

Tree-life history prior to death: two fungal root pathogens affect tree-ring growth differently

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Summary

1 This paper assesses whether tree-ring patterns found in recently dead mountain pines (*Pinus mugo* Turra) infected by *Armillaria* spp. differ from those infected by *Heterobasidion annosum*, and determines whether and to what extent tree rings may be used as indicators of tree-decline history (i.e. tree health conditions in relation to disease history) prior to death.

2 Dendroecological and phytopathological analyses were undertaken in the Swiss National Park. The calendar year of death of the standing dead trees was determined by cross-dating ring-width patterns of dead trees to reference chronologies from living trees. This procedure is not, however, exact as there may be multiple intermittent missing rings.

3 A remarkable discrepancy (up to 31 years) was found between the tree-death year estimated through crown condition assessment (i.e. the presence or lack of green needles) and the date of the outermost tree ring (when tree-ring production ceased). New needles may form and existing ones remain green for some years after the cambium at different heights along the stem has ceased activity and no new wood cells are being formed.

4 Ring-patterns in trees infected by *Armillaria* differ from those in trees infected by *H. annosum*. All dead trees infected by *Armillaria* had a slow growth decrease indicating suppression for several decades, and suggesting that *Armillaria* attacked trees that were already weakened by competition. In contrast, trees infected by *H. annosum* died over a very short period of time, although they may have been infected a long time previously. Nevertheless *H. annosum* seems to infect and kill trees directly, whereas *Armillaria*, at this site, is a secondary pathogen.

5 This study demonstrates that tree rings may be used as indicators of the history of tree decline prior to tree death. However, the history of tree disease is difficult to reconstruct fully, e.g. tree rings do not enable the onset of infection to be dated.

Key-words: dendroecology, discontinuous rings, missing rings, mortality, tree death

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Introduction

In a changing environment, forest ecosystems face changing types and levels of stress. Climatic and anthropogenic stresses may change the composition

and structure of forest ecosystems. Fungal diseases are one of the most frequent causes of tree mortality and play an important part in destabilizing alpine forest stands (Motta & Haudemand 2000). Climatic changes, causing movement or alteration of geographical range of pathogens and hosts, may change the occurrence and intensity of tree diseases. Understanding the ecology of the regeneration, life and mortality of trees is critical in both applied and basic forest ecology. Yet, despite this, a comprehensive understanding of

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processes leading to tree death is lacking (Franklin *et al.* 1987; Pedersen 1998).

Tree-ring records can provide information about the reactions of trees to past environmental stresses (Pedersen 1998), and disturbances (Cherubini *et al.* 1996, 1998, 1999). Dendrochronological techniques have been used to establish the time-since-death of standing dead trees ('snags'). The calendar year of tree death for snags is determined by cross-dating their ring-width patterns to stand ring-width chronologies (Brang 1988; Dynesius & Jonsson 1991; Johnson & Greene 1991; Pedersen & McCune 2002). Tree-ring growth, as an expression of tree productivity, has also been used as an indicator of tree health (Kozłowski *et al.* 1991; Manion 1991). Although controversial, there is some evidence of agreement between abrupt growth reductions and commonly used indicators of tree health, such as crown defoliation (e.g. Innes 1993a,b; Schmid-Haas 1994; Schmid-Haas *et al.* 1997; Solberg 1999; Solberg & Tveite 2000). However, the physiological relationships between light to medium crown transparency and tree-ring growth remain controversial (Innes 1993a; McClenahan 1995), and the value of tree-ring patterns as indicators of tree health is still doubtful.

Fungal diseases affect tree-ring growth via several different processes. Foliar pathogens can reduce the foliage area, thereby affecting the amount of assimilate available for growth (Oberhuber *et al.* 1999; Hansen *et al.* 2000). Shoot and stem pathogens may reduce growth by interfering with the movement of water, nutrients and assimilates in the stem and branches (Frei Raj & Schweingruber 1993; Kaitera *et al.* 1995; Davis *et al.* 1997). Root pathogens disturb the water availability and nutrition of the trees (Joseph *et al.* 1998), thus affecting growth indirectly (Wargo & Houston 1974; Shaw & Toes 1977; Hrib *et al.* 1983; Bendz-Hellgren & Stenlid 1997; Mallett & Volney 1999), and may influence the effects of other diseases on growth (Mallett & Volney 1990). The association between tree condition and growth rates is therefore well known, but it is still unclear whether tree rings may be used as indicators of tree health during disease development.

By measuring the tree-ring widths of recently dead mountain pines (*Pinus mugo* Turra) infected by two different root pathogens, *Armillaria* spp. (in the following referred to as *Armillaria*) and *Heterobasidion annosum* (Fr.) Bref., in an unmanaged subalpine stand, we tested the hypothesis that tree-ring patterns are influenced by fungal diseases in such a manner that they may be used as records of tree vigour prior to death, and that they may therefore be used to reconstruct the disease history. *Armillaria* and *H. annosum* are known to cause root and butt rot in many tree species (Guillaumin *et al.* 1993; Korhonen & Stenlid 1998), either as primary pathogens (Korhonen & Stenlid 1998; Rosso & Hansen 1998) when they infect and eventually kill vigorous trees, or as opportunistic secondary pathogens attacking weakened, stressed or wounded plants. We assessed whether tree-ring patterns differed between pathogens

in order to determine the extent to which these may be used as indicators of the history of declining tree health.

