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Temporal development of collar necroses and butt rot in association with ash dieback

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In recent years collar necroses and butt rot associated with the ash dieback disease occurred with alarming frequency in *Fraxinus excelsior*. We analysed tree ring structures to identify the year of necrosis initiation on a set of 507 necroses on 155 stem discs from nine severely diseased south-western German stands. The number of first-time infections of trees was highest from 2010 to 2012 and slightly decreased in 2013 and 2014, whereas the total number of newly emerging individual necroses remained high. Logistic modelling of disease progression suggests that collar rot infection has almost reached its maximum incidence and that a fraction of trees will remain healthy at the root collar. On average, *Hymenoscyphus fraxineus* was isolated more frequently from younger collar necroses, whereas older necroses were more often colonized by *Armillaria* spp. Advanced stages of rot that may pose a risk to forest workers, visitors and traffic were observed already in two years-old necroses infected by *Armillaria* spp.

Keywords: Ash Dieback, Collar Necrosis, Disease Progression, *Armillaria*, Butt Rot, Epidemiology

Introduction

Populations of Common ash (*Fraxinus excelsior* L.) and Narrow-leaved ash (*F. angustifolia* Vahl) in Europe are currently devastated by ash dieback, a disease of outstanding severity that strongly impairs the silvicultural utilization of these important broadleaf tree species. The agent of ash dieback is the ascomycete *Hymenoscyphus fraxineus* (T. Kowalski) Baral et al. (syn. *H. pseudoalbidus* Queloz et al.; anamorph: *Chalara fraxinea* T. Kowalski). According to current knowledge, the fungus has been introduced from Far East Asia to Europe about 25 years ago (Gross et al. 2013, Drenkhan et al. 2014). In south-western Germany, first traces of ash dieback have been dated back to the year 2006. Since 2009, the disease is omnipresent throughout this area (Metzler 2010).

Characteristic crown symptoms of ash dieback are necroses on leaves and dieback of shoots. Already in 2005, diseased root collars of ash trees have been reported in combination with crown symptoms of ash dieback, but were assigned to secondary pathogens (Lygis et al. 2005, Skovsgaard et al. 2010, Bakys et al. 2011). Only in 2012, it became clear that *H. fraxineus* can frequently be detected in diseased root collars (Husson et al. 2012).

The path of infection on root collars still remains unknown and it was not yet possible to directly demonstrate that *H. fraxineus* is the primary agent of these symptoms, but there is strong indirect evidence (Chandelier et al. 2016). Potential infection courts for *H. fraxineus* at root collars may be lenticels, as hypothesized by Husson et al. (2012). After successful infection by *H. fraxineus*, the cambium is killed and characteristic, tongue-shaped discoloured bark necroses develop at the root collar. The sapwood proximal to the affected area dies and turns to a darker, brownish colour. Bark cracks become visible within one or two years. Xylem proximal to necroses is colonized by secondary agents that can cause butt and root rot. Very frequent pathogens in this regard are species of honey fungus, mainly *Armillaria gallica* and *A. cepistipes*, but also *A. mellea* and *A. borealis* (Lygis et al. 2005, Bakys et al. 2011, Husson et al. 2012, Enderle et al. 2013, Hauptman et al. 2015, Chandelier et al. 2016, Marçais et al. 2016). In addition, some wood decay fungi of other genera and of minor importance have been reported (Heydeck & Langer 2014, Langer et al. 2015).

Spatial patterns of collar necroses prevalence suggest an influence of site factors and there are indications for a predisposition of humid and wet sites (Husson et al. 2012, Enderle et al. 2013, Muñoz et al. 2015, Marçais et al. 2016). Moreover, there is a genetic component in susceptibility to collar necroses (Muñoz et al. 2015), as previously demonstrated for crown symptoms of ash dieback (McKinney et al. 2014 and references therein, Enderle et al. 2015b). Collar necroses occur more frequently on trees with high susceptibility to crown symptoms, but can also be observed on otherwise healthy trees (Husson et al. 2012, Enderle et al. 2013, Muñoz et al. 2015). Underlying resistance mechanisms of the different symptoms and possible relationships between them are still unknown.

Collar rots can occur in high prevalence, often cause substantial mortality and eventually are the most damaging factor associated with *H. fraxineus* (Husson et al. 2012, Metzler & Herbstritt 2014, Chandelier et al. 2016, Marçais et al. 2016). Root and butt rot reduce the stability of the trees and can be a risk for foresty staff, forest visitors and traffic (Metzler et al. 2013, Kirisits & Freinschlag 2014, Metzler & Herbstritt 2014, Skovsgaard et al. 2017). Collar necroses also occur on narrow-leaved ash (*F. angus-*

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Tab. 1 - Location and characteristics of study sites. (1): According to forestry site maps (InFoGIS / ForstBW); (2): according to documents of local forest authorities or the mean number of year rings at stumps; (3): the number of stumps affected by collar necroses was counted either directly in the stands or on sampled stem discs.

