

# 10 Heart Rots, Sap Rots and Canker Rots

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## 10.1 Pathogens, Significance and Distribution

This chapter is mainly devoted to stem rots in temperate and boreal forests of the northern hemisphere, primarily focusing on stands subjected to various management regimes but, to a certain extent, also to nature conservation. Decays of urban and amenity trees in recreational areas are therefore omitted, as well as tree care and 'hazard tree' management practices. For this, refer to Burdekin (1979), Schwarze *et al.* (2000), Sinclair and Lyon (2005), Terho (2009), and the Western Hazard Tree Workshop (2010).

Heart rot is decay in the central stem wood or heartwood. The term heartwood here applies to a cylinder of wood in the centre of tree stems that contains no functional (living) cells and serves merely to provide mechanical support for the crown of the tree (Tainter and Baker, 1996). In certain cases, heart rot-causing fungi in living stems do attack sapwood, which then results in the formation of sap rot. The attacked sapwood might be either dead (e.g. beneath disrupted or dead bark) or functional (e.g. encasing rotten heartwood). When functional sapwood is killed by heart rot fungus this results in

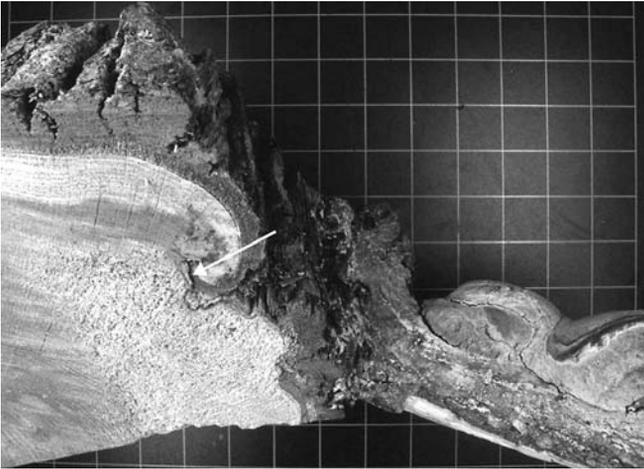
development of stem canker, and such a pattern of the decay is then called a canker rot. Consequently, the same fungus in the living tree might simultaneously cause heart rot, sap rot and canker rot. A typical example of this type of fungus is the polypore *Fomitiporia robusta* (P. Karst.) Fiasson & Niemelä in living English oak (*Quercus robur* L.) (Sunhede and Vasiliauskas, 2002; Fig. 10.1).

### 10.1.1 Ecological groups of heart rot fungi

In a living tree, the heartwood is encased by functionally intact sapwood, which is not susceptible to decay owing to its high moisture content and physiological properties. Moreover, the sapwood is covered by bark, which represents an additional effective barrier to fungal infections. Manion (1991) over-viewed four different concepts of the infection and colonization of a living tree by a decay fungus: (i) the 'Haddow–Etheridge' concept, which implies latent establishment in an intact tree (Haddow, 1938b; Etheridge and Craig, 1976); (ii) the 'Hartig' concept, which implies entry through heartwood-exposing injury (Hartig, 1874); (iii) the 'Shigo' concept

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**Fig. 10.1.** Stem cross-section of *Quercus robur* L. showing heart rot, sap rot and canker rot caused by *Fomitiporia robusta* (P. Karst.) Fiasson & Niemelä. The arrow indicates the part of the stem where the cambium and functional sapwood were killed, leading to canker formation. Note the presence of fruiting bodies (conks) of the fungus on a branch. The black squares in the background are 3 × 3 cm. Modified from Vasiliauskas *et al.* (2003). Credits: Audrius Menkis.

of fungal succession on sapwood wounds (Shigo, 1966); and (iv) the 'Boddy-Rayner' concept, explaining fungal colonization of a tree in terms of wood moisture content (Boddy and Rayner, 1983). It was suggested that it is possible that any of the four concepts might be correct, at least with regard to certain decay phenomena. In fact, while the first three concepts deal in particular with infection courts of fungi on living trees, the fourth mainly reflects patterns of their spread inside a tree. Here, an attempt will be made to demonstrate that all three of the first-mentioned infection concepts are indeed correct and that none of them contradicts any other. Moreover, each of the first three concepts represents a characteristic attribute for respective ecologically distinct groups of stem decay fungi, while the fourth provides a general explanation for the different colonization patterns observed and strategies exhibited by representatives of those ecological groups.