Materials and methods

STUDY SITE

The study site is located within the Swiss National Park, in the Engadine Valley, Swiss Central Alps (lat. 46°39'50" N, long. 10°13'51" E). Stands have not been affected by forestry activities since park establishment in 1914, although previously they experienced several centuries of severe anthropogenic disturbance, mainly from grazing, forest management and logging (Parolini 1995; Hauenstein 1998). The study area is located at an elevation ranging from 1890 to 1907 m a.s.l., in one of the plots of the *Langfristige Waldökosystem-Forschung (LWF)*. The slope (about 11%) is south-exposed and the plot is located on an alluvial fan that contains sediments rich in carbonates. The soil type is a rendzic leptosol. The forest is a pure mountain pine stand, classified as *Erico-pinetum montanae* (Ellenberg & Klötzli 1972), with sporadic *Pinus cembra* L. and *Larix decidua* in the understorey. The meteorological station at Buffalora, located at 2038 m a.s.l., 4 km from the site, recorded average annual total precipitation of 895 mm, with a maximum in summer and a minimum in winter and mean annual temperature of 0.4 °C for the period 1964–98.

PHYTOPATHOLOGICAL ANALYSES

The 2 ha study plot was established in 1995 and a first subsample of 31 recently dead mountain pine trees (called 'Pnz1') was taken in September 1998 with a second subsample of 30 trees ('Pnz2') in September 1999. Tree selection was based on the results of routine forest surveys, recorded in the *Sanasilva Inventory*, a systematic annual assessment of crown conditions in Switzerland, and considered only trees that had died during the 2 years prior to sampling. Root samples were taken from each tree and assessed for root rot fungi essentially as described by Dobbertin *et al.* (2001). Briefly, three main roots near the stem were selected from each tree. Saws and increment borers were sterilized in a solution of 70% ethanol between samples. Small wood pieces taken from root segments or cores were surface sterilized in 7% sodium hypochlorite before placing onto benomyl streptomycin malt agar plates (Maloy 1974), and incubating at 20–22 °C in the dark. The presence of *H. annosum* was recognized by its *Spiniger meinekellus* (Ohlson) Stalpers conidial stage (Worrall & Harrington 1992), whereas *Armillaria* species were identified by their typical hyphal brushes, which appeared on the surface of the wood. Pure cultures of *Armillaria* were isolated from the root samples to confirm their identity and to determine the species of each isolate (Daniel Rigling, unpublished data). A tree

was considered to be infected by *H. annosum* or *Armillaria* if these pathogens were identified on at least one out of the three analysed roots. Trees infected by both pathogens were excluded from further analysis, as were trees that showed visible signs of root rot (decay or discoloration in the root samples) but were uninfected by *H. annosum* or *Armillaria*.

DENDROECOLOGICAL ANALYSES

During 1999, all selected dead trees were sampled for dendroecological analyses. In May, we collected cores from 'Pnz1' trees, as well as from five living trees outside the plot (sample 'L'), whereas 'Pnz2' trees were cored in September. We took cores at two different heights from each tree (1 m and 20 cm) to assess growth rates in the juvenile period. The increment borer was sterilized in 70% ethanol between samples. Cores were mounted on channelled wood, seasoned in a fresh-air dry store for a few months, and then sanded and used for ring-width measurement.

Ring-widths were measured to the nearest 0.01 mm, using the Time Series Analysis Programme (TSAP)-measurement equipment, coupled to a stereomicroscope (60 \times magnification) and software package (Frank Rinn, Heidelberg, Germany). Raw ring-widths of the single curves of each dated tree were plotted, cross-dated visually and then cross-dated statistically by (i) the per cent agreement in the signs of the first-differences of two time series (the *Gleichläufigkeit*), and (ii) Student's *t*-test, which determines the degree of correlation between the curves. Locally missing or discontinuous rings were identified by cross-dating (i) the two tree-ring curves obtained from the same tree, and (ii) the chronologies of different trees. Standard methods were used to build an averaged series (Fritts 1976).

The year of death was determined by identifying the calendar year in which the outermost ring of each tree was formed (Dynesius & Jonsson 1991; Mast & Veblen 1994). We built a mean chronology using two ring-width series obtained from each of the five living trees (sample 'L') growing at the study site. As the site is located in a protected area, sampling was restricted to minimize damage to living trees. We then tried to cross-date the ring-width series of the cores obtained from dead trees, assigning a calendar year of formation to each tree ring, the outermost ring included. However, as a sample of five trees seemed unrepresentative of the stand, we also used two other mountain pine chronologies, the reference mean chronology 'R1' built by Fontana & Brang (unpublished data), and the reference mean chronology 'R2' (Stöckli 1996). These chronologies were built from trees growing under the same conditions as our sample trees, but approximately 200 m from our plot. Cross-dating to the reference chronologies was done visually and also statistically using TSAP (*Gleichläufigkeit* and Student's *t*-test).

Skeleton plots were used to determine stem age and other information on the life history of each tree.

During the skeleton plot analyses (Stokes & Smiley 1968; Schweingruber *et al.* 1990), performed with the help of a stereomicroscope (Wild M3Z Leica, Germany), we recorded the innermost rings (situated immediately next to the pith), the presence of tree rings characterized by crushed collapsed cells and traumatic parenchyma (frost rings, Glerum & Farrar 1966) and the presence of any abrupt growth changes, as well as any trends for slow decreases in growth. An abrupt growth change (AGC) is defined as a sudden change (increase or decrease) in annual increment occurring in the last 30 tree rings formed before tree death, lasting between 1 and 15 years, and differing by at least 40% from the average during the previous same number of years. A slow decreasing trend (SDT) is defined as a decrease in annual increment where no negative AGCs were detected.

Three dimensionless variables were used to characterize growth changes before tree death. The first (w_1-2) was the ratio of the widths of the last ring formed and the preceding ring, which may reflect the season in which the tree died. Ratios were also determined for the average width of the five rings formed before the last ring to the preceding 5 years ($w_2-6/7-11$), and of the 10 rings formed before the last ring to the preceding 10 years ($w_2-11/12-21$). These two variables should capture abrupt changes in radial growth during the 21 years preceding tree death, but exclude potential effects of the season in which the tree died. The two periods (2-6 vs. 7-11, and 2-11 vs. 12-21 years before tree death) were determined based on abrupt growth changes frequently found in the data. We also calculated the mean annual ring width, the variance, and the standard mean of the ring widths over the longest period available for all cores (1941-60).