Site	Coordinates	Altitude (m a.s.l.)	Site conditions (1)	Sampling date	Mean diameter	Age (2)	No. diseased (3)	Percentage diseased (3)
AC	48°38′ 01″ N 08°01′ 15″ E	135	Fresh fluvial loam	02.2014	21.8	25	229	77.6
WE	48°13′ 33″ N 07°13′ 50″ E	167	Moist floodplain	10.2014	36.0	45	27	54.0
SE	47°49′ 33″ N 09°31′ 06″ E	560	Marshy lower slope	12.2014	31.6	45	43	89.6
FR	47°53′ 34″ N 09°31′ 55″ E	575	Wet depression	12.2014	58.0	65	11	68.8
SH1	47°37′ 43″ N 07°47′ 24″ E	420	Fresh depression	05.2015	48.0	62	28	50.0
SH2	47°38′ 06″ N 07°50′ 01″ E	450	Humid depression	05.2015	20.0	23	39	78.0
MS	48°22′ 32″ N 09°33′ 53″ E	762	Moderately dry residual material from weathered limestone	05.2015	19.6	32	26	52.0
HS	48°19′ 45″ N 09°19′ 48″ E	750	Moderately dry residual material from weathered limestone	05.2015	15.5	24	48	96.0
TR	48°18′ 28″ N 09°14′ 26″ E	720	Moderately humid residual material from weathered limestone	05.2015	46.2	49	5	25.0

tifolia Vahl – Hauptman et al. 2015).

The aim of this study was to investigate the initiation and progression of this important disease in *F. excelsior* trees and stands, including the time course of the colonization of necroses by wood rotting fungi. The results are expected to provide a basis for decision-making and enhanced disease management in ash stands.

Material and methods

Study sites and sampling

In the context of consulting activities of the Forest Research Institute of Baden-Württemberg, nine pure ash stands with high prevalence of collar necroses have been reported by local forest authorities (Tab. 1). Harvesting operations were carried out shortly before investigation in these stands. Stumps of currently felled trees were investigated with differing intensity as described below. Discolorations of sapwood due to necroses and rots can be easily detected on stumps of recently felled trees (Fig. 1) and allow a more reliable survey of collar lesion prevalence than surveys on standing trees. In total, 155 stem discs with at least one necrosis were selected randomly (Tab. 2) and collected by sawing less than 10 cm above ground. The stem discs were about 4 cm in width.

Dating of collar necroses and reconstruction of prevalence history

The bottom sides of the stem discs were either grinded or planed. The year of necrosis formation was ascertained by analysing tree ring structures under a dissecting microscope. The year of the youngest unaffected tree ring was considered as the year of necrosis initiation. This was done for every individual necrosis separately except for stem discs from stand AC, where only the age of the oldest necrosis was identified per disc. These data and the data of prevalence of collar necroses at the time of sampling (Tab. 1) were used to retrospectively reconstruct the development of collar necrosis infection rate in the stands. A logistic curve was fitted to the mean percentage of infected trees by year of necrosis formation using the none-linear least squares method (R package "car" – Fox & Weisberg 2011). This model has the following form (eqn. 1):

$$y=\frac{\varphi_1}{1+e^{-(\varphi_2+\varphi_3+x)}}$$

where y is the percentage of infected trees, φ_1 is the upper asymptote, φ_2 and φ_3 are growing parameters and x is the year. Logistic models are widely used to describe disease growth in the analyses of plant disease epidemics (Campbell & Madden 1990, Van Maanen & Xu 2003, Nutter 2007). The upper asymptote and the inflexion point of the sigmoid curve can be indicators for the final disease incidence (Holb et al. 2005, Shearer et al. 2007). For a highly susceptible host, the asymptote would be expected to be located at an infection rate of 100 % and the inflexion point at an infection rate of 50 %. The inflexion point of the curve was determined with the R package "inflection" (Christopoulos 2016).

Characterization of collar necroses and rot

Sapwood proximal to necroses usually changes to darker, brownish colour after necrosis formation (Fig. 1a, Fig. 1b), but partly brightens up again with increasing degree of wood decay (Fig. 1c). The activity of certain wood-destroying fungi, *Armillaria* spp. in particular, is also indicated by the presence of demarcation lines in the wood (Fig. 1c).

All stem discs except discs from stand AC were visually categorized according to the proportion of the cross-section area that demonstrated indications of rot by using a ruler. They were divided into the following classes of rot intensity: (0) no indications of rot; (1) rot on less than 20 % of the cross-section area; (2) rot on more than 20 % of the cross-section area. Successful wound closure (Fig. 1e) was also recorded for

Tab. 2 - Number of first-time infections per site and year on 155 investigated trees.

