74	23	7	52	156
Total (%)	84 (49%)	23 (13%)	7 (4%)	58 (34%)	172 (100%)
Saplings (< 110 cm height)					
Symptomatic	5	1	0	3	9
Dead	117	38	2	26	183
Total (%)	122 (64%)	39 (20%)	2 (1%)	29 (15%)	192 (100%)
Total (%)	206 (57%)	62 (17%)	9 (2%)	87 (24%)	364 (100%)

Table 3. Armillaria species isolated from the roots of symptomatic or recently dead mountain pine trees and saplings[a]

Species	Trees	Saplings	Total
A. ostoyae	18	33	51 (72%)
A. cepistipes	8	2	10 (14%)
A. borealis	4	6	10 (14%)
Total	30	41	71 (100%)

[a]Trees ≥12 cm dbh; saplings <110 cm height.

Five out of six canopy gaps associated with Armillaria root rot were occupied exclusively by *A. ostoyae*. In one *Armillaria* gap, one tree was infected with *A. borealis*, while *A. ostoyae* was isolated from five trees. Only three gaps were associated with both *H. annosum* and *Armillaria* (*H. annosum* occurred in two gaps with *A. ostoyae* and in one gap with *A. cepistipes*). In 20 out of the 31 *H. annosum* gaps, a low incidence (one to three trees infected) of Armillaria root rot was observed (Figure 2). In nine gaps it was caused by *A. cepistipes*, in six gaps by *A. borealis*, and in three gaps by *A. ostoyae*. In two *H. annosum* gaps, two *Armillaria* species (*A. ostoyae* and *A. borealis*, or *A. borealis* and *A. cepistipes*) were found. Individual gaps ranged from 911 m^2 to 10,304 m^2 in size with a mean of 3199 m^2 (median 2447 m^2) (Table 4, Figure 1). *Armillaria* gaps were found to be significantly larger than *H. annosum* gaps (Wilcoxon rank sum test, $p = 0.05$).

Heterobasidion annosum gaps were mainly found in the western part of the study area along the former pass route, which ran from NW to SE crossing the grassland, and in the eastern part of the study area at lower elevations close to today's pass route (Figure 3). Within the eastern part of the study area, *Armillaria* gaps were found at higher elevations than gaps associated with *H. annosum* (Wilcoxon rank sum test, $P = 0.04$).

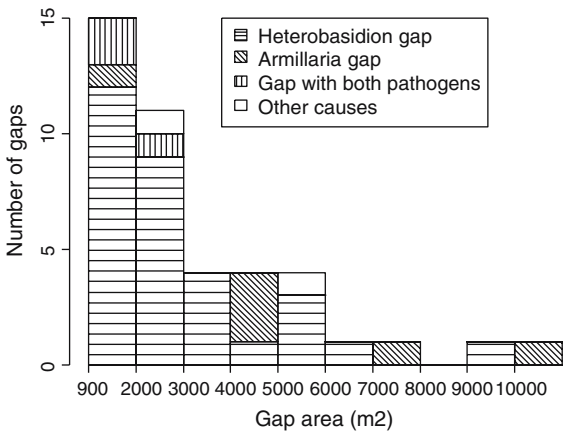

Figure 1. Size-frequency distribution of canopy gaps ($n = 42$) in the mountain pine forests of the Swiss National Park.

Discussion

The root rot fungi *Heterobasidion annosum* s.str. and *Armillaria* spp. occur over a large spatial area in the mountain pine forests of the Swiss National Park and are a major cause of tree mortality. Approx. 75% of the sampled symptomatic or recently dead trees and saplings within or at the edge of canopy gaps were infected with *H. annosum* and/or *Armillaria*. *Heterobasidion annosum* was the dominant pathogen on both trees and saplings. Both pathogens were found significantly more often on large compared to small saplings. This suggests that the sapling root system needs to attain a certain size before becoming infected. Competition for light and nutrients or trampling by red deer may be more important death factors than root rot pathogens for small saplings.

The reason why *H. annosum* is so widespread in the area is not yet fully understood, but it may be due to intense logging in the past. Mining activities in this area between the 14th and 17th century

Table 4. Characteristics of canopy gaps associated with *Heterobasidion annosum* and/or *Armillaria* in the mountain pine forests of the Swiss National Park

Gap associated with	*n*	%	Mean elevation (m a.s.l. ± S.D.)	Mean area (m^2 ± S.D.)	Median area (m^2)
H. annosum	31	74	1982 ± 74	2898 ± 1898	2428
Armillaria ostoyae	6	14	2044 ± 101	5281 ± 3141	4695
H. annosum + *Armillaria* spp.	3	7	1956 ± 72	1813 ± 445	1837
Other factors	2	5	2122 ± 43	3705 ± 2151	3705
Total/mean/median	42	100	1996 ± 83	3199 ± 2195	2447