Based on infection pathways, heart rot fungi are traditionally categorized as 'true heart rots' that infect trees through natural infection courts, and 'wound decay fungi' (or in other words, 'wound heart rots') that infect trees through mechanical wounds (Hansen and Lewis, 1997). Yet, such categorization

could be modified and expanded while adapting it to the three infection concepts discussed above, by distinguishing: (i) true heart rots that gain entry to the heartwood of an intact tree using known or considered natural courts of infection and correspond to the Haddow-Etheridge concept; (ii) true heart rots that directly colonize heartwood exposed by natural injuries, such as broken large branches and tops, fire scars and stem cracks, and are thus are grouped under the classical Hartig concept; and (iii) wound heart rots entering heartwood through exposed dead sapwood, which comply with the Shigo infection concept. Table 10.1 presents the most relevant stem rot fungi in respect of those three categories, and includes also a fourth category, root rots and butt rots, which are not covered by other chapters in this volume.

The suggested categorization agrees well with the opinion on stem decay infection courts expressed in the classical work of Boyce (1961). Hyphae from germinating spores cannot penetrate bark or living sapwood. Consequently, a spore must alight on heartwood or exposed deadwood directly connected with heartwood for decay to start in a living tree. However, all the dead branches form bridges from the outside heartwood, as

**Table 10.1.** Main heart rot agents in forest stands of the northern hemisphere. Apart from the citations in the table, the fungi listed are referred to as heart rot and stem decay agents on living trees in classic compendia on forest pathology by Boyce (1961), Hepting (1971) and Sinclair and Lyon (2005).

Fungus	Geographic distribution	Principal host genera	Forest	Referred to as rot agents of living trees	Remarks
<b>1. True heart rots of intact tree stems (infection according the 'Haddow–Etheridge' concept)</b>					
<i>Echinodontium tinctorium</i> (Ellis & Everh.) Ellis & Everh.	Western N. America, Mexico to Alaska	<i>Abies</i>	Old natural <sup>a</sup>	Allen <i>et al.</i> , 1996; Hansen and Lewis, 1997; Holsten <i>et al.</i> , 2001	Inoculated on to living stems to promote wildlife habitats (Filip <i>et al.</i> , 2011)
<i>Fomes fomentarius</i> s.l., clade A (in Judova <i>et al.</i> , 2012)	Temperate and boreal north hemisphere	<i>Alnus</i> , <i>Betula</i> , <i>Fagus</i>	Old natural (when on living trees)	Butin, 1995; Allen <i>et al.</i> , 1996; Holsten <i>et al.</i> , 2001; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007	In Europe, biodiversity component of old-growth beech ( <i>Fagus sylvatica</i> L.) forest (Skov and Thomsen, 2003)
<i>Fomitiporia robusta</i> (P. Karst.) Fiasson & Niemelä	Temperate Eurasia	<i>Quercus</i>	Old natural	Černý, 1989; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007	On over-mature oaks (Sunhede and Vasiliauskas, 2002)
<i>Fomitopsis officinalis</i> (Vill.) Bondartsev & Singer	Temperate and boreal Asia and western N. America	Wide range, coniferous	Old natural	Allen <i>et al.</i> , 1996; Holsten <i>et al.</i> , 2001; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007	Inoculated on to living stems to promote wildlife habitats (Filip <i>et al.</i> , 2011)
<i>Fomitopsis pinicola</i> (Sw.) P. Karst.	Temperate and boreal north hemisphere	Wide range, coniferous and deciduous (when on dead wood)	Old natural (when on living trees)	Allen <i>et al.</i> , 1996; Holsten <i>et al.</i> , 2001; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007	Inoculated on to living stems to promote wildlife habitats (Filip <i>et al.</i> , 2011); mortality agent in pristine forests of north Eurasia (Renvall <i>et al.</i> , 1991; Dai, 1996; Länneppää <i>et al.</i> , 2008)
<i>Inonotus obliquus</i> (Ach. ex Pers.) Pilát	Temperate and boreal north hemisphere	<i>Betula</i>	Old natural	Allen <i>et al.</i> , 1996; Holsten <i>et al.</i> , 2001; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007	
<i>Mensularia radiata</i> (Sowerby) Lázaro Ibiza	Temperate Eurasia	<i>Alnus</i>	Managed and natural	Phillips and Burdekin, 1982; Dai <i>et al.</i> , 2007; Arhipova <i>et al.</i> , 2011a, 2012	
<i>Phellinus chrysoloma</i> (Fr.) Donk	Temperate and boreal Europe	<i>Picea</i>	Old natural	Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007; Tomšovský <i>et al.</i> , 2010a	In Europe, indicator of forest value for nature conservation (Nitare, 2000); mortality agent in pristine forests (Länneppää <i>et al.</i> , 2008)
<i>Phellinus hartigii</i> (Allesch. & Schnabl) Pat.	Temperate Eurasia, boreal N. America	<i>Abies</i> , <i>Tsuga</i>	Old natural	Černý, 1989; Allen <i>et al.</i> , 1996; Holsten <i>et al.</i> , 2001; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007	On <i>Abies</i> in Eurasia, mainly on <i>Tsuga</i> in N. America