Site	Sum	2007	2009	2010	2011	2012	2013	2014
AC	19	0	0	4	8	7	0	-
FR	11	0	0	0	7	3	1	0
HS	20	0	0	1	6	8	4	1
MS	17	0	0	1	6	4	4	2
SH1	4	0	1	2	0	0	1	0
SH2	6	0	0	2	2	1	1	0
SE	46	0	0	9	19	6	4	8
TR	5	1	0	0	1	1	0	2
WE	27	0	2	9	8	7	1	0
Sum	*155*	*1*	*3*	*28*	*57*	*37*	*16*	*13*
Percentage	*100*	*0.6*	*1.9*	*18.1*	*36.8*	*23.9*	*10.3*	*8.4*

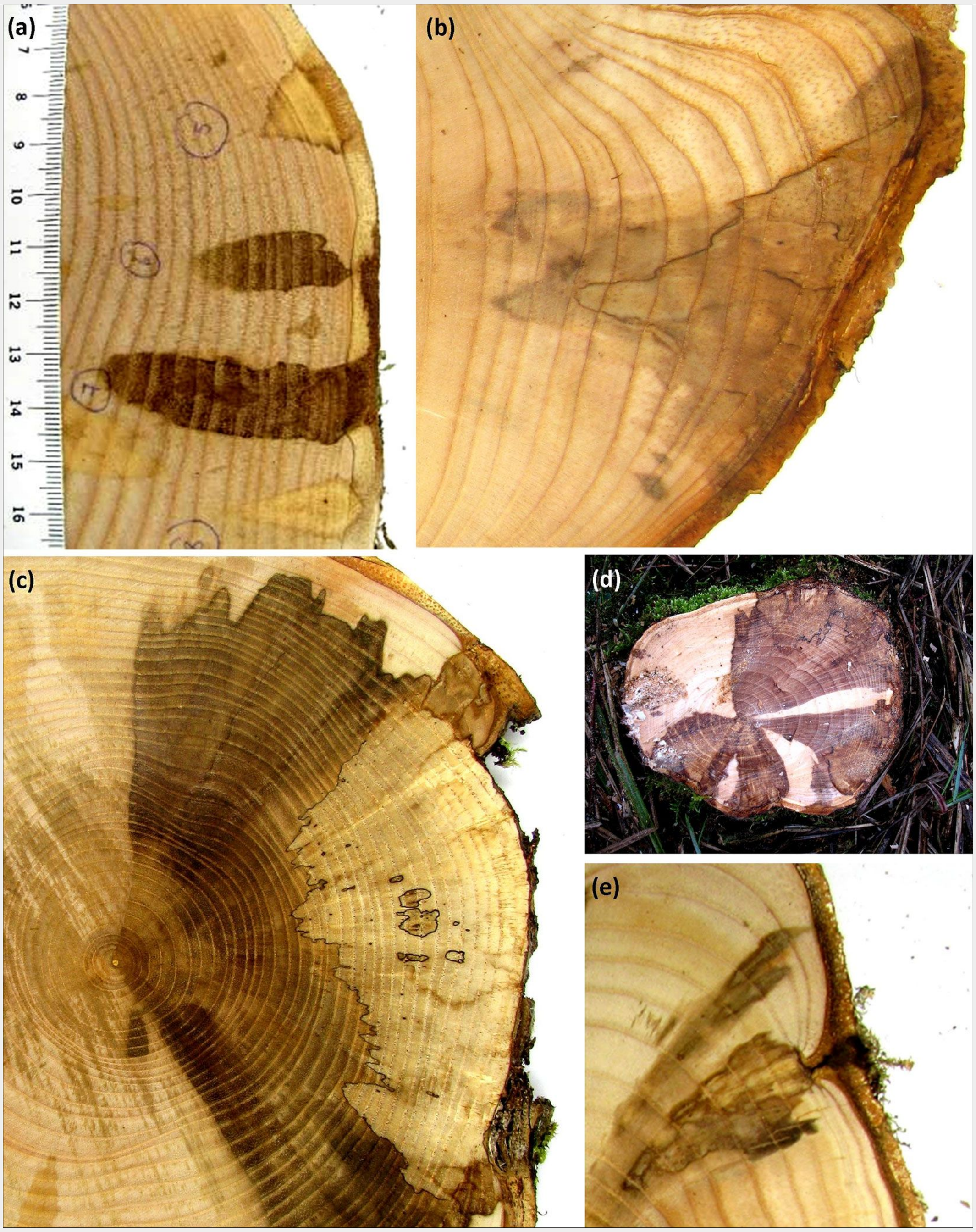

Fig. 1 - Overview of differently developed collar necroses on investigated stem discs. (a): Stem disc with several young necroses; (b): advanced discoloration proximal to a bark necrosis; (c): partly brightening of discoloration due to wood decay and demarcation lines caused by *Armillaria* sp.; (d): severely affected cross section; (e): occasionally, successful wound closure was observed.

these stem discs. For all stem discs that originated from the sites HS, MS, SH1, SH2 and TR, the width of necrosis was measured along the cambium with a tape line.

