



# Orman Fakültesi Dergisi

Seri : A

Sayı: Özel Sayı

Yıl : 2009

ISSN: 1302-7085



Faculty of Forestry Journal  
Süleyman Demirel University



ISPARTA

Guest Editor

H. Tuğba DOĞMUŞ-LEHTIJÄRVI



**SDU  
FACULTY  
OF  
FORESTRY  
JOURNAL**

**SPECIAL EDITION  
2009**

**PROCEEDINGS OF  
THE CONFERENCE OF  
IUFRO WORKING  
PARTY 7.02.02  
EĞİRDİR, TURKEY**

**11-16 MAY 2009**

**Guest Editor  
H. Tuğba  
DOĞMUŞ-LEHTIJÄRVI**





**SDU**  
**FACULTY OF FORESTRY JOURNAL**  
**Serial: A, Number: Special Edition, Year: 2009, ISSN: 1302-7085**

**Indexed in**

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TÜBİTAK

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Fakülte Kitabevi-İSPARTA

SDU Faculty of Forestry Journal is a refereed journal and published twice a year.  
Responsibility for the published papers concern to the Authors  
2009 – SDU FFJ

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Special edition of the journal is financially supported by  
**The Scientific and Technological Research Council of Turkey (TÜBİTAK)**  
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## *Preface*

*The meeting of IUFRO Working Party (WP) 7.02.02 "Foliage, Shoot and Stem Diseases of Forest Trees" was held in Eğirdir, Isparta, Turkey. Local organizers were Dr. H. Tuğba Dođmuş -Lehtijärvi and her colleagues from the Faculty of Forestry, Süleyman Demirel University. In the opening ceremony, vice rectors of the university, Dr. Vecihî Kurdemir and Dr. Mehmet Ali Koyuncu and also dean of the Forestry Faculty, Dr. Musa Genç and the Coordinator of the IUFRO Forest Health Division, Dr. Gaston Laflamme welcomed the participants of the WP. We thank the attendees who presented oral and poster presentations, local organisers for their great effort, Süleyman Demirel University for their kind support and The Scientific and Technological Research Council of Turkey (TUBİTAK) for financial support.*

*Forest pathology has developed a lot during the past 40 years. The most remarkable progress is the possibility to use DNA methods in studying genetics of pathogens and host plants. DNA methods are helping us also when we try to find out the origin of new diseases, alien or original? What is the next step? Also the development of information technology has affected a lot of our daily working compared to time before computers and internet. The first step in forest pathology is to describe the pathogen and disease symptoms. The pathogenicity should be tested according to Koch's postulates. Then the ecology of the disease should be examined experimentally including the interactions between the pathogen, host, other microbes and environment. DNA methods can be used in studying the variation of pathogens, taxonomy, endophytes and pathogenesis.*

*The first meeting of the IUFRO Working party 7.02.02 was arranged in 1973 in Minneapolis, USA. Now Turkey was the 10th country to host the meeting so far. In the first meetings one of the main subjects was Scleroderris canker which was an important disease in Europe, Northern America and Japan. Surprisingly, the subjects of the presentations in this meeting were scattered, including some other important biotic and abiotic diseases of forest trees.*

*When new disease appears we should start from the beginning. Thanks to new methods or tools we can get the same knowledge much faster than in the 1900 's. It seems that new diseases appear continuously, f. ex. Phytophthora alni and Chalara fraxinea in Europe. The human interest to grow exotic tree species and even the commercial international seedling trade keeps the forest pathologists in work in future too.*

*The climate change means also challenges to forest pathologists. The warming climate is a fact based on the laws of physics. The concentration of carbon dioxide and other greenhouse gases are rising fast in atmosphere. Near the arid areas the warming means the drought problems and in the north it means the new pathogens from milder climates together with faster forest growth. The climate change can disturb the evolutionary balance between the plants and the pathogens. But the climate change highlights also the importance of forests. At the same time, forests produce renewable materials and energy and bind the carbon dioxide from the air. A healthy forest is important in controlling the warming. This is a fact which is very important to get to a common knowledge of people and this is our task.*

*Nowadays we can exchange information quickly by internet. Why to fly to another side of the earth to meet colleagues? I think the human being needs human contacts and conversation. This is an excellent opportunity to discuss and to start co-operation. The internet has not yet changed human genes. We had once more a very successful meeting in Eğirdir with very sincerely and relaxed atmosphere and found the opportunity to share the experiences and create the new ideas coming from basically all age groups, from very young to seniors, and we had close to 50 participants from 15 countries with 29 oral presentations and 15 posters. This proceeding includes full papers as well as extended and short abstracts and we would like to mention that the responsibility for the published papers lies with the authors.*

*Finally, we would like to see you in the next meeting to be held in Spain, 2011 organised by new deputy Julio Javier Diez Casero!*

*Antti Uotila  
Coordinator  
IUFRO WP 7.02.02*

*H. Tuğba Doğmuş -Lehtijärvi  
Local organizer & Deputy*

## THE CURRENT SITUATION OF ASH DIEBACK CAUSED BY *Chalara fraxinea* IN AUSTRIA

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### ABSTRACT

In many parts of Europe common ash, *Fraxinus excelsior*, is presently affected by a serious dieback of shoots, twigs and branches, causing decline and mortality of trees of all age classes. Initially thought to be primarily incited by abiotic damaging factors, accumulating evidence suggests that ash dieback is a new infectious disease caused by the hyphomycete *Chalara fraxinea* and its teleomorphic state, *Hymenoscyphus albidus*. In Austria, ash dieback was first observed in 2005 and in 2008 it occurred in all Austrian provinces. In heavily affected forests mortality is common amongst saplings and young trees. Moreover, in some areas dying of mature trees has started to occur. *Chalara fraxinea* was for the first time recorded in Austria in June 2007. Subsequent surveys have shown that the pathogen is widespread in the country. Until June 2009 it was isolated from symptomatic ash trees at 82 localities in eight out of the nine Austrian provinces. Apart from *F. excelsior*, *C. fraxinea* was isolated from narrow-leaved ash, *F. angustifolia* subsp. *danubialis* and from weeping ash, *F. excelsior* 'Pendula'. *Chalara fraxinea* was consistently isolated at high frequencies from ash shoots, twigs and stems showing early symptoms of disease. In inoculation experiments using potted *F. excelsior* and *F. angustifolia* seedlings, Kochs postulates were fulfilled for *C. fraxinea*, clearly suggesting that this fungus is the primary causal agent of ash dieback. It also displayed pathogenicity to *Fraxinus ornus* seedlings. Besides reviewing the situation of ash dieback in Austria and summarizing the results of some of our research since 2007, we generally review the knowledge on this emerging disease in Europe, describe its symptoms, present a hypothetical disease cycle for ash dieback and discuss options for disease management.