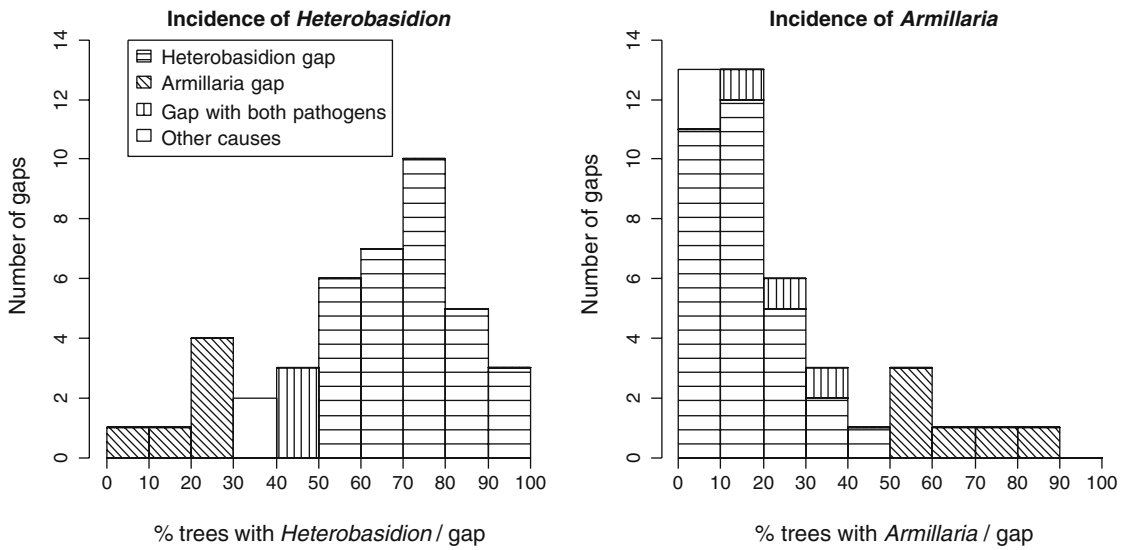

Figure 2. Incidence of *Heterobasidion annosum* and *Armillaria* in canopy gaps (n = 42) associated with either or both root rot pathogens in the mountain pine forests of the Swiss National Park.

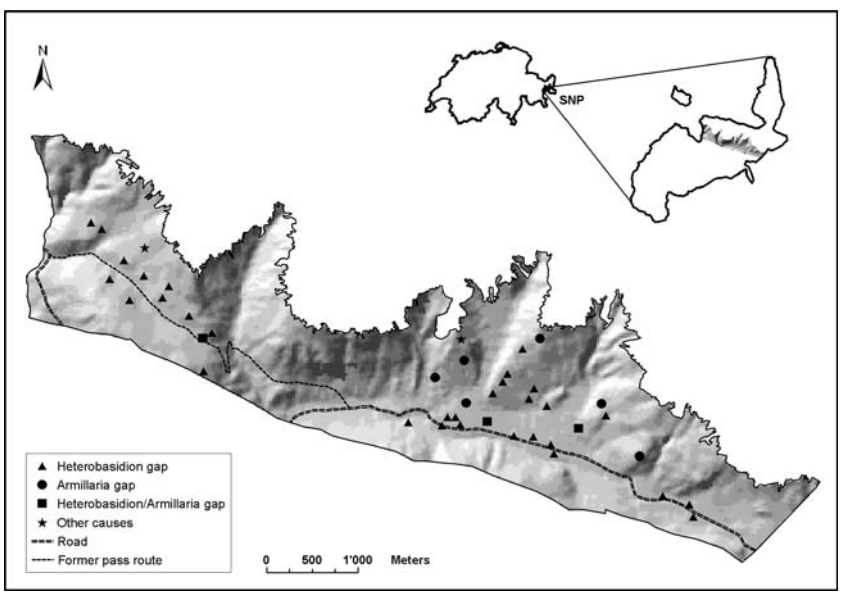

Figure 3. Spatial distribution of canopy gaps associated with *Armillaria* and/or *Heterobasidion annosum* in the mountain pine forests of the Swiss National Park (SNP). Sources: borderline, GIS-SNP, unpublished material; DHM25©1994 Bundesamt für Landestopographie.

required timber and fuel and led to the first significant human-induced changes in the forests. A second important influence was the intensive logging carried out between the 17th and 19th century (Parolini, 1995). *Heterobasidion annosum* may have spread through spores infecting stumps and then become widely established in the forests. After the widespread clear-cuts, it was mainly mountain pines that were able to quickly establish on the rocky limestone soils. The trees developed to relatively even-aged stands, which today represent the dominant forest type in the Park, with the *Erico-Pinetum montanae* being the dominant forest association. The homogeneous stands further favoured the spread of root rot fungi via root contacts. A reason for trees and saplings infected

with *H. annosum* being found at lower elevations than those infected with *Armillaria* might be related to differences in former forest management, as 'lower elevations' coincide with 'proximity' to the pass route. Historically, forest patches located in these areas were logged more intensively, which favoured the dispersal of *H. annosum* through spore infection of stumps.