Occurrence of Armillaria spp., H. fraxineus and other microbes

Necroses with characteristic rhizomorphs and white mycelial fans between bark and wood (*Rhizomorpha subcorticalis*) were classified as infected by *Armillaria* spp. (Garraway et al. 1991). All individual necroses were inspected in this way, except for stem discs from AC and WE. Here, infections by *Armillaria* spp. were documented only on the level of trees. A total of 73 necroses from the sites of HS (37 necroses) and MS (36 necroses) were randomly chosen for isolations of microbes. Xylem not deeper than 2 cm below the cambial necroses was radially split in the lateral advancing zone of the discoloration with a rack and pinion press (Metzler et al. 1993, Metzler 1997). Four specimens per necrosis (292 in total) of about 12 mm^3 were taken immediately from the new, untouched surfaces with a cork borer under sterile airflow. Two specimens per necrosis were placed on synthetic nutrient-poor agar (SNA – Nirenberg 1981) and ash leaf malt agar (Kirisits et al. 2013), respectively, and incubated for three weeks at room temperature. The two culture media were used for a comparison of isolation success. Eight of the resulting *Armillaria* isolates were further analysed by molecular means according to Tsykun et al. (2013) in order to identify the *Armillaria* species.

Results

Development of symptom prevalence

The first collar necrosis in the nine stands developed in 2007 in stand TR (Tab. 2). In stands WE and SH1, first necroses occurred in 2009, in the majority of stands in 2010. In 2011, collar necroses occurred in all stands. The majority of trees were infected in 2011 for the first time at the stem base. In subsequent three years, the number of first-time infected trees decreased. The asymptote of the logistic model was located at y = 65.3, the inflection point at y = 34.2 (Fig. 2), both indicating that final disease incidence will be less than 100 %.

Initially, the temporal development of individual necroses followed a similar pattern and only few necroses occurred before

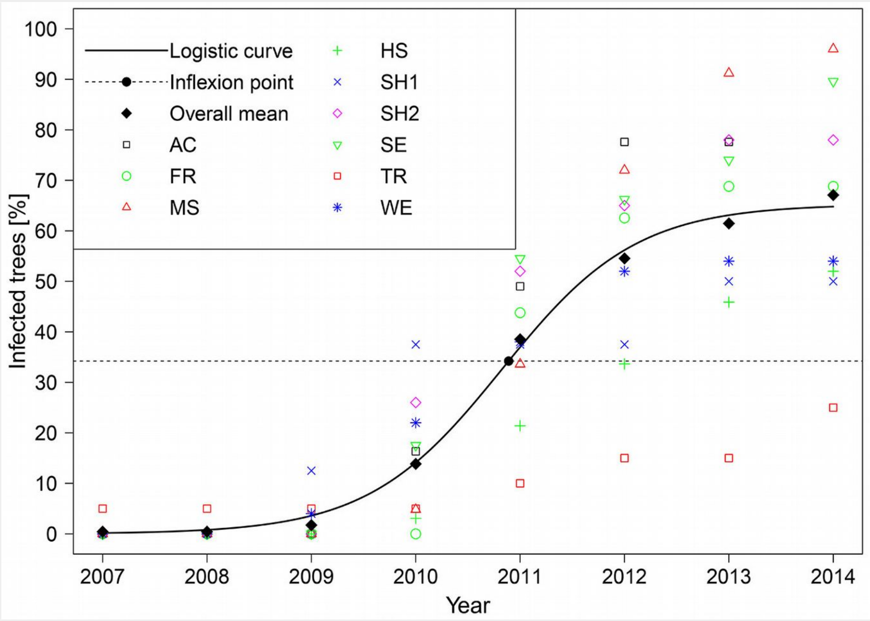

Fig. 2 - Temporal development of the proportion of infected trees in total and per stand, calculated from the year of first infection per tree and the proportion of infected trees at the time of sampling (see Tab. 1). Data for the stand AC ends in 2013.

Tab. 3 - Number of individual necroses and year of their formation.