**Keywords:** *Hymenoscyphus albidus*, *Fraxinus excelsior*, *Fraxinus angustifolia* subsp. *danubialis*, emerging disease, fungal disease, new forest health problem

## 1. INTRODUCTION

Since the early 1990s common ash, *Fraxinus excelsior*, has been affected by an unprecedented, serious dieback of shoots, twigs and branches, causing decline and mortality of trees of all age classes. Ash dieback was first noticed around 1992 in Poland (Kowalski and Holdenrieder, 2008), where it has been causing serious damage (Przybył, 2002; Kowalski, 2006; Kowalski and Holdenrieder, 2008). It was subsequently recorded in many other European countries and threatens common ash in large parts of its distribution range. By 2009 ash dieback has been reported to occur in Lithuania (Lygis et al., 2005), Latvia (T. Gaitnieks, personal communication), Estonia (M. Hanso and R. Drenkhan, personal communication), area Kaliningrad (Russia, R. Vasaitis, personal communication), Denmark (Thomsen et al., 2007; Skovsgaard et al., 2009), Sweden (Bakys et al., 2009a; 2009b), Norway (Talgø et al., 2009), Finland (J. Hantula, personal communication), Germany (Schumacher et al., 2007), Slovakia (A. Kunca, personal communication), Czech Republic (Jankovský et al., 2008), Austria (Cech, 2006b; Halmschlager and Kirisits, 2008; Kirisits et al., 2008a; 2008b; 2009), Hungary (Szabó, 2008), Slovenia (Ogris et al., 2009), Rumania (D. Chira, personal communication), Switzerland (Engesser et al., 2009) and eastern France (Chandelier et al., 2009; Ioos et al., 2009) It can be expected that this emerging forest health problem will in the future also occur in other parts of Europe, where it has thus-far not been found.

Initially, ash dieback was suspected to be primarily incited by abiotic damaging factors (frost, drought and abrupt changes of periods with warm and cold weather conditions), with secondary, weakly virulent fungal pathogens and endophytes contributing to the syndrome (Przybył, 2002; Pukacki and Przybył, 2005; Cech, 2006b; Cech et al., 2007). This view changed with the discovery and description of the anamorphic fungus *Chalara fraxinea* that was in Poland frequently isolated from shoots in the early phase of the pathological process (Kowalski, 2006). In the meanwhile, *C. fraxinea* has been detected in many of the above mentioned countries and accumulating evidence suggests that it is the cause of ash dieback (Schumacher et al., 2007; Halmschlager and Kirisits, 2008; Szabó, 2008; Kowalski and Holdenrieder, 2009a; Talgø et al., 2009; Bakys et al., 2009a; 2009b; Engesser et al., 2009; Ogris et al., 2009; Kirisits et al. 2009; Chandelier et al., 2009; Ioos et al., 2009).

Because of the sudden appearance, the rapid spread and the high intensity of ash dieback, *C. fraxinea* was thought by some forest pathologists to be an alien invasive organism (Halmschlager and Kirisits, 2008; Kirisits and Halmschlager, 2008; Kowalski and Holdenrieder, 2008; Ogris et al., 2009). However, *Hymenoscyphus albidus*, a discomycete native to Europe has recently been identified as the teleomorph of *C. fraxinea* (Kowalski and Holdenrieder, 2009b). This ascomycete fungus has been known since 1850 as harmless decomposer of leaf rachises (referred to as leaf petioles by Kowalski and Holdenrieder [2009b] but we think that 'leaf rachis' is the more appropriate botanical term) of common ash

and it is unknown, why this fungus suddenly causes a serious, emerging disease on *F. excelsior* (Kowalski and Holdenrieder, 2009b). Kowalski and Holdenrieder (2009b) proposed that the fungus they assigned to the morphospecies *H. albidus* may have undergone genetic change by mutation or hybridization with an unknown introduced species. Another possibility is that the teleomorph of *C. fraxinea* is not the ‘original’ *H. albidus*, but an exotic invasive species, that is morphologically virtually identical to *H. albidus*. Finally, the fungus may show unprecedented aggressiveness towards ash because of environmental factors or/and weather extremes, that could either have predisposed the host trees to fungal attack or provided ideal conditions for fungal infections (Kowalski and Holdenrieder, 2009b). These three theories are the conceptual basis for future research regarding the question what triggered the epidemic of *H. albidus* and its anamorphic state *C. fraxinea*.

Ash dieback is presently amongst the most important forest health problems in Austria. Here we review the situation of this emerging disease in this Central European country. We also summarize some research that has been conducted since 2007, present a hypothetical disease cycle for ash dieback and discuss options for disease management.

## 2. ASH SPECIES IN AUSTRIA

Three ash species are native in Austria including common ash, *Fraxinus excelsior*, also known as European ash, narrow-leaved ash, *F. angustifolia* subsp. *danubialis* and flowering ash, *F. ornus* (Adler et al., 1994). While European ash is widespread on appropriate sites in many parts of the country (Schadauer, 1994), the two other species are at the edge of their distribution ranges in Austria and are thus rare (Adler et al., 1994; Zukrigl, 1997).

With a share of 2.5% (based on the number of trees) and 1.8% (based on the growing stock) ash species are the third most frequent group of hardwood species in managed forests in Austria (Table 1). All three species are included in the relative proportions reported in Table 1, but the vast majority of the share of *Fraxinus* spp. refers to *F. excelsior*. Based on the growing stock only European beech (*Fagus sylvatica*) and oak species (mainly *Quercus petraea* and *Quercus robur*) occur more frequently than *Fraxinus* spp. and based on the number of trees *F. sylvatica* dominates amongst hardwood species, while European hornbeam (*Carpinus betulus*) is slightly more frequent than ash. The share of ash in the nine Austrian provinces is shown in Table 1. Ash is particularly abundant in the provinces Upper Austria, Lower Austria, Vorarlberg and Vienna and occurs least frequently in the province Tyrol that is to a large extent located in areas of the Alps that are inappropriate for the growth of *F. excelsior*.



**Table 1:** Share (%) of ash, based on number of trees and based on growing stock in managed forests in the nine Austrian provinces and in entire Austria. The data include all three ash species native in Austria, but the vast majority is *F. excelsior*, while the proportions of *F. angustifolia* and *F. ornus* are negligible. Source: Austrian Forest Inventory 2000-2002, Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW), Department of Forest Inventory (<http://bfw.ac.at/rz/bfwcms.web?dok=35>).