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Table 10.1. Continued.

Fungus	Geographic distribution	Principal host genera	Forest	Referred to as rot agents of living trees	Remarks
<i>Phellinus himalayensis</i> Y.C.Dai	Temperate Asia	<i>Picea</i>	Natural	Dai <i>et al.</i> , 2007; Tomšovský <i>et al.</i> , 2010a	
<i>Phellinus igniarius s.l.</i>	Temperate and boreal Asia and N. America	Wide range, deciduous	Natural mature	Allen <i>et al.</i> , 1996; Holsten <i>et al.</i> , 2001; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007	Limited material from USA indicates certain speciation within the group (Fischer and Binder, 2004)
<i>Phellinus jezoënsis</i> (Yamano) Parmasto	Temperate Asia	<i>Picea</i>	Old natural	Dai <i>et al.</i> , 2007; Tomšovský <i>et al.</i> , 2010a	
<i>Phellinus nigricans</i> (Fr.) P. Karst.	Boreal and temperate Europe	<i>Betula</i>	Old natural	Niemelä 1975; Černý, 1989; Tomšovský <i>et al.</i> , 2010b	
<i>Phellinus populicola</i> Niemelä	Temperate and boreal north hemisphere	<i>Populus</i>	Old natural	Manion, 1991; Tainter and Baker, 1996; Fischer and Binder, 2004; Dai <i>et al.</i> , 2007	In Europe, indicator of forest value for nature conservation (Nitare, 2000); red listed (Larsson, 1997)
<i>Phellinus tremulae</i> (Bondartsev) Bondartsev & P.N. Borisov	Temperate and boreal Eurasia and N. America	<i>Populus</i>	Natural	Niemelä, 1974; Černý, 1989; Allen <i>et al.</i> , 1996; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007	Destructive pathogen, limiting economic life of aspen ( <i>Populus</i> spp.) to 40–50 years (Manion, 1991; Tainter and Baker, 1996)
<i>Porodaedalea laricis</i> (Jacz. ex Pilát) Niemelä	Temperate and boreal Eurasia	<i>Larix</i>	Old natural	Dai <i>et al.</i> , 2007; Tomšovský <i>et al.</i> , 2010a	
<i>Porodaedalea pini</i> (Brot.) Murrill	Temperate and boreal Eurasia	<i>Pinus</i>	Old natural	Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007; Tomšovský <i>et al.</i> , 2010a	In Europe, indicator of forest value for nature conservation (Nitare, 2000)
<i>Porodaedalea pini s.l.</i>	Temperate and boreal N. America	<i>Picea</i> , <i>Pinus</i> , <i>Pseudotsuga</i> , <i>Tsuga</i>		Allen <i>et al.</i> , 1996; Tainter and Baker, 1996; Holsten <i>et al.</i> , 2001	Consists of five host-specific groups (Fischer, 1996); in the USA, inoculated on to living stems to promote wildlife habitats (Filip <i>et al.</i> , 2011)
<b>2. True heart rots associated with heartwood-exposing natural injury (broken branches and tops, stem cracks, fire scars; infection according the 'Hartig' concept)</b>					
<i>Fistulina hepatica</i> (Schaeff.) With.	Temperate Europe and N. America	<i>Quercus</i>	Old natural	Phillips and Burdekin, 1982; Butin, 1995	In the past, referred to in Europe as important pathogen of mature oaks ( <i>Quercus</i> spp.) (Aufsess, 1973; Černý, 1989); red listed in north Europe (Larsson, 1997) and indicator of forest value for nature conservation (Nitare, 2000)