Site	Sum	2007	2009	2010	2011	2012	2013	2014	Mean no. per tree	Maximum no. per tree
FR	60	0	0	0	13	19	13	15	5.5	12
HS	61	0	0	1	10	18	14	18	3.1	7
MS	51	0	0	1	9	12	13	16	3.0	8
SH1	19	0	1	3	0	1	12	2	4.8	8
SH2	13	0	0	2	4	2	3	2	2.2	4
SE	232	0	0	16	49	33	31	103	5.0	16
TR	12	1	3	1	1	1	2	3	2.4	5
WE	59	0	2	14	12	20	10	1	2.2	5
Sum	*507*	*1*	*6*	*38*	*98*	*106*	*98*	*160*	*3.3*	*12*
Percentage	*100*	*0.2*	*1.2*	*7.5*	*19.3*	*20.9*	*19.3*	*31.6*	*-*	*-*

2010 (Tab. 3). In the years 2011 to 2013, about a fifth of the investigated necroses emerged, respectively. Even more individual necroses occurred in 2014, particularly in the site SE.

Isolates

The results of the isolation experiment are presented in Tab. 4. In total, *H. fraxineus* was isolated 94 times and detected in 58.9 % of the investigated necroses and 67.6 % of the stem discs. There was almost no difference in frequency of detection between the two stands (MS and HS) and the two culture media. *Armillaria* mycelium was isolated from 10 specimens. Bacteria (not further identified) emerged from 88 specimens. A total of 35 isolates were assigned to other fungal species: *Fusarium* sp. (three isolates), *Phialophora* sp., *Cladosporium* sp. and *Acremonium* sp. (two isolates, respectively), *Trichoderma* sp., *Scytalidium lignicola, Exophiala* sp. and *Phoma* sp. (one isolate, respectively) and 22 not identified fungal mycelia. No growth of microbes could be observed on 80 specimens (27.4 %).

Characteristics of necroses of differing age

Infections by *Armillaria* were detected on 58.4 % of the 437 necroses that were tested either by isolation or by observation of characteristic mycelium or rhizomorphs. The temporal development of the colonisation by *Armillaria* spp. is presented in Fig. 3. Only 10.4 % of young necroses that experienced one complete growing season at maximum were infected by *Armillaria*. After two complete growing seasons 79.3 % of necroses were colonized by *Armillaria* and the fungus was observed on 95.8 % of necroses that experienced five complete growing seasons. A Mann-Whitney test for the year of necrosis formation between necroses infected and not infected by *Armillaria* was highly significant ($p < 0.001$). A contrary tendency was detected for the number of *H. fraxineus* isolates (Fig. 4), although the smaller sample number did not reveal significance in this case (Mann-Whitney test, $p = 0.055$). Successful isolation of *H. fraxineus* was particularly high for necroses that experienced only one complete growing season at maximum (78.3 %) and was smaller for older necroses. The pathogen could still be isolated from a necrosis that experienced five complete growing seasons.

The necroses width was significantly correlated with the time of necrosis formation (Spearman correlation, $\rho = -0.661$; $p < 0.001$). On average, older necroses colonized by *Armillaria* spp. were considerably wider than younger necroses. In contrast, such relationship was not evident when only necroses without *Armillaria* infection were considered (Fig. 5). Successful wound closure (Fig. 1e) of individual necroses was observed on 21 of 137 stem discs (15.4%).

Almost one fifth (19.9 %) of the inspected stem discs were assigned to rot intensity class 2 (more than 20 % of the cross-section

Tab. 4 - Number of isolated microbes per site (ME and HS), culture medium and in total and number of individual necroses with respective microbe detections.

Counts	*H. fraxineus*	*A. gallica*	Other fungi	Bacteria	Without growth of microbes
Total no. of isolates	94 (32.2 %)	10 (3.4 %)	35 (12.0 %)	88 (30.1 %)	80 (27.4 %)
No. isolates in ME	42 (29.2 %)	5 (3.5 %)	24 (16.7 %)	49 (34.0 %)	32 (22.2 %)
No. isolates in HS	52 (35.1 %)	5 (3.4 %)	11 (7.4 %)	39 (26.4 %)	48 (32.4 %)
No. isolates on ash leaf agar	45 (30.8 %)	7 (4.8 %)	12 (8.2 %)	44 (30.1 %)	40 (27.4 %)
No. isolates on synthetic nutrient-poor agar	49 (33.6 %)	3 (2.1%)	23 (15.8 %)	44 (30.1 %)	40 (27.4 %)
No. of necroses with isolates	43 (58.9 %)	7 (9.6 %)	24 (32.9 %)	50 (68.5 %)	2 (2.7 %)
No. of stem discs with isolates	25 (67.6 %)	6 (16.2 %)	17 (45.9 %)	31 (83.8 %)	1 (2.7 %)