GROWING SPACE

In order to assess whether competition was the cause of the mortality observed at this site, we calculated the growing space available for each tree. Thiessen polygons can be used to define the potential growing space of trees (Mead 1966). We delineated Thiessen polygons around all trees alive in 1995 using a toroidal edge correction (Dobbertin *et al.* 2001). As the boundary effect diminishes with increasing observations (Kenkel 1988) it should have little impact on our study, with approximately 1800 trees used for the polygon delineation.

STATISTICAL ANALYSIS

We compared the diameter distribution and the Thiessen polygon area of the trees infected by *H. annosum* with those infected by *Armillaria*. As the distributions were not normally distributed (SAS 1989), we applied a Wilcoxon's rank-sum test (also known as Mann-Whitney test) to test for differences between the two groups of trees. The degree of correlation between the ring-width chronologies was determined by the

Gleichläufigkeit, and Student's *t*-test. In order to establish a function that discriminated between trees infected with *Armillaria* or *H. annosum*, we analysed 26 trees in Pnz1 and 22 in Pnz2. A forward selection method was used to select those quantitative variables that revealed differences between trees infected by the two pathogens at a *P*-level of 0.15. The discriminant function used non-phytopathological observations to predict the mortality cause (*Armillaria* or *H. annosum*) of each individual tree. To test the predictive accuracy of this function, Pnz1 was used as a calibration, and Pnz2 as a validation data set, and misclassification rates were calculated for both data sets. Each tree in Pnz2 was classified using a discriminant function computed from the other observations on Pnz1, and this classification was compared with the actual infection

found in the field. For the validation set, misclassification rates were derived assuming a multivariate normal distribution, using a parametric discriminant procedure. Misclassification rates for the calibration set were calculated using a cross-validation procedure. Furthermore, we used Bartlett's modification of the likelihood ratio test (Morrison 1976) to decide if the covariance matrices of the two tree groups (infected by *Armillaria* or *H. annosum*) could be pooled for calculating the squared distance.

Results

Mean ring-width chronologies for all the recently dead trees (two cores of 61 trees) are shown in Fig. 1. Correlation coefficients between the single-core

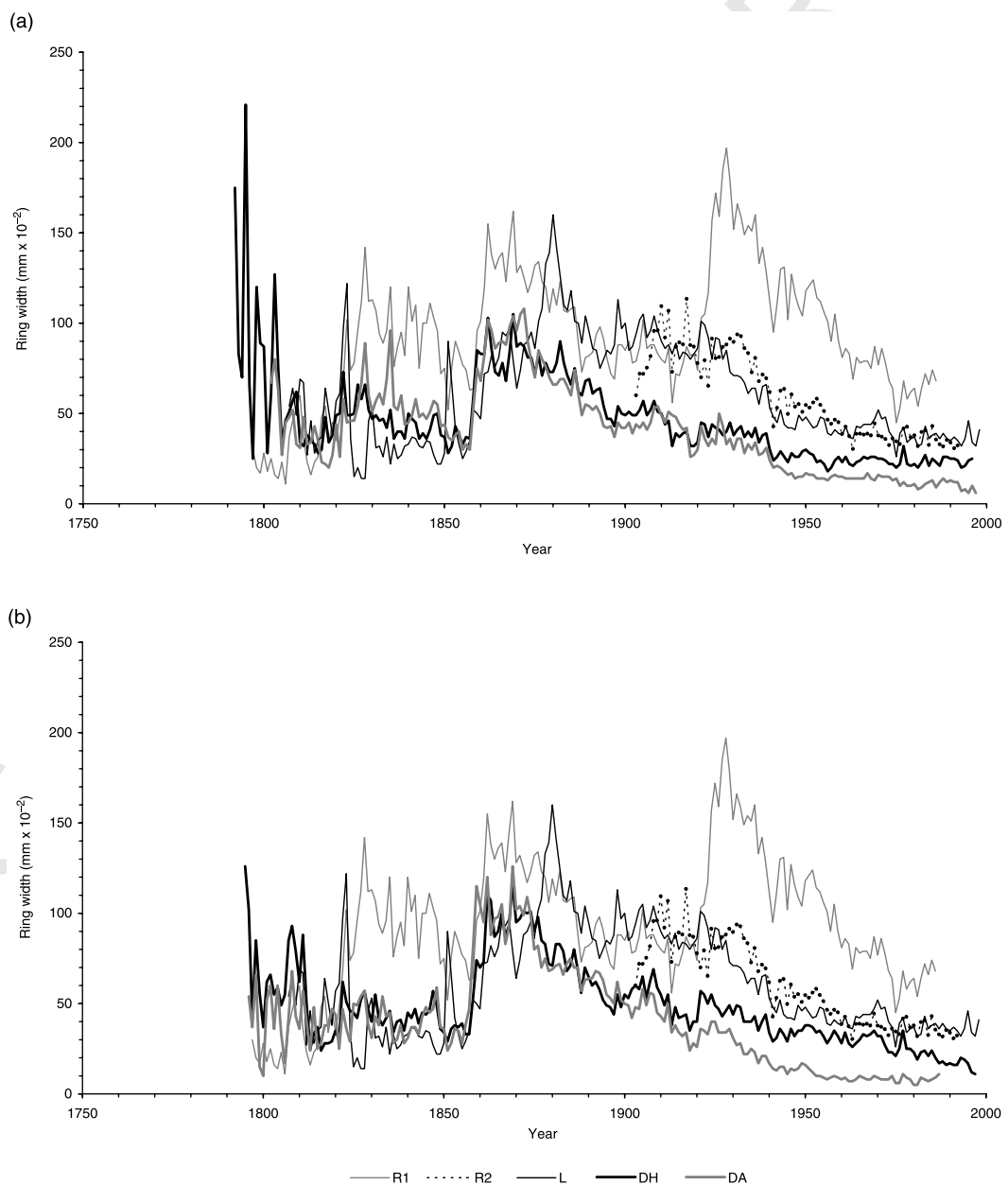


Fig. 1 Reference chronologies (R1 and R2), mean ring-width chronology obtained from living trees (L), and mean chronologies of the dead trees infected by *Heterobasidion annosum* (DH) and by *Armillaria* (DA), for (a) Pnz1 and (b) Pnz2.