<i>Fomitopsis cajanderi</i> (P. Karst.) Kotl. & Pouzar	Western N. America, Pacific Northwest	Coniferous	Natural	Scharpf, 1993; Hansen and Lewis, 1997	Inoculated on to living stems to promote wildlife habitats (Filip <i>et al.</i> , 2011)
<i>Hapalopilus croceus</i> (Pers.) Donk	Temperate Europe and N. America	<i>Quercus</i>	Old natural	Černý, 1989; Sunhede and Vasiliauskas, 2003b	In Europe, in nature conservation areas (Jahn, 1990); red listed (Larsson, 1997) and indicator of forest value for nature conservation (Nitare, 2000)
<i>Inonotus dryophilus</i> (Berk.) Murril	Temperate Europe and N. America	<i>Quercus</i>	Old natural	Berry and Lombard, 1978; Kuzmichev <i>et al.</i> , 2004	In the past, referred to in Europe as important pathogen of mature oaks (Aufsess, 1973; Granatov, 1973); red listed in north Europe (Larsson, 1997)
<i>Laetiporus conifericola</i> Burds. & Banik	Western N. America, California to Alaska	<i>Abies, Picea,</i> <i>Tsuga</i>	Old natural	Burdsall and Banik, 2001; Holsten <i>et al.</i> , 2001	On mature and over-mature trees
<i>Laetiporus cremeiporus</i> Y. Ota & T.Hatt.	Cool temperate and boreal Asia	<i>Quercus</i>	Natural	Dai <i>et al.</i> , 2007; Ota <i>et al.</i> , 2009	
<i>Laetiporus gilbertsonii</i> Burds.	Western N. America, Mexico to Washington	<i>Quercus</i>	Natural	Burdsall and Banik, 2001	
<i>Laetiporus huroniensis</i> Burds. & Banik	Eastern N. America, Great Lakes area	<i>Tsuga</i>	Old natural	Burdsall and Banik, 2001	On mature and over-mature trees
<i>Laetiporus montanus</i> Černý ex Tomšovský & Jankovský	Cool temperate and boreal Eurasia	<i>Abies, Larix,</i> <i>Picea, Pinus</i>	Old natural	Černý, 1989; Dai <i>et al.</i> , 2007; Ota <i>et al.</i> , 2009	In Europe, on over-mature trees
<i>Laetiporus sulphureus s.l.</i> , clades C and E (in Vasaitis <i>et al.</i> , 2009)	Temperate Europe and N. America	<i>Quercus</i>	Old natural	Vasiliauskas <i>et al.</i> , 2003; Banik <i>et al.</i> , 2010	In Europe, on over-mature oaks
<i>Laetiporus versisporus</i> (Lloyd) Imazeki	Warm temperate Asia	<i>Quercus</i>	Natural	Dai <i>et al.</i> , 2007; Ota <i>et al.</i> , 2009	

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Table 10.1. Continued.