<b>Austrian province</b>	<b>Based on number of trees</b>	<b>Based on growing stock</b>
Burgenland	2.1	1.2
Carinthia	1.7	1.0
Lower Austria	3.4	2.9
Salzburg	2.0	1.1
Styria	1.6	1.2
Tyrol	0.4	0.1
Upper Austria	5.2	3.7
Vienna	9.4	7.5
Vorarlberg	4.6	2.2
<b>Austria total</b>	<b>2.5</b>	<b>1.8</b>

Common ash has its optimum on moist, nutrient-rich sites, but in areas with limestone as geological bedrock it can also occur on drier sites (Mayer, 1984). It is mainly found from the lowlands up to elevations of 900 m asl. (Schadauer, 1994; Nationalpark Kalkalpen, 2007) In the Alps it rarely occurs at elevations higher than 1200 m asl. (Mayer, 1984; Schadauer, 1994; Nationalpark Kalkalpen, 2007). *Fraxinus excelsior* occurs in a large number of forest types. It is a characteristic component of floodplain forests along big rivers, forests along streams and in glens, but also occurs in other hardwood-dominated forests on moist and sometimes drier sites (Jelem, 1974; Mayer, 1974; 1984; Nationalpark Kalkalpen, 2007). For forest owners managing riparian forests, along the Danube for example, common ash is usually the most economically important timber species (Jelem, 1974). In many areas, especially on sites at lower elevations it has received much attention for the production of valuable timber and as an alternative to Norway spruce (*Picea abies*) (Wolf and Jasser, 2003). It is also important for various ecosystem services, for example stabilization of riverbanks and slopes (Mayer, 1984). Moreover, *F. excelsior* is an attractive and appreciated landscape tree in the countryside and shade tree in urban areas. Due to its nutrient-rich foliage it was the most preferred tree species for lopping in the Alps, providing fresh or dry fodder for cattle, sheep and other domestic animals.

Narrow-leaved ash, *Fraxinus angustifolia* subsp. *danubialis* (hereafter referred to just as '*F. angustifolia*'), is mainly distributed in lowland areas of south-eastern Europe. In eastern Austria it reaches one of its distribution limits and is therefore rare (Jelem, 1974; 1975; Adler et al., 1994; Zukrigl, 1997). It forms part of riparian forest ecosystems along the lower reaches of the rivers March, Danube, Fischa

(province Lower Austria) and Leitha (provinces Lower Austria and Burgenland) (Jelem, 1974; 1975; Adler et al., 1994; Zukrigl, 1997). Hybrids between *F. angustifolia* and *F. excelsior* have been reported to occur in areas in Austria, where the distribution ranges of the two species overlap (Jelem, 1974; 1975). While it is mainly a botanical curiosity and of interest for nature conservation, this ash species is an economical important timber species in floodplain forests along the March (Jelem 1975; Damm, 1997).

Flowering ash mainly occurs in southern and south-eastern Europe, but its natural distribution range just reaches southern Austria (Mayer, 1974; Adler et al., 1994; Zukrigl, 1997). It is mainly found in southern and eastern Carinthia (Adler et al., 1994), where it usually occurs on steep, rocky, warm and dry sites on limestone (Zukrigl, 1997). Together with European hop-hornbeam, *Ostrya carpinifolia*, *F. ornus* often forms dense bush forests on such sites (Mayer et al., 1974; Zukrigl, 1997). Apart from Carinthia, flowering ash also occurs in other Austrian provinces (Eastern and Northern Tyrol, Styria, Lower Austria and Burgenland), where it is generally rare (Adler et al., 1994; Zukrigl, 1997). Most of the occurrences in these provinces are likely not native, but *F. ornus* has become naturalized in some areas (Zukrigl, 1997). This ash species has no importance for forestry in Austria, but is of interest for nature conservation, as it forms part of rare and ecologically valuable forest types. It is occasionally used as shade and ornamental tree and planted in shelterbelts (Zukrigl, 1974).

Green ash (*F. pennsylvanica*) and white ash (*F. americana*), two introduced species from North America are occasionally planted as ornamentals (Adler et al., 1994). Some decades ago they also received some interest as plantation trees in floodplain forests, but as their growth potential and timber quality did not fulfill the expectations of foresters they are presently no longer planted. *Fraxinus pennsylvanica* has become naturalized in some riparian areas, especially in those along the lower reach of the Danube and the March (Essl and Rabitsch, 2002). It is therefore considered as alien invasive species in Austria (Essl and Rabitsch, 2002; Essl et al., 2006).

### 3. SYMPTOMS OF ASH DIEBACK

The symptoms of ash dieback share characteristics of a bark disease, a vascular wilt disease and a leaf disease (Figure 1 and 2; Thomsen et al., 2007; Halmschlager and Kirisits, 2008; Kirisits et al., 2008a; 2008b; Kowalski and Holdenrieder, 2008; Szabó, 2008; Bakys et al., 2009b; Engesser et al, 2009; Kirisits and Cech, 2009; Kirisits et al., 2009; Ogris et al., 2009). Typical symptoms occur in the bark, phloem and wood of shoots, twigs, branches and stems as well as on leaves of ash trees. Necrotic lesions and wood discoloration can also extend into the roots, from where the fungus infects coppice sprouts, but the disease clearly starts at above-ground parts of the tree (Kowalski and Holdenrieder, 2008).



**Figure 1.** A stand of common ash severely affected by shoot, twig and branch dieback (Laussa, Upper Austria, July 2007).

The most obvious symptom is dieback of shoots, twigs and branches (Fig. 1). Shoot dieback is caused by localized necrotic lesions that initially are small, but as they expand they girdle the phloem and sapwood occlusion occurs, too. When phloem girdling and sapwood occlusion take place in winter time, shoots do not flush in spring, however, when they happen during the vegetation period, simultaneous wilting of leaves above the lesions occurs (Fig. 2A). Leaves then dry, turn brown to black and remain attached to the shoots for a long time. Elongated, often elliptical necrotic lesions and cankers in the bark are characteristic symptoms of ash dieback (Fig. 2B and 2C). These lesions either form around a dead side twig (Fig. 2B) or occur around a leaf scar (Fig. 2C). On larger shoots, twigs, branches as well as on younger stems, the tree often defends itself against the pathogen attack, at least for some time, leading to perennial cankers.

Necrotic lesions and cankers are usually accompanied by brownish to grayish discoloration of the wood (Fig. 2D) that frequently extends longitudinally beyond necrotic areas in the bark. Diseased trees react with prolific formation of epicormic shoots and the silhouettes of heavily affected trees look tousled and distorted (Fig. 1). *Chalara fraxinea* also causes symptoms on leaves, resulting from direct leaf infections (Kirisits et al., 2008b; Ogris et al., 2009; Bakys et al., 2009b). These symptoms include brown to blackish necrotic lesions on leaf rachises and leaflet veins, followed by wilting of parts of the leaves distal to the necrotic lesions. Early leaf shedding is often a consequence of these leaf symptoms.