5
Tree-life history
prior to death

chronologies and the reference chronologies (Table 1) showed highly significant correlation coefficients ($P \leq 0.001$) for 85 cores (70%). Their chronologies were therefore cross-dated, enabling the year of death to be identified for 58 of the 61 trees. Ten cores (6% of those analysed) were not cross-dated to the reference curves because the statistical correlation values were non-significant.

Armillaria isolates obtained from the root samples of 16 trees were identified to species level. Half the isolates belonged to *A. borealis* Marxmüller and Korhonen, and half to *A. cepistipes* Velenovsky. Because of the small sample size and the fact that both fungi have a similar pathological behaviour (Guillaumin *et al.* 1993), the tree-ring data for both *Armillaria* species were combined.

We built a mean chronology using all dead trees infected only by *Armillaria* (Fig. 1, DA), and a separate one for those infected only by *H. annosum* (DH), in each subsample Pnz1 and Pnz2.

The age structure (Fig. 2) shows no difference between *Armillaria* and *H. annosum* infected trees: in both cases the oldest trees are approximately 200 years old. All the mean chronologies showed an age trend characterized by an abrupt growth increase around 1858 (Fig. 1), with this release from suppression recorded in 51 cores of 32 trees. Comparing growth trends of dead trees with those of reference chronologies built from living trees (L, R1, R2), all dead trees show a more pronounced decreasing recent trend in ring-width.

We found significant correlation coefficients between the mean chronologies and the two reference chronologies R1 and R2. All the chronologies have a similar trend and synchronous pointer years (Fig. 1). The highest *Gleichläufigkeit* (Glk) values with the reference chronologies (Table 2) and with the mean chronology of all the dead trees (Fig. 3) were found for the *H. annosum* mean chronologies. Significant correlation coefficients were found between living (L) and dead

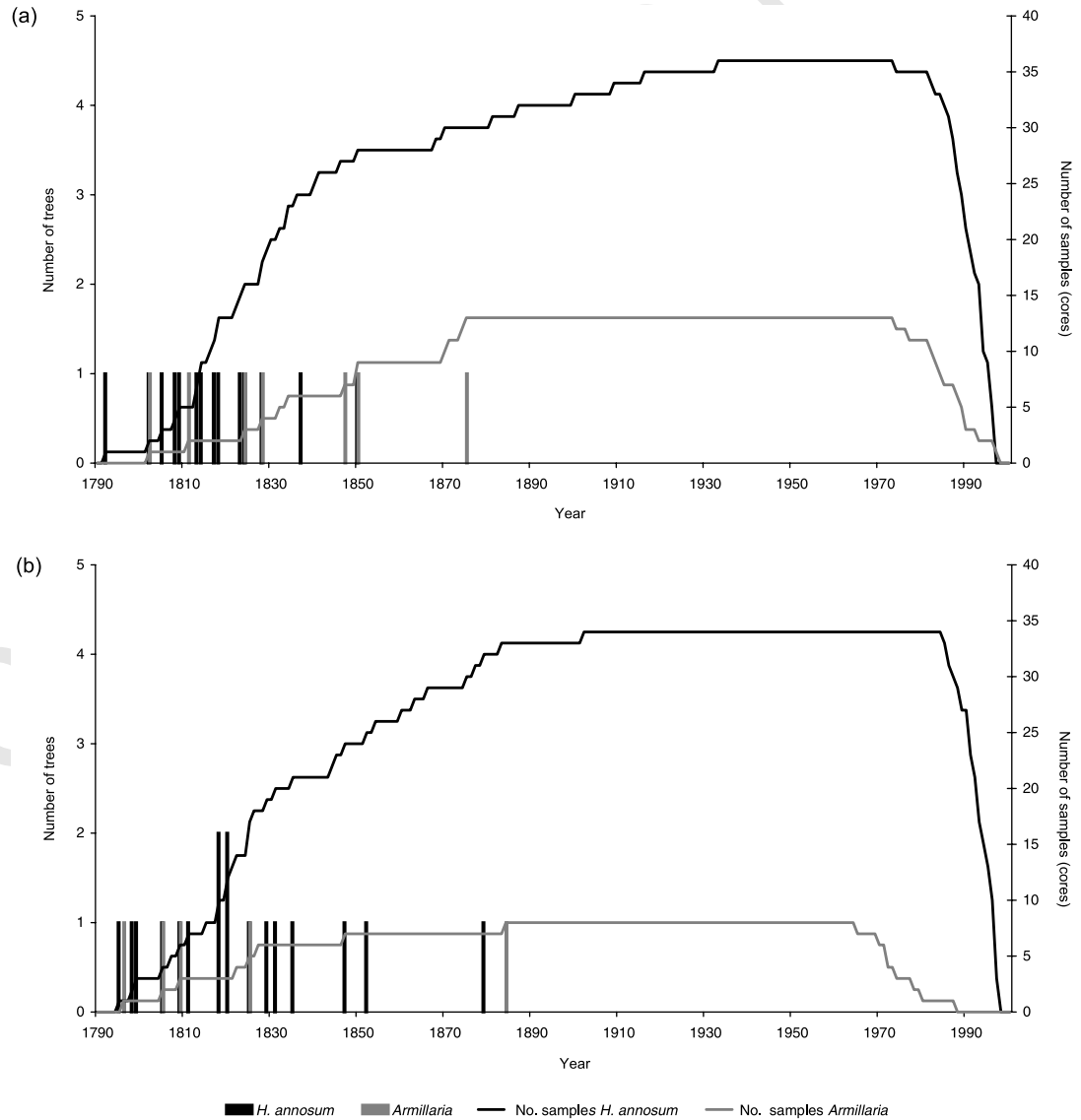


Fig. 2 Age structure and sample depth for (a) Pnz1 and (b) Pnz2.