Fungus	Geographic distribution	Principal host genera	Forest	Referred to as rot agents of living trees	Remarks
<i>Pholiota adiposa</i> (Batsch) P. Kumm., <i>P. squarrosa</i> (Vahl) P. Kumm.	Temperate and boreal northern hemisphere	<i>Abies</i> , <i>Betula</i> , <i>Tsuga</i>	Old natural	Scharpf, 1993; Tainter and Baker, 1996; Holsten <i>et al.</i> , 2001; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007	Root/butt rot of deciduous trees (Phillips and Burdekin, 1982; Butin, 1995); stem rot of alder/spruce (Arhipova <i>et al.</i> , 2011a; Cleary <i>et al.</i> , 2013); wound rot of birch ( <i>Betula</i> ) (Shigo, 1966)
<i>Stereum gausapatum</i> (Fr.) Fr.	Temperate Europe and N. America	<i>Quercus</i>	Managed and natural	Aufsess, 1973; Berry and Lombard, 1978; Phillips and Burdekin, 1982	Produces fruiting bodies on old standing trunks and still attached branches (Eriksson <i>et al.</i> , 1984)
<i>Xylobolus frustulatus</i> (Pers.) Boidin	Temperate Europe and N. America	<i>Quercus</i>	Natural	Aufsess, 1973; Berry and Lombard, 1978; Butin, 1995	In Europe, on old-growth oaks (Sunhede and Vasiliauskas, 1996)
<b>3. Wound heart rots associated with artificial mechanical damage (logging, bark stripping, pruning wounds; infection according the 'Shigo' concept)</b>					
<i>Amylostereum areolatum</i> (Chaillat ex Fr.) Boidin	Temperate and boreal Eurasia	<i>Picea</i> , <i>Pinus</i>	Managed	Hansen and Lewis, 1997; Vasiliauskas, 1998a, 2001 and references therein	Fruiting bodies common on woody debris of spruce ( <i>Picea</i> spp.) (Breitenbach and Kränzlin, 1986; Jahn, 1990)
<i>Amylostereum chaillatii</i> (Pers.) Boidin	Temperate and boreal northern hemisphere	Wide range, coniferous	Managed	Hansen and Lewis, 1997; Vasiliauskas, 1998a, 2001 and references therein	Fruiting bodies common on woody debris of fir ( <i>Abies</i> spp.) (Breitenbach and Kränzlin, 1986); often on left logs (Eriksson and Ryvarde, 1973)
<i>Chondrostereum purpureum</i> (Pers.) Pouzar	Temperate and boreal northern hemisphere	<i>Alnus</i> , <i>Betula</i>	Managed	Shigo, 1966; Phillips and Burdekin, 1982; Butin, 1995; Arhipova <i>et al.</i> , 2011a, 2012	Fruiting bodies common on stumps (Eriksson and Ryvarde, 1973); on dead wood of broadleaved trees (Breitenbach and Kränzlin, 1986)
<i>Coniophora puteana</i> (Schumach.) P. Karst., <i>C. arida</i> (Fr.) P. Karst.	Temperate and boreal western N. America and Europe	<i>Fraxinus</i> , <i>Quercus</i> , <i>Picea</i> , <i>Tsuga</i>	Natural and managed	Černý, 1989; Vasiliauskas, 1998b,c; Vasiliauskas and Stenlid, 1998b; Cleary <i>et al.</i> , 2013	Fruiting bodies on dead wood (Jahn, 1990; Ryman and Holmåsén, 1992); consistent latent infections to living trees/intact sapwood; mortality agents in pristine boreal conifer forests (Holsten <i>et al.</i> , 2001; Länneppää <i>et al.</i> , 2008)