#### 4. ASH DIEBACK IN AUSTRIA

In Austria, first unambiguous observations of ash dieback were made in 2005, mainly on young trees (Cech, 2006a; 2006b). From 2006 to 2007 damage levels increased dramatically, particularly in the provinces Lower and Upper Austria as well as Styria (Cech and Hoyer-Tomiczek, 2007; Hagen, 2007; Fachabteilung Forstwesen-Forstdirektion, 2009). In 2008 the phenomenon was widespread and symptoms were observed in all Austrian provinces (Kirisits et al., 2008a; Kirisits and Cech, 2009).

Prior to the widespread occurrence of dieback of shoots, twigs and branches, early leaf shedding on ash trees, occurring already in late August and early September, was observed in parts of the provinces Lower and Upper Austria in 2005 and Styria in 2006 (Cech, 2005; Hagen, 2005; Fachabteilung Forstwesen-Forstdirektion, 2009). In the following year, thus in 2006 in Lower and Upper Austria and in 2007 in Styria, ash dieback was for the first time recorded at high intensity (Cech, 2006b; Hagen, 2007; Fachabteilung Forstwesen-Forstdirektion, 2009). Originally, this early shedding of *F. excelsior* leaves was thought to be caused by powdery mildews (*Phyllactinia fraxini*) and other microfungi (Cech, 2005). However, as *C. fraxinea* is now known to cause also symptoms on ash leaves (Thomsen et al., 2007; Bakys et al., 2009b; Kirisits and Cech, 2009; Ogris et al., 2009), it is likely that the episodes of early leaf shedding in 2005 and 2006 were the first obvious indications of ash dieback. In 2008 leaf symptoms and early leaf shedding occurred again, for example in parts of Styria (Fachabteilung Forstwesen-Forstdirektion, 2009).

Incidence and severity of ash dieback varies considerably in different parts of the country. It appears to be most serious in the Northern Limestone Alps in the provinces Lower and Upper Austria, Styria and Salzburg. Likely, there are still areas, where the disease does not occur, especially in parts of the Alps, where common ash is present at a low density (Kirisits and Cech, 2009). Apart from *F. excelsior*, dieback also occurs on narrow-leaved ash and weeping ash (*Fraxinus excelsior* 'Pendula'), an ornamental variety of common ash (Kirisits et al., 2008a; 2009; Kirisits and Cech, 2009). No symptoms have thus far been observed on

*F. ornus* as well as the exotic *F. pennsylvanica* and *F. americana* (Kirisits, 2008; Kirisits et al., 2008a; Kirisits and Cech, 2009).

The disease occurs on ash trees of all ages, both on natural regeneration and planted trees and on the entire spectrum of sites and forest types, where ash is found (Cech, 2008). Ash dieback is damaging on both forest and shade trees and it also causes serious problems in nurseries, where rearing of healthy ash seedlings has become difficult, if not impossible. In heavily affected forests mortality is common amongst saplings and young trees. Moreover, in some areas dying of mature trees has started to occur. It is expected that the future use of *F. excelsior* as economically and ecologically valuable noble hardwood species will be substantially impaired by this emerging disease.



**Figure 2.** Symptoms of ash dieback: (A) Wilting of leaves due to girdling of the phloem and sapwood occlusion, (B) A necrotic lesion in the bark with a small dead twig in the centre, (C) A necrotic lesion in the bark with a leaf scar (arrow) in the centre, (D) Discoloration of the wood.

A number of surveys are presently underway to obtain more precise information on the geographical distribution, incidence, severity and temporal development of ash dieback in Austria. In 2007 and 2008 monitoring plots have been established in Lower Austria (Cech, 2008) and additional plots in other provinces will be installed in 2009. On these plots, disease intensity will be monitored on permanently marked ash trees over the next years. From 2009 onwards the disease is also included in the 'Documentation of forest damage factors' (German: 'Dokumentation der Waldschädigungsfaktoren – DWF'), a monitoring system that is based on expert opinions and appraisals of staff of the district forest authorities (Steyrer et al., 2008). Finally, assessments on the geographical distribution and incidence of ash dieback will be carried out as part of the field work of the Austrian Forest Inventory.

### **5. *Chalara fraxinea* ASSOCIATED WITH ASH DIEBACK IN AUSTRIA**

Starting in June 2007, we aimed to examine the role of *C. fraxinea* in ash dieback in Austria. Shoots, twigs, branches, stems and leaves of young *F. excelsior* trees showing symptoms of the disease were collected in many different parts of the country. From January 2008 onwards special attention was given to collect only samples from trees showing early symptoms of ash dieback, particularly shoots with small, localized necrotic phloem lesions. About 4 to 6 cm long segments, containing the transition between necrotic and healthy phloem tissues and/or discolored and healthy xylem were cut from symptomatic ash organs. These segments were surface sterilized as described by Kowalski (2006). Thereafter, the outer bark was carefully peeled off and 3 to 10 mm small discs containing wood and phloem tissues were cut under aseptic conditions and put onto malt extract agar (MEA; 20 g malt extract, 16g agar, 1000 ml tap water supplemented after autoclaving with 100 mg streptomycin sulphate). In the earlier isolation series until January 2008, the outer bark was not peeled off and not discs, but small pieces of phloem or wood were removed and placed on MEA plates.

Initially the isolation plates were incubated at room temperature (23-25°C), but from August 2008 onwards they were immediately stored at low temperatures (approximately +4°C) in refrigerators. At cool temperatures, the growth of many fungi competing with *C. fraxinea* is more inhibited than that of *C. fraxinea* itself. In addition, phialophore formation of *C. fraxinea* is greatly enhanced by low temperatures (Halmschlager and Kirisits, 2008; Kirisits et al., 2008a). Both factors increase the likelihood to detect the fungus. *Chalara fraxinea* was identified based on morphological characteristics (colony morphology, phialophores and conidia; Kowalski, 2006; Halmschlager and Kirisits, 2008; Kowalski and Holdenrieder, 2008; Kirisits et al., 2008a).