Table 1 Overview of all the samples used in the study (a) Pnz1 and (b) Pnz2, with the statistical values and results of the cross-dating procedure. The most recent year of formation of the outermost ring was assumed to be the last tree ring formed before death, and defined as the year of tree mortality. The most likely year of death for each tree (considering both of the cores of each tree) is shown in bold. See text for details

(a) Cross-dating statistics (Pnz1)

Pnz1 Tree ID	Core	GLK	GSL	Innermost– outermost ring	F	Pnz1 Tree ID	Core	GLK	GSL	Innermost– outermost ring	F
1300	a	70	***	1830– 1992	H	523	a	58	*	1828– 1989	A
	b	63	***	1828–1989	H		b	67	***	1870–1989	A
1299	a	66	***	1823– 1986	H	5393	a	65	***	1811–1973	A
	b	70	***	1832–1986	H		b	62	***	1832–1997	A
1442	a	74	***	1808– 1994	H	79	a	61	**	1850–1976	A
	b	74	***	1818–1993	H		b	57	*	1850– 1987	A
5150	a	63	***	1836– 1993	H	6081	a	54	*	1847– 1983	A
5343	a	75	***	1841– 1985	H	6162	b	65	***	1874–1981	A
	b	67	***	1814–1982	H		a	68	***	1834–1984	A
1108	a	62	**	1824– 1993	H	964	b	73	***	1802– 1988	A
	b	65	***	1828–1985	H		a	?		?	A
6388	a	67	***	1816– 1996	H	6272	b	65	***	1875– 1982	A
	b	60	**	1809–1993	H		a	64	**	1871–1992	A
1045	a	67	***	1834– 1990	H	5218	b	61	**	1824– 1996	A
	b	64	***	1818–1973	H		a	68	***	1864– 1987	H + A
5556	a	61	**	1805–1991	H	5220	b	73	***	1880–1985	H + A
	b	73	***	1829– 1995	H		a	61	*	1875– 1994	H + A
54	a	76	***	1887– 1993	H	5449	b	67	***	1817–1990	H + A
	b	65	***	1813–1993	H		a	67	***	1835– 1988	?
5893	a	78	***	1909– 1996	H	6010	b	60	**	1844–1988	?
	b	61	*	1900–1996	H		a	63	**	1883–1995	?
5282	a	71	***	1813–1981	H	5680	b	66	***	1901– 1996	?
	b	66	***	1802– 1989	H		a	60	*	1865–1996	?
5130	a	65	***	1881– 1990	H	5750	b	64	**	1878– 1997	?
	b	65	*	1933–1988	H		a	71	***	1869– 1996	?
1505	a	67	***	1822– 1996	H		b			?	?
	b	64	***	1817–1984	H						
750	a	65	***	1834– 1996	H						
	b	63	***	1792–1987	H						
6386	a	63	**	1870– 1989	H						
	b	65	***	1850–1987	H						
5021	a	67	***	1840– 1995	H						
	b	55	*	1814–1995	H						
468	a	58	*	1868–1987	H						
	b	61	**	1846– 1988	H						
5367	a	71	***	1916– 1991	H						

(b) Cross-dating statistics (Pnz2)

Pnz2 Tree ID	Core	GLK	GSL	Innermost– outermost ring	F	Pnz2 Tree ID	Core	GLK	GSL	Innermost– outermost ring	F
603	a	67	***	1820– 1992	H	1452	a	65	***	1822–1971	A
	b	68	***	1875–1991	H		b	70	***	1809– 1973	A
1009	a	64	***	1815– 1992	H	388	a			?	A
	b	63	***	1795–1992	H		b	70	***	1884– 1987	A
992	a	64	***	1807–1996	H	770	a	60	**	1847– 1979	A
	b	73	***	1799– 1997	H		b	68	***	1796–1969	A
1183	a	73	***	1860– 1985	H	1325	a			?	A
	b	72	***	1829–1985	H		b			?	A
1301	a	72	***	1826– 1997	H	488	a			?	A
	b	69	***	1818–1996	H		b			?	A
198	a	65	***	1863– 1992	H	6099	a	71	***	1825– 1977	A
	b	61	**	1847–1988	H		b			?	A
5778	a	66	***	1845– 1997	H	6369	a	65	***	1827– 1971	A
	b	69	***	1835–1996	H		b	64	***	1805–1964	A
5833	a	69	***	1818– 1995	H	5831	a	72	***	1886– 1996	H,A
	b	62	***	1822–1994	H		b	67	***	1889–1996	H,A
6032	a	72	***	1825–1991	H	1096	a	64	***	1832– 1993	?
	b	76	***	1809– 1994	H		b	68	***	1823–1988	?