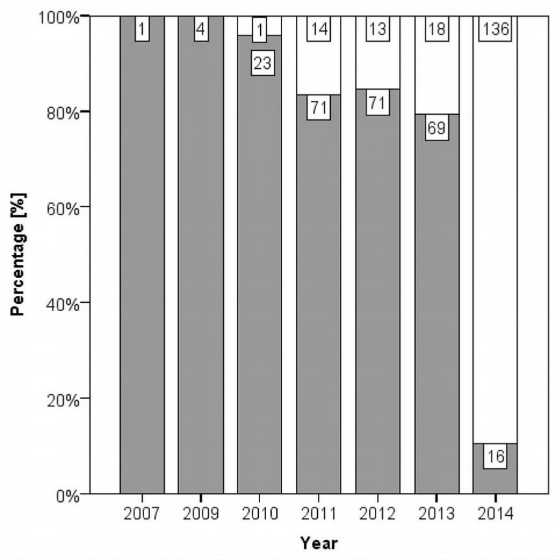

Fig. 3 - Proportion of individual necroses colonized (grey bars) and not colonized (white bars) by *Armillaria* spp. per year of necrosis formation. The number of necroses per category is displayed, respectively. There was no data for necroses from stands AC and WE.

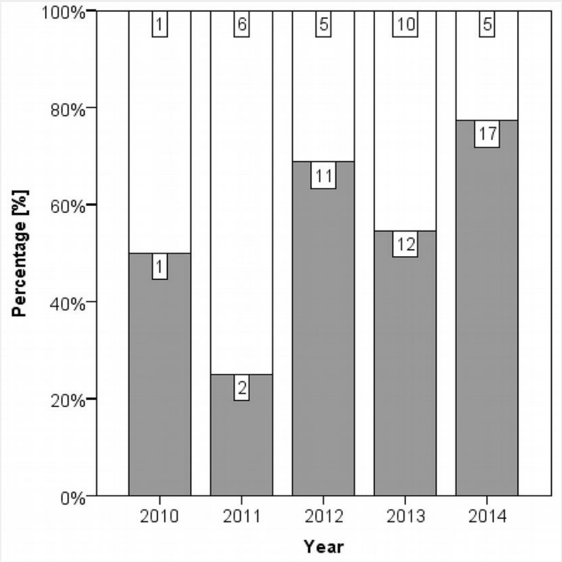

Fig. 4 - Proportion of necroses from stands HS and MS with detection by isolation of *H. fraxineus* (grey bars) and without detection (white bars) separated by year of necrosis formation. The number of necroses per category is displayed, respectively (70 in total).

area). Less pronounced rot was observed on 64.7 % of stem discs (rot intensity 1), whereas 15.4 % of discs showed discoloration but no indications of rot (rot intensity 0). Rot intensity was significantly correlated with the time of first necrosis formation (Spearman, $\rho = -0.420$; $p < 0.001$). Indications for rot occurred on 23.1 % of the discs that did not become diseased before 2014, but were local and all of rot intensity class 1. 81.2 % of stem discs with oldest necroses from 2013 exhibited rot and one disc was even assigned to rot intensity class 2. The proportion of discs with rot intensity 2 increased with the time of infection and reached 41.7 % for stem discs that were infected in 2010 for the first time. Significantly stronger rot intensity (Mann-Whitney test, $p < 0.001$) was observed on stem discs that were colonized by *Armillaria* spp., whereas rot intensity class 2 occurred only once on a disc that appeared

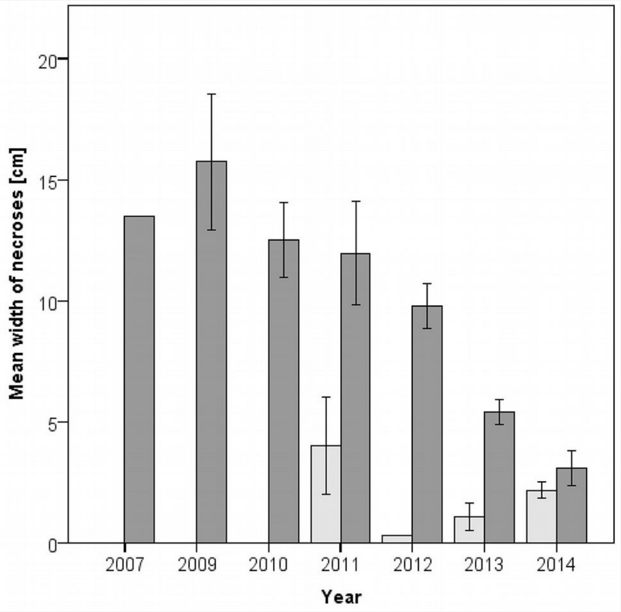

Fig. 5 - Mean width of 151 necroses of different age from stands HS, MS, SH and TR, separated by necroses with (dark grey) and without (light grey) indications of *Armillaria* colonization. Error bars (± standard error) are missing when only one necrosis was present in a category.