*Chalara fraxinea* was for the first time isolated in Austria in June 2007, at one locality in Upper Austria (Edt bei Lambach, 48°06'51" N, 13°53'29" E) and another one in Styria (Altaussee, 47°38'34" N, 13°45'36" E) (Halmschlager and Kirisits,

2008; Kirisits and Halmschlager, 2008). Subsequent surveys have shown that the pathogen is widespread in the country and apparently occurs everywhere, where ash dieback is present. Until June 2009 the fungus was obtained from symptomatic ash trees at 82 localities in eight out of the nine Austrian provinces (Table 1). The differences in the number of records of *C. fraxinea* in the various provinces (Table 1) do not allow inferring about the intensity of ash dieback in various parts of Austria, but just reflect differences in the intensity of sampling. In the future it is planned to examine more samples and sites in those provinces, where extensive collections have thus far not been conducted, especially in Tyrol, Vorarlberg, Burgenland and Carinthia

In the early isolation series carried out in 2007 *C. fraxinea* was rarely isolated, because samples were mainly collected from ash trees showing relatively late symptoms of disease. We suppose that on such plant material the slow growing *C. fraxinea* is in most cases already outcompeted by fast-growing endophytic and saprotrophic fungi (Kowalski and Holdenrieder, 2008). However, when isolations were made from shoots, twigs and stems showing early symptoms of disease, *C. fraxinea* was the most consistently and most frequently isolated fungus and in most cases the only one that was recovered. For example, isolation frequencies of *C. fraxinea* at ten localities in six Austrian provinces ranged from 81% to 100% of the examined shoots and necrotic lesions (Table 2). Overall, the fungus was obtained from 94% of the samples, from which isolations were made. Isolation of *C. fraxinea* was successful throughout the year, given that samples were collected from ash trees showing early disease symptoms (Table 2).

Apart from *F. excelsior*, *C. fraxinea* was isolated from young, planted *F. angustifolia* trees in floodplain areas along the river Morava near Hohenau/March and from symptomatic seedlings of this species in a nursery in Lower Austria (Kirisits et al., 2009; Table 2). In addition, it was obtained at a few localities from *F. excelsior* 'Pendula' (Table 2). To our knowledge, these are the first and thus far only European records of the fungus from hosts other than *F. excelsior*. The fungal isolations from *Fraxinus* ssp. have shown that *C. fraxinea* is associated with early symptoms of ash dieback, as it is typical for the primary causal agent of a plant disease. These results agree well with other studies in Europe, in which this fungus was consistently isolated or detected with molecular markers from diseased ash trees (Kowalski, 2006; Bakys et al., 2009b; Ioos et al., 2009; Chandelier et al., 2009).

In May 2008 potted, one-year-old common ash seedlings were wound-inoculated with five *C. fraxinea* isolates and in June 2008 with five other strains. Similarly, potted, two-year-old narrow-leaved ash seedlings were inoculated with one *C. fraxinea* isolate in May 2008 (Kirisits et al., 2009) and with two other isolates in June 2008. Inoculum consisted of small pieces of autoclaved *F. excelsior* phloem (approximately 10 x 4 x 2-3 mm) that had been placed for 15 to 30 days on the various *C. fraxinea* cultures on MEA.

**Table 2:** Overview of the records of *Chalara fraxinea* in eight Austrian provinces from June 2007 to June 2009. Only in Tyrol the fungus has thus-far not been reported, although its presence as causal agent of ash dieback in this province is also very likely.

Austrian province	First record (month, year, locality)	Ash species and varieties	Number of localities, where <i>C. fraxinea</i> has been recorded
Burgenland	October 2008, BOKU Forest Demonstration Centre 'Rosalia'	<i>F. excelsior</i>	1
Carinthia	August 2008 Saberda, Sattnitz	<i>F. excelsior</i>	3
Lower Austria	August 2007 Langau	<i>F. excelsior</i>	30
Salzburg	October 2008 Fuschl	<i>F. angustifolia</i> subsp. <i>danubiensis</i> <i>F. excelsior</i> <i>F. excelsior</i> 'Pendula'	14
Styria	June 2007 Altaussee	<i>F. excelsior</i> <i>F. excelsior</i> 'Pendula'	10
Upper Austria	June 2007 Edt bei Lambach	<i>F. excelsior</i>	11
Vienna	January 2008 Neuwaldegg, 17 <sup>th</sup> district	<i>F. excelsior</i> <i>F. excelsior</i> 'Pendula'	12
Vorarlberg	May 2009 Götzis	<i>F. excelsior</i>	1
<b>Total</b>	-	-	<b>82</b>



**Table 3:** Isolation frequencies of *Chalara fraxinea* from young common ash (*Fraxinus excelsior*) trees showing early symptoms of ash dieback (recently died shoots as well as shoots, twigs and stems with localized necrotic lesions and wood discoloration) at ten localities in six Austrian provinces. Isolations were done from August 2008 to May 2009 and localities are arranged in chronological order of the date of isolation.

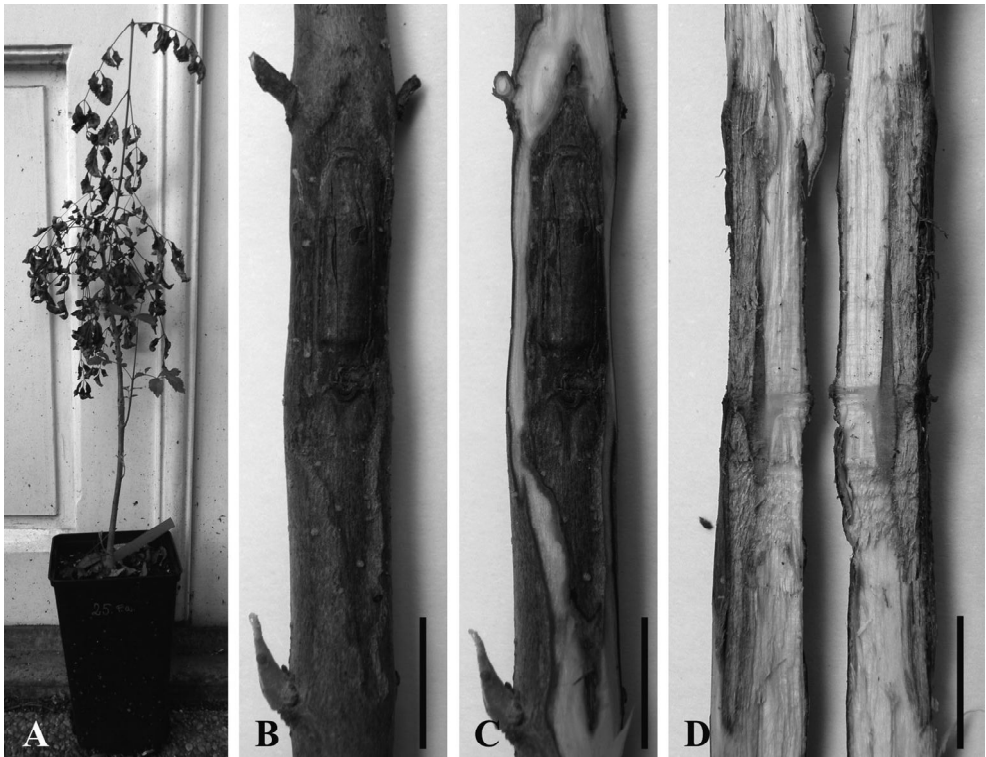
Locality	Austrian province	Date	Necrotic shoots or necrotic lesions <sup>1</sup>	
			Number of samples	Isolation frequency of <i>Chalara fraxinea</i> (%) <sup>2</sup>
Saberda, Sattnitz	Carinthia	August 2008	17	100
Wien, Hermannskogel	Vienna	November 2008	14	93
Muggendorf, Unterberg	Lower Austria	December 2008	14	93
Wien, Steinhofgründe	Vienna	January 2009	17	100
Lofér	Salzburg	April 2008	11	100
Ungerdorf, Hinterleiten	Styria	April 2009	8	88
Bad Gleichenberg <sup>3</sup>	Styria	April 2009	11	91
Feldkirchen an der Donau <sup>3</sup>	Upper Austria	May 2009	21	81
Kaumberg-Arabung	Lower Austria	May 2009	8	100
Leutschach	Styria	May 2009	9	100
<b>All ten localities</b>	-	-	<b>130</b>	<b>94</b>