<i>Pleurotus ostreatus</i> (Jacq.) P. Kumm., <i>P. dryinus</i> (Pers.) P. Kumm.	Temperate and boreal northern hemisphere	Deciduous and coniferous	Managed and natural	Phillips and Burdekin, 1982; Černý, 1989; Vasiliauskas, 1989; Butin, 1995; Dai <i>et al.</i> , 2007	Fruiting bodies on stumps and lying stems; cultivated on dead wood as a culinary species (Butin, 1995)
<i>Postia caesia</i> (Schrad.) P. Karst.	Boreal and temperate Eurasia	<i>Picea</i>	Managed	Vasiliauskas, 1989; Butin, 1995	Fruiting bodies on rotten conifer and hardwood logs and slash (Ryvarden and Gilbertson, 1994); on stumps (Breitenbach and Kränzlin, 1986)
<i>Postia stiptica</i> (Pers.) Jülich	Temperate and boreal northern hemisphere	<i>Picea</i>	Managed	Phillips and Burdekin, 1982; Černý, 1989; Butin, 1995; Vasiliauskas, 1998b	Fruiting bodies on rotten conifers and hardwoods (Ryvarden and Gilbertson, 1994); on stumps (Breitenbach and Kränzlin, 1986)
<i>Resinicium bicolor</i> (Alb. & Schwein.) Parmasto	Temperate and boreal northern hemisphere	<i>Picea</i>	Managed	Vasiliauskas, 1998a,b; Cleary <i>et al.</i> , 2013	Fruiting bodies on rotten barkless stumps (Breitenbach and Kränzlin, 1986); important as decomposer of dead wood (Eriksson <i>et al.</i> , 1981)
<i>Sistotrema brinkmannii</i> (Bres.) J. Erikss.	Temperate and boreal northern hemisphere	<i>Picea</i>	Managed	Vasiliauskas, 1998a,b	Fruiting bodies mostly on much decayed wood (Eriksson <i>et al.</i> , 1984); on dead wood of broadleaves and conifers (Breitenbach and Kränzlin, 1986)
<i>Stereum hirsutum</i> (Willd.) Pers.	Temperate and boreal northern hemisphere	<i>Quercus</i>	Managed	Shigo, 1966; Jahn, 1990; Vasiliauskas, 1998c	Fruiting bodies on dead deciduous wood (Eriksson <i>et al.</i> , 1984; Breitenbach and Kränzlin, 1986)
<i>Stereum sanguinolentum</i> (Alb. & Schwein.) Fr.	Boreal and temperate Eurasia	Wide range, coniferous	Managed	Phillips and Burdekin, 1982; Butin, 1995; Allen <i>et al.</i> , 1996; Hansen and Lewis, 1997; Dai <i>et al.</i> , 2007	Especially common on newly dead logs and stumps (Eriksson <i>et al.</i> , 1984); typical decomposer of logging residues (Vasiliauskas, 1989)
<i>Trametes versicolor</i> (L.) Lloyd	Temperate and boreal northern hemisphere	<i>Betula</i> , <i>Quercus</i>	Managed	Shigo, 1966; Phillips and Burdekin, 1982; Butin, 1995; Vasiliauskas, 1998c	Probably the most common wood rotting fungus on dead hardwoods (Ryvarden and Gilbertson, 1994)
<b>4. Root and butt rots (not covered by other chapters in this volume)</b>					
<i>Climacocystis borealis</i> (Fr.) Kotl. & Pouzar	Temperate and boreal northern hemisphere	<i>Picea</i> , <i>Pinus</i> , <i>Tsuga</i>	Old natural	Černý, 1989; Holsten <i>et al.</i> , 2001; Kuzmichev <i>et al.</i> , 2004	In Europe, indicator of forest value for nature conservation (Nitare, 2000)

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Table 10.1. Continued.