Table 1 Continued

Pnz2						Pnz2					
Tree ID	Core	GLK	GSL	Innermost– outermost ring	F	Tree ID	Core	GLK	GSL	Innermost– outermost ring	F
6170	a	68	***	1883–1995	H	6333	a	63	***	1829– 1995	?
	b	69	***	1879– 1996	H		b	66	***	1803–1994	?
6387	a	60	**	1852– 1996	H	5564	a	63	***	1841–1987	?
	b	63	**	1902–1996	H		b	66	***	1840– 1993	?
6497	a	60	**	1805– 1990	H	1390	a	71	***	1813– 1966	?
	b	75	***	1866–1988	H		b	65	***	1793–1958	?
5245	a	67	***	1854–1995	H						
	b	71	***	1825– 1996	H						
5615	a	70	***	1831–1984	H						
	b	74	***	1877– 1987	H						
6511	a	72	***	1820–1990	H						
	b	69	***	1825– 1993	H						
6031	a	60	**	1844– 1993	H						
	b	69	***	1811–1990	H						
1121	a			?	H						
	b			?	H						
6209	a	67	***	1821–1986	H						
	b	59	**	1798– 1990	H						

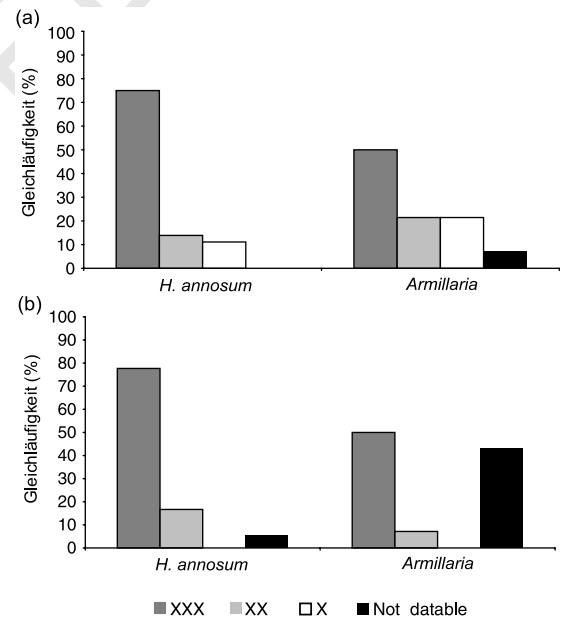
GLK, *Gleichläufigkeit*; F, fungi isolated from the roots; H, *H. annosum*; A, *Armillaria* sp.; ?, root rot detected, but identification of causal agent not successful.

GSL, statistical significance of the GLK: ***99.9%; **99%; *95%.

Table 2 *Gleichläufigkeit* values between the *H. annosum* and *Armillaria* mean chronologies for the sub-samples Pnz1 and Pnz2 and the two reference-chronologies R1 (G. Fontana and P. Brang unpublished data) and R2 (Stöckli 1996)

	Cross-dating values for trees infected by	
	R1 (1797–1986)	R2 (1903–1992)
Pnz1		
<i>H. annosum</i> (1792–1996)	72%	66%
<i>Armillaria</i> (1802–1997)	63%	39%
Pnz2		
<i>H. annosum</i> (1795–1997)	72%	66%
<i>Armillaria</i> (1796–1987)	64%	62%

tree chronologies (Pnz1: 61% Glk 1792–1997, Pnz2: 63% Glk 1793–1997). However, in establishing the calendar year of formation of the outermost ring of the two cores obtained from the same dead tree, i.e. cross-dating the two ring-width chronologies of a single tree, different years were found in 79% of the 61 trees. The difference between the two calendar years of tree death ranged from 1 to 24 years, indicating that, for a period prior to death, ring growth occurred in only part of the tree circumference. The more recent year was assumed to be the last tree ring formed before death, and defined as the year of tree mortality. In the stand, the outermost rings of trees were formed between 1966 and 1997 (Table 1). There was also a marked discrepancy (up to 31 years) between the last

**Fig. 3** *Gleichläufigkeit* values (%) between the single ring-width chronologies of dead trees infected by *Heterobasidion annosum* and by *Armillaria* and the mean chronology of all the successfully cross-dated dead trees for (a) Pnz1 and (b) Pnz2. Statistical significance: ×, 95%; ×, 99%; ×××, 99.9%.

year of ring formation and the date of death as recorded in the visual inventories of crown condition. Usually, the trees still had needles when their cambial activity, as assessed by analysing their tree-ring patterns, had ceased.

The difference in the age of the pith between the 20-cm and 1-m-height cores was also computed. The mean time needed by the trees to reach 1 m height was

Table 3 Mean circumference and polygon area of trees infected only by *H. annosum* and only by *Armillaria*, and Wilcoxon's rank sum test statistics for significant differences between groups

Infection agent	<i>n</i>	Mean circumference (mm)	Mean polygon area (m ²)
<i>H. annosum</i>	37	55.4	13.0
<i>Armillaria</i>	14	46.6	7.1
Wilcoxon's rank sum test		0.025	0.005

Table 4 Coefficients of the function discriminating between trees infected by *Armillaria* and *Heterobasidion*

	<i>H. annosum</i>	<i>Armillaria</i>
Constant	-104.9	-86.0
<i>Gleichläufigkeit</i>	2.5	2.3
w2-6/7-12	24.8	19.5
w2-11/12-21	-10.1	4.8
dbh	1.7	1.3

w2-6/7-12, relation between diameter increment of years 2-6 and that of years 7-12 before the last annual ring; w2-11/12-21, relation between diameter increment of years 2-11 and that of years 12-21 before the last annual ring.

22 years. Frost rings were detected in tree rings formed in 1835 (10 cores), and in 1865 (5 cores).

The proportion of trees with *H. annosum* and *Armillaria* was similar in the two subsamples taken in 1998 and in 1999. The trees infected by *H. annosum* had a significantly higher d.b.h and a significantly larger growing space than trees infected by *Armillaria* (Table 3).