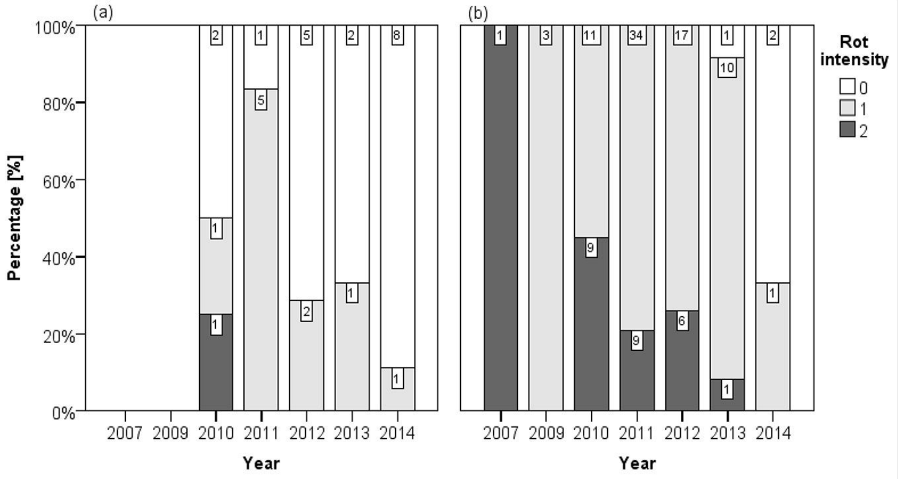

Fig. 6 - Percentage in classes of rot intensity and year of first infection per stem discs without (a) and with (b) indications of colonization by *Armillaria* spp. Rot intensity: (0) no indications of rot; (1) rot on less than 20 % of the cross-section area; (2) rot on more than 20 % of the cross-section area. The number of stem disc per category is displayed, respectively.

to be not infected by this fungus (Fig. 6).

Discussion

The retrospective approach of analysing tree ring structures revealed comprehensive information about the temporal development of collar necroses and butt rot including the colonization by the main pathogens *H. fraxineus* and *Armillaria* spp. New insights about the pathogenesis and recommendations for practitioners can be inferred from these results. In contrast to most other studies, we examined stumps of cut trees. This allowed investigating also young necroses that would not have been detectable on standing trees.

Prevalence of collar necroses and site conditions

The high prevalence of collar necroses in the investigated stands can be explained with their targeted selection. Moreover, it can be assumed that infection pressure by *H. fraxineus* and *Armillaria* spp. is higher in pure ash stands than in mixed stands. According to a representative survey for south-western Germany, ash trees with collar necroses accounted for only 17.5 % of the total ash stock, whereby infection rate decreased with tree age (Enderle et al. 2015a). In this survey on standing trees, however, young necroses were probably not yet detectable.

The locally high frequency of collar necroses suggests site effects for prevalence. Indeed, data of several studies indicate that humid, wet, waterlogging and floodplain sites are predisposing for collar necroses (Husson et al. 2012, Enderle et al. 2013, Muñoz et al. 2015, Marçais et al. 2016). The majority of sites investigated in this study were humid, which supports the above cited findings. However, prevalence was also high in the sites ME and HS, which were categorised as moderately dry. Apparently, there are important factors other than site humidity that influence prevalence of collar necroses. Further studies that include, for example, the influence of tree age, are needed to clarify these very important interdependencies.

Fungal isolates

The method of sterile sampling used for isolation from fresh surfaces is advantageous over surface sterilisation, which can bias the isolation success. *H. fraxineus* was isolated with high frequency. *Armillaria* strains were isolated only scarcely, because specimens were sampled from the margins of discolorations, where the presence of *Armillaria* spp. is rather unlikely. Another study was able to detect *H. fraxineus* in 98 % and *Armillaria* spp. in 41 % of necroses by molecular methods (Chandelier et al. 2016). These necroses did not provide any visual indications for the presence of *Armillaria* spp., and the authors assumed that frequency of this fungus can be underestimated in visual surveys. The two tested culture media (SNA and ash leaf agar) were similar in effectiveness for the isolation of *Armillaria* spp. and *H. fraxineus*. The latter grew faster on ash leaf agar, but phialides, which are important for the morphological identification of *C. fraxinea*, were easier to identify in SNA.