Fungus	Geographic distribution	Principal host genera	Forest	Referred to as rot agents of living trees	Remarks
<i>Ganoderma applanatum</i> (Pers.) Pat.	Temperate and boreal northern hemisphere	Wide range, deciduous and coniferous	Natural and managed	Allen <i>et al.</i> , 1996; Holsten <i>et al.</i> , 2001; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007	In North America, serious pathogen of deciduous forests (Ross, 1976; Manion, 1991); urban in Europe (Terho, 2009)
<i>Grifola frondosa</i> (Dicks.) Gray	Temperate Europe and N. America	<i>Quercus</i>	Old natural	Berry and Lombard, 1978; Phillips and Burdekin, 1982; Černý, 1989; Butin, 1995	Red listed in northern Europe (Larsson, 1997); indicator of forest value for nature conservation (Nitare, 2000)
<i>Inonotus leporinus</i> (Fr.) Gilb. & Ryvar den	Boreal and temperate Eurasia	<i>Picea</i>	Old natural	Černý, 1989; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007	Mortality agent in pristine forests of north Europe (Län nenpää <i>et al.</i> , 2008); red listed (Larsson, 1997) and indicator of forest value for nature conservation (Nitare, 2000)
<i>Perenniporia subacida</i> (Peck) Donk	Boreal and temperate N. America and Asia	Wide range, coniferous	Old natural	Scharpf, 1993; Allen <i>et al.</i> , 1996; Hansen and Lewis, 1997; Dai <i>et al.</i> , 2007	Old-growth conifer forests
<i>Phaeolus schweinitzii</i> (Fr.) Pat.	Temperate and boreal northern hemisphere	Wide range, coniferous	Old natural	Scharpf, 1993; Allen <i>et al.</i> , 1996; Hansen and Lewis, 1997; Holsten <i>et al.</i> , 2001; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007	In Europe, indicator of forest value for nature conservation (Nitare, 2000)
<i>Pseudoinonotus dryadeus</i> (Pers.) T. Wagner & M. Fisch.	Western N. America, Mexico to British Columbia, Europe, Asia	<i>Abies, Quercus</i>	Old natural	Hansen and Lewis, 1997; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007	Red listed in northern Europe (Larsson, 1997); indicator of forest value for nature conservation (Nitare, 2000)
<i>Sparassis crispa</i> (Wulfen) Fr.	Boreal and temperate Eurasia	<i>Larix, Pinus</i>	Old natural	Phillips and Burdekin, 1982; Černý, 1989; Butin, 1995; Dai <i>et al.</i> , 2007	In Europe, indicator of forest value for nature conservation (Nitare, 2000)

<sup>a</sup>In geographic regions with intensive forestry, old natural forest is as a rule synonymous with protected forest.

does the exposed dead sapwood where the bark has been knocked off by injuries such as lightning wounds, breaking branches, falling trees and many others. Broken tops give direct access to the heartwood, as do fire scars when the fire has eaten deeply enough into the tree. Notably, the injuries considered in this fundamental work as the most important are those arising during natural ecosystem processes, and are typical attributes of old-growth forest. Consequently, the work of Boyce (1961), which has already been cited, reflects the infection pathways of the first two heart rot categories in Table 10.1.

Recent decades of forestry have been marked by a rapid increase in the area of forest plantations that is intensively managed for wood and/or wildlife. Characteristic of such stands is the presence on living stems of logging and bark stripping wounds, and in certain forest areas trees without such injuries have become uncommon (Steyrer, 1992). The wounds result in sapwood exposure, thus providing access for decay fungi to the heartwood. The exposed sapwood then becomes subject to fungal succession, and certain fungi, upon reaching the heartwood, are able to cause heart rot in living wounded trees (Shigo, 1965; Vasiliauskas, 1998a, 2001). Such heart rot will subsequently be referred to as a wound heart rot. Traits and impacts of all three categories of heart rots, and of certain butt rots and root rots, as well as of the saprotrophs (agents of sap rot in dead stems) will be discussed elsewhere in this chapter. It will be demonstrated that fungi from each group possess a number of rather distinct ecological traits and differ markedly in their infection biology, host colonization strategies, ecological roles and pathological impacts.

### 10.1.2 Pathogens

All the wound heart rot pathogens listed in the Table 10.1 were traditionally known as saprotrophic decomposers of various kinds of woody debris. Yet, seemingly, those species are adapted to penetrate the stem of a tree through exposed dead sapwood, become established and cause heart rot in

a living stem. Still, due to the presence of a large number of wounded trees in managed forests, these fungi emerged as pathogens, threatening sustainable production of wood over large territories, e.g. in Europe (Vasiliauskas, 2001). In a way, these saprobes should now be considered to be more important heart rot pathogens than the classical true heart rot fungi that have been previously treated in texts of forest pathology.