All the cores from trees infected with *Armillaria* showed a slow decreasing growth trend, whereas cores from trees infected with *H. annosum* showed abrupt growth reductions. In the discriminant analysis, the forward selection of variables discriminating between trees infected by *Armillaria* and *H. annosum* resulted in the retention of four variables *Gleichläufigkeit*, w2-6/7-11, w2-11/12-21 and d.b.h. (Table 4). All others showed $P > 0.15$. There was a higher probability of infection by *H. annosum* for trees with higher *Gleichläufigkeit*, higher relative growth in the 10 years before death, i.e. no long-term growth decrease, lower relative growth in the 5 years before death, i.e. abrupt growth decrease prior to death, and higher d.b.h. The most accurate model correctly predicted an *Armillaria* infection in the calibration data set in five out of seven cases (71%), and an *H. annosum* infection in 14 out of 19 cases (74%) with similar success in the validation data set (*Armillaria*-infected trees: four out of five cases, 80%; *H. annosum*-infected trees: 13 out of 17 cases, 76%). In a model with only d.b.h., the portion of correct predictions was slightly lower (Pnz1 71% and 63%, Pnz2 80% and 71%).

Discussion

CROSS-DATING THE DEAD TREES

Dendrochronology is a useful tool for dating the death of trees. At our site it was possible to assign a year of death for all but a few trees. Analysing the curves of single trees, significant correlation coefficients with the reference chronologies were found, enabling cross-dating, and a year of death to be assigned to 58 trees. Significant correlation coefficients were also found between mean and reference chronologies. All these chronologies had similar, synchronous pointer years, indicating a common, site-dependent signal, and validating the cross-dating. We therefore confirm previous observations on the potential use of dendrochronological methods for roughly estimating tree mortality rates for different time spans (Dynesius & Jonsson 1991; Mast & Veblen 1994).

However, the calendar year of formation of the outermost ring often differed markedly for the two cores taken from the same tree. The two cores were taken at different heights, suggesting that tree rings are not formed regularly every year throughout the stem: entire tree rings may be missing, or they may be only partially present.

Discontinuous and missing rings were detected in many samples: trees do not always lay down a continuous sheath of xylem over the entire stem, especially under conditions of environmental stress (Kramer & Kozłowski 1979). Rings are said to be 'missing' if no visible increment was laid down at any point along the circumference at a specific height, and 'discontinuous' or 'partial' if the ring is incompletely formed (Lorimer *et al.* 1999). The frequency of discontinuous or missing rings is higher in suppressed trees than in dominant canopy trees (Tuberville & Hough 1939; Bormann 1965; Lorimer *et al.* 1999). Discontinuous rings are most evident during prolonged periods of suppression (Tuberville & Hough 1939), but they are not uncommon in extremely slow-growing trees in harsh environments (Kelly *et al.* 1992). Asymmetric radial growth of the shoot may be imposed by partial cambial mortality caused by death of a spatially connected sector of the root system, i.e. disruption of the upward movement of water in hydraulically separate sections of the xylem (Larson *et al.* 1993). The number of missing rings in a particular tree will therefore depend on both the duration of the suppressed period and the actual growth rate during the episode (Lorimer *et al.* 1999). In our case, trees, particularly those infected by *Armillaria*, were stressed and suppressed for a long time. The large differences found in the year of formation of the outermost ring on the two cores of the same tree can be explained by the growth behaviour of dying trees, in which radial growth can continue for many years along some sections of the tree's circumference, while other portions are dead as a result of cambial dieback (Daniels *et al.* 1997).

The most recently formed ring in either core represents the best dendrochronological estimate for the year of death, rather than the actual year that the tree died. As already suggested by Mast & Veblen (1994), using dendrochronological methods to determine the date of tree death is prone to some error, mainly because trees may fail to produce complete rings in the last years before death, and death may occur some years after the outermost ring is formed.

Cross-dating the trees, i.e. assigning a year of tree-death to each tree, was inconclusive mainly because of multiple missing rings in the final segments of the cores. If a long trouble-free segment was present at the beginning of the tree-ring series (for example from 1850 until 1960), cross-dating tended to be statistically significant. Even then, however, the final segment may be affected by multiple intermittent missing rings so that the determination of the year of death is impossible. In contrast, other authors have been able to assign a calendar year to the death of trees attacked by fungi (e.g. Davis *et al.* 1997). Lorimer *et al.* (1999) suggest that errors caused by multiple missing rings can often be corrected by cross-dating. However, the later period of suppression usually has multiple missing rings and, because the specific years in which these missing rings occurred were not known and were not necessarily consecutive, it was impossible for a cross-dating program properly to interpret the pattern of peaks and low points during the period of suppression. Mast & Veblen (1994) did not consider samples with fewer than 60 years present because of the possibility of spurious cross-dating from short records. Our results indicate that cross-dating may be inconclusive even for very long ring-width series.

From a methodological point of view, our results show that some ring-width chronologies may not be successfully cross-dated, despite the presence of the same pointer years in different chronologies, leading to incorrect determination of date of death despite high correlation values.

YEAR OF TREE DEATH: SHEDDING OF LEAVES OR CEASING CAMBIAL ACTIVITY?

The discrepancy (1–31 years) found between the year of death estimated through crown condition assessment (i.e. the presence or lack of green needles) and the year of formation of the outermost tree ring in the cores (when the tree-ring production ceased) can be explained by dieback of the tree, or by the fact that green needles may exist for some years after the cambium at different heights along the stem has ceased activity and no new wood cells are formed. There is therefore a difference between the year of cessation of cambial activity and the year of cessation of photosynthesis and other needle activities. *P. mugo* at this site usually maintains needles for 8–10 years before shedding (Dobbertin personal observations), and the crown may survive without new wood formation.