<sup>1</sup> Usually one shoot or necrotic lesion per tree was used for fungal isolation, but occasionally more than one sample was collected from a single tree. <sup>2</sup> In most cases *C. fraxinea* was obtained in pure culture and only occasionally in mixed culture with other fungal species (data not shown). <sup>3</sup> Seed orchards affected by ash dieback.

Inoculation of seedling stems was done by cutting an approximately 2 cm-long slit into the bark, to the level of the cambium, pulling the bark slightly away, inserting inoculum and wrapping parafilm around the wound to seal the bark flap back to the stem, to minimize contamination and to prevent rapid drying of the phloem and wood. Each isolate was inoculated onto 20 seedlings and twenty other seedlings of each ash species were inoculated with sterile pieces of ash phloem to serve as control. In each experiment, seedlings were observed for external symptoms during a period of approximately three months. Thereafter, they were dissected and lengths of necrotic lesions and longitudinal extension of wood discoloration were recorded.

On both ash species all isolates tested caused symptoms virtually identical to those occurring on naturally infected trees: wilting of leaves and dieback (Fig. 3A) due to girdling of the phloem and sapwood occlusion around the inoculation site, necrotic lesions in bark (Fig. 3B), phloem (Fig. 3C) and cambium as well as brown-greyish discoloration in the wood (Fig. 3D) (Kirisits et al. 2008a; 2009). On the control seedlings the inoculation wounds were partly or entirely closed and no necrotic lesions or wood discoloration occurred. The three isolates that were tested on both ash species caused more intensive symptoms (longer necrotic lesions, more plants displaying wilt and dieback) on *F. angustifolia* than on *F. excelsior*, which may indicate that the former species is more susceptible to *C. fraxinea* than the latter species. *Chalara fraxinea* was consistently re-isolated from the inoculated seedlings, while it was not recovered from any of the control plants. On *F. excelsior* the re-isolation rates of the various *C. fraxinea* isolates ranged from 25 to 73 %. On *F. excelsior* and *F. angustifolia* Kochs postulates were thus fulfilled for *C. fraxinea*, clearly suggesting that this fungus is the primary causal agent of ash dieback. This is in agreement with studies in Poland (Kowalski, 2006; Kowalski and Holdenrieder, 2008; 2009a), Sweden (Bakys et al., 2009b), Hungary (Szabó, 2008), Slovenia (Ogris et al., 2009) and Norway (Talgø et al., 2009).

Flowering ash was also included in the inoculation experiments. Two *C. fraxinea* isolates, one in May 2008 and the other one in June 2008, were wound-inoculated onto one-year-old seedlings of this ash species as described above. In both experiments *C. fraxinea* displayed pathogenicity to *F. ornus*. While in the first experiment some plants showed wilting of leaves and dieback, and necrotic lesions of similar size as those on *F. excelsior* developed, no dieback occurred in the second experiment and necrotic lesions were rather small. Flowering ash may be less susceptible to *C. fraxinea* than the other two European ash species which is supported by the fact that natural infections have thus-far not been observed. Further disease surveys and inoculation trials are, however, required to definitely appraise the susceptibility of *F. ornus* to the ash dieback pathogen.



**Figure 3.** Symptoms on potted *Fraxinus angustifolia* seedlings following wound-inoculation with *Chalara fraxinea*: (A) Wilting of leaves, (B) Superficially visible necrotic lesion in the bark, (C) Necrotic lesion in the phloem, (D) Discoloration of the wood (Bar for B, C and D [each showing the same inoculation point] = 1 cm). See Kirisits et al. (2009) for colored versions of the photographs.

## 6. INFECTION BIOLOGY OF *Chalara fraxinea* AND HYPOTHETIC AL DISEASE CYCLE OF ASH DIEBACK

Until recently, the infection biology of *C. fraxinea* was totally enigmatic. There were no published reports of the fungus sporulating on dead shoots, necrotic lesions or cankers and its mode of dispersal was unknown. The conidia of *C. fraxinea* are sticky, accumulate in droplets on the top of phialophores and do not appear to be adapted to wind-dispersal (Kowalski, 2006; Kowalski and Holdenrieder, 2008). It was therefore speculated that the fungus is transmitted by animal vectors such as the ash bark beetle *Leperesinus varius* (Kowalski and Holdenrieder, 2008). No clear evidence was found, however, that vectors are involved and circumstantial evidence, for example the occurrence of the disease on trees of all age classes and the low degree or lack of association between insect infestations and ash dieback, made vector-dispersal of the fungus unlikely.



**Figure 4.** Apothecia of *Hymenoscyphus albidus* on leaf rachises of *Fraxinus excelsior* from the previous year (Neuwaldegg-Dornbach, Vienna, 14 and 16 June 2009).

The enigma, how the ash dieback pathogen is transmitted was solved, at least partly, by Kowalski and Holdenrieder (2009b) who discovered the teleophorph of *C. fraxinea* and linked it to *Hymenoscyphus albidus*. Similar as in other ascomycetes, the ascospores of *H. albidus* are likely to be wind-dispersed (Kowalski and Holdenrieder, 2009) and appear to play the key role in inciting infections of ash trees. Ascospore dispersal by wind would also explain the rapid spread of the ash dieback pathogen in Europe, if it had changed genetically or were an invasive alien organism (Kowalski and Holdenrieder, 2009b). In contrast, we suppose that the spores of *C. fraxinea* are unable to cause infections and they may play a different, if any role in the biology of *H. albidus*. In May 2008 we inoculated ash shoots and leaves with suspensions of *C. fraxinea* spores, but no symptoms developed on any of the test seedlings. In addition, we repeatedly aimed to test the germination of spores of *C. fraxinea*, but without any success. They did not germinate on MEA, V8 agar or an agar medium containing an extract from ash leaves that stimulated mycelial growth of *C. fraxinea*, but not conidial germination. The spores also did not germinate after *in vitro* inoculation of detached ash leaflets. We thus speculate that the spores of *C. fraxinea* are not conidia, but probably

spermatia that play a role in exchanging nuclei and in fertilization of the fungus, if they are of any biological significance.