Temporal development of collar necroses and rots

According to the data presented, collar necroses started to become problematic in south-western Germany in 2010, which is four years after the first indications of the presence of *H. fraxineus* (Metzler 2010). Also in France, the first collar necroses occurred later than crown symptoms and several years after the arrival of the pathogen (Husson et al. 2012, Marçais et al. 2016). The year 2011 was an inflexion point, as the number of first-time infected trees decreased in subsequent years (Fig. 2, Tab. 2). In theory, an inflexion point would be expected at an infection rate of 50 % (Nutter 2007) and an asymptote for disease progression at an infection rate of 100% (Neher & Campbell 1992), under the presumption that all individuals will become diseased. Inflexion points at lower infection rates suggest a lower final incidence of the disease (Holb et al. 2005). A similar assumption can be done for the asymptote (Shearer et al. 2007). The observed development suggests that a fraction of trees will remain in healthy conditions. This can be expected when assuming that currently uninfected individuals are less susceptible towards the symptom (Muñoz et al. 2015). Another possible explanation is that the remaining ash trees are growing in micro locations that are not suitable for collar infections. Of course, further monitoring is needed, as the presented time series comprises only few years and is too short for a reliable prediction of future infection development. However, general conditions in the years after 2011 apparently have been favourable to infection, as many collar necroses occurred at already infected trees (Tab. 3). Since most infections likely occur during the main time of sporulation, one may speculate that the high number of emerging individual necroses in 2014 is connected to the extraordinarily high precipitation during summer 2014 in the region: the mean precipitation in the Federal State of Baden-Württemberg was 191.6 mm in July and 115.6 mm in August, according to DWD (the German Meteorological Service).

The more frequent detections of *Armillaria* spp. on older necroses (Fig. 3) and the opposite pattern for *H. fraxineus* (Fig. 4) indicate that the necroses are primarily caused by the latter pathogen (Chandelier et al. 2016). Nevertheless, *Armillaria* spp. play an important aggravating role in this pathosystem. Obviously, necroses infected by *Armillaria* strongly enlarge over time (Fig. 5) and increasingly girdle the root collar, which is crucial for tree mortality. Collar girdling can also occur because of the accumulation of necroses (Marçais et al. 2016). Although other wood decaying fungi can cause rot in ash collar necroses (Heydeck & Langer 2014, Langer et al. 2015), our data demonstrate that extensive rots rarely occur in absence of *Armillaria* spp.

Implications for forest management

In forest management, collar necroses are relevant for two main reasons: (i) they dramatically increase tree mortality; and (ii) they reduce the stability of trees, which can be crucial for the safety of forestry workers, forest visitors and traffic. For timber marketing, collar necroses are of moderate importance, as they affect usually less than 1 m of the basal trunk. The wood quality of the remaining trunk is not compromised, if trees are harvested in time, *i.e.*, before trees have lost more than 70% of the canopy or even have died (Metzler et al. 2013).

In the majority of cases, the anticipated mortality of the next years dictates the need for action in management of ash dieback affected stands. For the assessment of future mortality it is recommended to rate not only crown symptoms. At least on a random sample of trees, root collars should be inspected for the presence of necroses and butt rot, as described by Skovsgaard et al. (2017). Prevalence of these symptoms can change drastically within few years and operational decisions should not be made on a basis of older observations. Rot on more than 20 % of the cross-section area was detected on a necrosis that was only two years old. We estimate that such extent of rot can already be a risk for forest workers and traffic.

Most trees affected by collar necroses are expected to die within a few year and/or their growth performances to be strongly reduced. Such trees should be removed during thinnings similar to trees with strongly defoliated crowns (exceeding 70 % – Metzler et al. 2013, Skovsgaard et al. 2017) in order to minimize risk of accidents. Exceptions may be trees with small, already closed necroses. Trees appearing resistant to the disease, also regarding collar necroses, should be conserved and their regeneration promoted.

The presence of *Armillaria* spp. is not to be expected in afforestation sites where thinnings were not yet conducted. The same likely holds for solitary trees, *e.g.*, in parks or alongside roads. Under these circumstances, the situation of collar necroses can be considered much less severe. In the absence of *Armillaria* spp., rot was observed only rarely and only on several years old necroses.

Conclusions

Dating the time of collar necrosis formation by tree ring analyses revealed a typical sigmoid disease progression in a set of 155 trees from nine south-western German severely infested stands. Modelling of disease progression suggests that comparatively few trees will become first-time infected in the future and a fraction of trees will not become affected by collar necroses in the long term. However, future monitoring of disease incidence is necessary to confirm these results. The data supports the hypothesis that *H. fraxineus* is the major agent of collar necroses in ash, although *Armillaria* spp. play an important aggravating role. Ash trees colonized by *Armillaria* spp. begin to pose risks to forestry staff and forest visitors within two years after necrosis formation. Five years after necrosis formation, 41.7 % of the affected root collars exhibited decay to a degree which we assume to be potentially hazardous.

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