Our observations confirm the hypothesis proposed by Mast & Veblen (1994) that tree-ring production typically stops some (in their study 1–3, in our study probably more) years before actual tree death, as defined by lack of green foliage. Trees appear to survive without forming any new continuous conducting tissue from the soil to the crown, possibly because the tree is still using old conduits. Alternatively water could be supplied by systems other than the stem, but given the low air humidity at our site, it seems to be unlikely that this can contribute sufficient moisture to maintain even a limited number of needles after the supply of water from the xylem has stopped.

TREE-RING PATTERNS AS INDICATORS OF THE LIFE HISTORY OF TREES PRIOR TO DEATH?

The age of the innermost ring on the cores taken at stump height (Table 1) gives an approximate age for each tree, and therefore provides information about its establishment date. The difference between the number of tree rings counted on the two cores from different heights shows that, on average, trees reached 1 m height after 22 years. These juvenile growth-rates suggest low competition for resources among trees. The trees may have established after a clearcut or other disturbance (at this site, probably, fire). Forest management plans and written records for the area confirm both the presence of intense forest management activities and the occurrence of forest fire (Parolini 1995). However, after 1858, the mean ring-width chronologies show a distinct growth release, which may be explained by logging, and this is confirmed by historical sources (Parolini 1995; Hauenstein 1998). As a rule, trees that have become established after clear-cutting do not show any release after suppression in the juvenile period. The presence of growth releases at our site suggests that several trees, removed some time after 1857, survived the stand-initiating disturbance event (probably a fire).

All dead trees show a more pronounced decreasing trend in ring-width patterns than the reference chronologies. This trend reflects long-term increasing stress, probably caused by reduced availability of resources as a result of increasing competition or root infections.

Cross-dating the chronologies of single trees with *H. annosum* and *Armillaria* to the reference chronologies, we found higher *Gleichläufigkeit* values for *H. annosum* than for *Armillaria* infected trees (Fig. 3, Table 4). All the *Armillaria* cores presented a slow reduction in annual growth, whereas c. 60% of the *H. annosum* cores presented an abrupt growth reduction, confirmed by the discriminant analysis (Table 4). The low values of cross-dating tests for the two *Armillaria* mean chronologies are due to the gradual reduction in growth (after 1923 for Pnz1 and after 1913 for Pnz2) prior to death (Fig. 1). Trees infected by *H. annosum* were larger

(Table 3, variable d.b.h. in Table 4), and had more growing space than trees infected by *Armillaria*.

Chronologies of trees infected by *Armillaria* that exhibited a long-term growth decrease were further evaluated for any indication of predisposing conditions or events, such as gradual microenvironmental changes (e.g. increasing competition from neighbouring trees), or as one or more growth shocks due to physical damage (e.g. frost injury) or physiological stress such as drought (McClenahan 1995), a so-called 'inciting' factor *sensu* Manion (1991). Late-frost injury, which triggers frost-ring formation (observed in 1835 and 1865), may render young conifers more susceptible to weakly parasitic fungi than they would otherwise be (Rhoads 1923). Mechanical wounds that may enable pathogen entry are thought to contribute to frost-related incidence of canker in European larch (Day 1931). At our site, a frost event occurred in 1923 (Stöckli 1996) and a subsequent pathogen attack may be a possible explanation for the loss in productivity, as already suggested for other sites (Hrib *et al.* 1983). *Armillaria* attacks were first reported in the Swiss National Park in 1923 (Gäumann & Campell 1932).

Armillaria is one of the most widespread causes of decay and death in trees. The fungus has been described variously as an aggressive primary pathogen of healthy trees, as a secondary pathogen of stressed trees and as a saprophytic decayer of dead trees (Wargo & Shaw 1985; Gregory *et al.* 1991). This behavioural variability was previously ascribed to a single species *A. mellea*, *sensu lato*, but can now be attributed to several closely related, but reproductively distinct, *Armillaria* species (Wargo & Shaw 1985), with differing regional distributions, host ranges and pathogenic capabilities (Guillaumin *et al.* 1993).

In our study, the low cross-dating statistical values found for trees infected by *Armillaria* indicate that these trees were declining for a long time before dying, whereas the higher values found for trees infected by *H. annosum* indicate that this pathogen caused rapid death. Whether the *H. annosum* trees died shortly after being infected or were infected for a long time before a final rapid decline and death is not known. In another study (Vausiliauskas 1999), *P. mugo* was reported to decline slowly over many decades while being infected by *H. annosum*. The slow decline observed for the trees with *Armillaria* could be the cause or result of the infection. Trees with *Armillaria* showed growth habits typical for suppressed trees and were smaller with less growing space than trees infected by *H. annosum*. This suggests that trees infected by *Armillaria* were suppressed while trees infected by *H. annosum* represent the originally dominant trees. This conclusion is further supported by the fact that the two *Armillaria* species identified, *A. borealis* and *A. cepistipes*, are known as saprotrophs or weak pathogens which sometimes attack trees stressed by other factors (Guillaumin *et al.* 1993). The results of this study are consistent with the hypothesis that *H. annosum* acts

as a primary pathogen in this mountain pine forest (Dobbertin *et al.* 2001).

Conclusions

Tree-ring patterns of recently dead trees infected by *Armillaria* are different from those found in recently dead trees infected by *H. annosum*. This indicates that under certain circumstances, tree rings can be used as indicators of the history of tree decline prior to death. Although the year of death could not be determined precisely because of the irregular tree-ring formation shortly before death, tree rings are a useful means of describing mortality patterns, as they provide an important contribution to the understanding of the ecology of pathogen–host systems. However, we stress that the history of tree disease is difficult to reconstruct fully, e.g. tree rings do not enable the onset of infection to be dated.

Tree rings may help us to understand tree senescence and its contribution to mortality. However, a particularly intriguing question remains unanswered: what are the parameters that determine when a tree is dead?

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