Independent from the discovery of *H. albidus* by Kowalski and Holdenrieder (2009b), from September 2008 onwards we started to comprehend the importance of leaf rachises for the infection biology and epidemiology of the ash dieback pathogen. Fungal isolation from necrotic lesions on leaf rachises in September and October 2008 has shown that *C. fraxinea* is clearly associated with these leaf symptoms, as it was the most frequently isolated fungus and was often obtained in pure culture. Repeated isolations from shed leaf rachises collected from the forest floor in autumn, winter and spring confirmed that *C. fraxinea* persists and overwinters in these parts of ash trees. Given that isolation of *C. fraxinea* from dead shoots and necrotic lesions can be difficult (e. g. Bakys et al., 2009a), it was surprising to isolate it as the most frequent fungus from decaying leaf remnants collected on the ground. Occasionally, also phialophores of *C. fraxinea* were found, sometimes abundantly. Furthermore, from late November 2008 onwards, most leaf rachises were covered by black, pseudosclerotial plates, resembling the structures often occurring in cultures of *C. fraxinea*, and now, with hindsight, known to be associated with *H. albidus* (Kowalski, 2006; Kowalski and Holdenrieder, 2008; 2009b; Halmschlager and Kirisits, 2008; Kirisits et al., 2008a).

While the discovery of *H. albidus* as teleomorph of *C. fraxinea* (Kowalski and Holdenrieder, 2009b) came surprising for us, we were not so surprised that the apothecia of this fungus are predominantly formed on leaf rachises from the previous year. In spring 2009 we repeatedly inspected leaf rachises for the occurrence of *H. albidus*. At one site in Vienna, developing apothecia with unripe ascospores were first seen at the end of May, while in mid-June the first fully developed fruiting bodies with ripe, germinating ascospores occurred abundantly (Fig. 4). Since then, apothecia of *H. albidus* have been recorded at several sites in various parts of Austria, indicating that they occur widespread and in high numbers. Intriguingly, apothecia were observed much earlier in the year (June) than previously reported in the literature (Kowalski and Holdenrieder, 2009a and references therein).

Based on the discovery of *H. albidus* as the teleomorph of *C. fraxinea*, published information on the disease as well as own observations and studies, we propose a hypothetical disease cycle for ash dieback (Fig. 5). This scheme (Fig. 5) shall also emphasize knowledge gaps and form the conceptual basis for future investigations on the infection biology and epidemiology of *H. albidus*/*C. fraxinea*. Infection of ash trees is thought to occur by wind-dispersed ascospores of *H. albidus* which form mainly on leaf rachises from the previous year, lying on the forest floor (Kowalski and Holdenrieder, 2009b; Fig. 5). Occasionally they also occur on dead shoots (Kowalski and Holdenrieder, 2009b). Ascospores are likely released from June to early October (Fig. 5). The length of the infectious period will depend on the local climate and will likely vary from year to year according to the weather conditions.

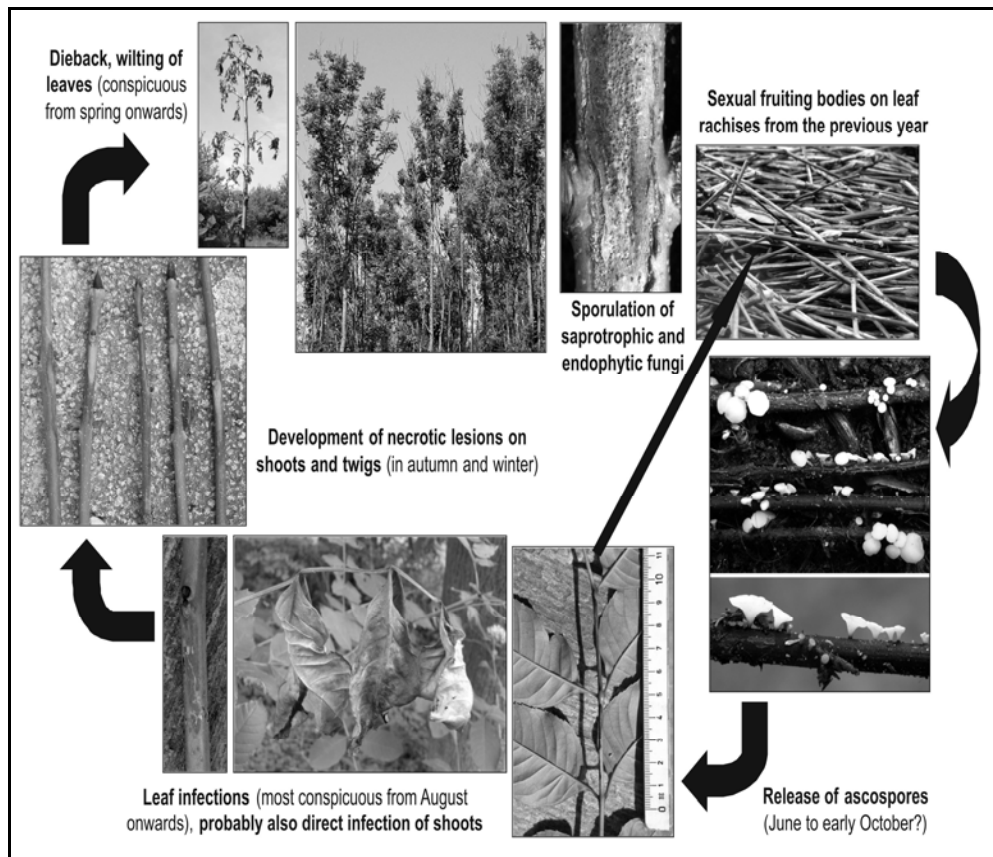
How infection by ascospores exactly takes place is unknown, but careful observations of symptoms suggest that leaves are an important target for infections (Fig. 5). In 2008 we observed leaf symptoms occasionally already in June and July, but they were most conspicuous from August onwards. In our opinion they can lead to early leaf shedding in late August and in September, as it has been repeatedly observed in Austria since 2005 (Cech, 2005; Hagen, 2005; Fachabteilung Forstwesen-Forstdirektion, 2009). We suppose that *H. albidus* is able to grow from the leaves into the shoots of ash trees (Fig. 5), where it causes necrotic lesions and wood discoloration. When examining numerous young ash trees showing early stages of disease, necrotic lesions occurred either around leaf scars (Fig. 2B) or around dead side twigs (Fig. 2C), but lesions were never seen in other positions. Dead side twigs are for sure entrance points of the pathogen into main shoots, bigger branches and stems of ash trees and the location of lesions around leaf scars may support the suspicion that the pathogen can enter the phloem and xylem via leaves. Direct infections of shoots possibly also occur (Fig. 5). Whatever organ is concerned, we assume that wounding is not required for infection. Environmental factors, particularly high amounts of precipitation and high levels of air humidity are likely conducive for ascospore release and for infections to be successful.