A promoting effect of past forest management on the current incidence of *Heterobasidion* was also shown by Slaughter and Rizzo (1999) in forest stands of California. These authors suggested that the numerous stumps created by management activities in the first half of the 20th century probably favoured the establishment of *Heterobasidion* through primary infection of the stumps with basidiospores. The pathogen then spread from the initial infection points to the surrounding forests and created numerous gaps in the forest (Slaughter and Rizzo, 1999).

Two recently dead Swiss stone pine (*Pinus cembra*) saplings (26 and 50 cm height) were found in our study, and both were infected with *H. annosum* s.str. (not shown). Only recently has it been reported that *Heterobasidion* spp. can infect this tree species (Gonthier et al., 2003). The isolation of *H. annosum* from two saplings proves the ability of the fungus to also infect and kill regenerating Swiss stone pines under natural conditions. While *H. annosum* kills saplings of both *P. mugo* and *P. cembra*, symptoms in adult trees seem to be different. In adult *P. cembra*, *H. annosum* and *H. parviporum* are reported to cause butt rot (Gonthier et al., 2003), compared to mountain pine where *H. annosum* causes root rot and mortality. The incidence of butt rot is an unusual characteristic in pines; however, it is also known from *P. sibirica*, which is closely related to *P. cembra* (Gonthier et al., 2003).

Although *Heterobasidion* can readily produce fruiting bodies on infected host tissues, we observed them only on a limited number of trees and saplings. *Armillaria* fruiting bodies were reported to be rare in this area (Favre, 1960), and during our field work, no *Armillaria* fruiting bodies could be found. The scarcity of *H. annosum* and the lack of *Armillaria* fruiting bodies can be attributed to the low precipitation and the cold climate of the study area.

Most of the canopy gaps studied were associated with *H. annosum*. These canopy gaps were concentrated in the western part of the study area where the former pass route ran, and in the eastern part at lower elevations along today's and the former pass route. This pattern of *H. annosum* gaps might be attributed to the past human activities in the area that favoured the establishment of *H. annosum* close to the pass route where trees were cut more frequently. Gaps associated with *Armillaria* were all found in the eastern part of the study area, and were concentrated at higher elevations. All these gaps were associated with *A. ostoyae*, a well-known pathogen of conifers in forest ecosystems (Durrieu et al., 1985; Guillaumin et al., 1993). Interestingly, *A. ostoyae* was not found in a previous study conducted on a smaller scale in the area (Rigling, 2003). The other two *Armillaria* species, *A. cepistipes* and *A. borealis*, seem to play a minor role in gap formation in our study area, and probably only cause tree mortality as secondary pathogens (Cherubini et al., 2002; Dobbertin et al., 2001). Only two canopy gaps showed low incidence of root disease and were probably associated with other disturbance factors, such as windthrow.

In our study, *Armillaria* gaps were significantly larger than gaps associated with *H. annosum*. Rizzo and Slaughter (2001) found the opposite in canopy gaps in California where the gaps associated with *Heterobasidion* were significantly larger than the *A. mellea* gaps. Large *Armillaria* gaps suggest that *A. ostoyae* has been active in our study area for a longer time than *H. annosum* and maybe was even established before the intensive logging activities in these forests. Some of the large *Armillaria* gaps may have also resulted from smaller coalescing gaps (Rizzo and Slaughter, 2001).

The strong positive skewness of the gap-size distribution we found, with a few large and many small canopy gaps, is a common phenomenon in coniferous forests (e.g., Liu and Hytteborn, 1991; Rizzo and Slaughter, 2001). In our study, the minimum gap size mapped was 900 m^2, which, compared to other studies, represents a relatively large area. But the mountain pine forests in the Swiss National Park are rather open, so that the delineation of the numerous smaller canopy gaps on aerial photographs becomes increasingly subjective and would have required very detailed maps of the areas similar to those used by Rizzo and Slaughter (2001).

Generally, assigning the causes of canopy gaps is often a rather subjective process. Defining gap causes was not always unambiguous in our study, as we only used the criterion of a high incidence of root disease. With a few exceptions, however, most gaps were also characterized by a large amount of standing or lying dead wood in different stages of decomposition. This suggests that the trees died at different times over several decades, which is what we would expect in gaps caused by root rot fungi. Only in five gaps, all of which were found in the western part of the study area, were comparatively low quantities of dead wood found. Nevertheless, *H. annosum* was the dominant pathogen in four of these gaps. Two explanations could account for the smaller amounts of dead wood in some gaps: they either represent remnants of former grazing meadows in the forest, or the dead wood was removed before the foundation of the National Park. Gäumann and Campell (1932) reported that people used to cut the standing dead trees in this area. In two of these five gaps, seasonally wet areas could also have played a role in the preservation of the canopy gaps. Regeneration was found to be abundant in almost all canopy gaps and was not a useful criterion for classifying the gaps.

In conclusion, our data suggest that *H. annosum* and, to a lesser extent *A. ostoyae*, are the main reasons for the large-scale mortality of mountain pines and the enlargement of canopy gaps in the Swiss National Park. The large-scale incidence of trees and saplings infected with *H. annosum* is probably related to past human land uses before the foundation of the National Park.

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