In 2008 small, localized necrotic lesions on shoots, often located around leaf scars (Fig. 5), where leaves had already been shed, were first observed in early August, but more commonly in September and October. These symptoms must have originated from current-years infections. Observations from 2007 to 2009 suggest, however, that many infections may remain latent for a while and that most of the host colonization and symptom progression takes place outside the vegetation period (Fig. 5). This view is supported by wound-inoculation of *F. angustifolia* with *C. fraxinea* in early December, resulting in dieback of many test seedlings in early spring. Because symptom development occurs to a large extent in autumn and winter, high damage levels become obvious in spring, when shoots do not flush and die, wilting of leaves occurs and trees show extensive dieback (Fig. 5). On bark tissues killed a while ago, saprotrophic or endophytic fungi sporulate (Fig. 5) and outcompete *C. fraxinea*, making isolation of the primary pathogen difficult or impossible. With the occurrence of *H. albidus* apothecia on leaf rachises on the forest floor (Fig. 5), the disease cycle starts again.

## 7. RECOMMENDATIONS FOR DISEASE MANAGEMENT

Ash dieback is another example of a serious disease damaging a valuable hardwood tree species in Europe, thereby causing problems for forestry, nature conservation and shade tree management. Common ash is not amongst the main timber species in Austria, but on many sites and forest types it is an economically and ecologically important species. On some sites there are hardly any or no attractive alternatives to ash for the selection of tree species. If ash dieback in Austria develops similar as in other countries, so that also old trees are seriously

affected, considerable losses will occur and ash may lose much of its importance in silviculture.



**Figure 5.** Hypothetical disease cycle of ash dieback caused by *Hymenoscyphus albidus*/*Chalara fraxinea*. See text for explanations

Although many aspects are still unknown, much progress has recently been made to better understand ash dieback and, based on this knowledge, to recommend measures for disease management. However, this new phenomenon reminds us, how little can in most cases be done against emerging forest health problems. As a consequence of ash dieback the silvicultural characteristics of ash need to be re-appraised. While it used to be a ‘stable’ tree species that was little affected by diseases, insect pests and abiotic damaging factors, it is presently threatened by this new phenomenon. It is therefore recommended to plant common ash less extensively as before and mix it with other site-adapted tree species. Plants for planting should be carefully inspected for the occurrence of symptoms by nursery managers, forest owners and foresters. Likewise, it should be avoided to bring diseased seedlings into areas, where ash dieback has thus far not been recorded. Wherever it is possible, leaves shed in autumn and leaf rachises on the

ground prior to the occurrence of apothecia of *H. albidus* should be removed, ploughed into the soil or covered with soil. Such sanitation measures are probably possible and economic feasible in nurseries and urban areas. However, the dispersal distances of ascospores of *H. albidus* are presently unknown and it will depend on these distances, whether infections can be effectively prevented by local removal of leaflets and leaf rachises. In nurseries fungicide application to protect plants from infections by ascospores may be another measure, but thus far there is no experience regarding the fungicides to be effectively used as well as the precise timing of the applications. It is likely that infections can occur over a long period of time, from June to early October (Fig. 5), which would make many applications necessary. While fungicide treatments may be a useful method to raise healthy ash seedlings, their general importance for disease management will be limited, as seedlings will become infected after having been planted in the field.

Thus far there are no reliable recommendations for the silvicultural treatment of stands affected by ash dieback. It is, however, recommended not to abandon ash too early, and, if there are no other reasons, to harvest only dead and severely damaged trees. It has been observed that *C. fraxinea* can grow from epicormic shoots into the wood of ash stems and causes discoloration there (Kowalski and Holdenrieder, 2008; Thomsen et al., 2009), thereby lowering the timber quality and value. To avoid such losses as well as damage caused by wood-decay fungi, timely felling of severely diseased trees is recommended. Ash dieback will likely weaken the populations of ash trees and secondary pathogens such as *Armillaria* spp. and ash bark beetles may become more important and need to be considered (Kowalski and Holdenrieder, 2008; Thomsen et al., 2009). When intensive care is possible, individual trees can be rescued by cutting infected shoots, twigs and branches. Likewise, young trees can be cut to rescue the stump and root system, from where suckers will develop. However, in both cases, new infections of *H. albidus*/*C. fraxinea* are likely to occur and thus, trees need to be inspected and treated repeatedly.

The most promising potential option for disease management may be the existence of considerable levels of resistance or tolerance within the populations of common ash. In heavily affected areas it is not rare to see severely diseased ash trees growing beside still healthy or little affected trees. Likewise, investigations in seed plantations in Denmark strongly suggest that there are considerable differences in the resistance levels of ash clones towards ash dieback, with some clones hardly being affected (Olrík et al., 2007; Kjær et al., 2009). Preliminary assessments in clonal seed orchards in Austria support this view (C. Freinschlag, C. Jasser, A. Gaisbauer and T. Kirisits, unpublished data). It is therefore recommended that forest owners and foresters record, mark and promote healthy and slightly diseased ash trees growing in severely affected stands and promote natural regeneration of these potentially resistant or tolerant trees. Thereby they may facilitate that resistance levels in the ash populations are maintained, get



stabilized or even increase. Breeding for resistance may be another, more intensive option for disease management in the future.

## 7. REFERENCES

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**Acknowledgements:** The financial support by the Austrian Federal Ministry of Agriculture, Forestry, Environment and Water Management (BMLFUW research project no. 100343, BMLFUW-LE.3.2.3/0001-IV/2/2008), the provincial governments of Lower Austria, Carinthia, Salzburg, Burgenland, Upper Austria and Styria as well as the Austrian Federal Forests (ÖBf AG) is gratefully acknowledged. We thank the Forest Authorities of all Austrian provinces as well as numerous District Forest Authorities and forest owners for the support of our research on ash dieback. The information on the occurrence of ash dieback in various European countries was collected as part of the Coordination Action 'European Network on emerging diseases and threats through invasive alien species in forest ecosystems (FORTHEATS)', contract no. 044436, within the 6<sup>th</sup> Framework Programme of the European Union.