Apart of those listed in Table 10.1, there are a few other heart rots that are deemed relevant for forest health in certain geographic areas. For example, *Inonotus andersonii* (Ellis & Everh.) Černý and *Perenniporia compacta* (Overh.) Ryvarden & Gilb. were reported as the most destructive heart rots of oaks (*Quercus* spp.) in the central USA (Berry and Lombard, 1978); *I. glomeratus* (Peck) Murrill is a common cause of canker rot in maples (*Acer* spp.) and beeches (*Fagus* spp.) in north-east USA (Manion, 1991); *Oxyporus populinus* (Schumach.) Donk cause hollows in the stems of maple and other hardwoods (Manion, 1991; Tainter and Baker, 1996); and *I. hispidus* (Bull.) P. Karst. is a heart rot agent on oaks, birches (*Betula* spp.), ashes (*Fraxinus* spp.) and other hardwoods in the USA and Europe (Butin, 1995; Tainter and Baker, 1996) – although in north-eastern Europe this fungus is rare and is red listed (Larsson, 1997). The only ascomycete to be mentioned in this chapter is *Kretzschmaria deusta* (Hoffm.) P.M.D. Martin, a cause of butt rots of many deciduous trees in the USA and Europe (Manion, 1991; Butin, 1995; Tainter and Baker, 1996). On conifers, conspicuous heart rot pathogens include *Tyromyces amarus* (Hedgc.) J. Lowe on cedar (*Chamaecyparis* spp.), and *Poria sequoiae* Bonar on redwood (*Sequoia sempervirens* (Lamb. ex D. Don) Endl.), both occurring in old-growth stands of the Pacific coast, and both strictly specific to their respective hosts (Scharpf, 1993; Tainter and Baker, 1996). A relevant example of butt heart rot of regional importance is *Hericium abietis* (Weir ex Hubert) K.A. Harrison, which infects old-growth true firs (*Abies* spp.) on the Pacific coast (Scharpf, 1993; Hansen and Lewis, 1997), and hemlock (*Tsuga* spp.) and spruce (*Picea* spp.) in Alaska (Holsten *et al.*, 2001).

### 10.1.3 Habitats

The infection courts of true and wound heart rot fungi fundamentally differ. As a rule, representatives of the first group are not capable of entering (younger) trees via artificial sapwood wounds, while the representatives of the second group are unable to infect (older) trees via natural pathways. As true heart rots are normally associated either with intact ageing stems or with stem injuries arising during natural ecosystem disturbance, one might argue that true heart rot fungi have evolved simultaneously with the evolution of forest ecosystems and are natural components of these ecosystems. Because with stand age numbers of both ageing weakened trees and of natural injuries in stands tend to increase, true heart rots become increasingly common in older forests, and currently represent the typical attributes of natural old-growth forest. In fact, the same also applies to root and butt heart rots. In comparison, wound heart rot fungi infect heartwood through artificially inflicted mechanical injuries, such as logging and bark stripping wounds (note that bark stripping does not normally occur in pristine forests) (Shigo, 1966; Vasiliauskas, 1998a, 2001), pruning damage (Risley and Silverborg, 1958; Metzler, 1997) or parent stumps (Berry and Lombard, 1978), so they are characteristic pathogens in forest stands managed for timber and big game. Stands are subjected to logging damage (and pruning) from the age of around 30 years, and to bark stripping damage mostly at the age of 30–50 years (Vasiliauskas, 1989, 1998a, 2001). Consequently, wound heart rots are typical attributes of younger forests. Therefore, different fungi infect tree stems in natural forests and managed stands, and the communities of heart rots in those habitats differ fundamentally.

Such a trend had already been noted in an early study by Maloy and Robinson (1968), in which the true heart rot *Echinodontium tinctorium* (Ellis & Everh.) Ellis & Everh. was not once isolated from the heartwood of 15–30 year old stems of grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.) with open and healed scars, despite them showing decay similar to that caused by the fungus (a white rot); instead, only the wound heart rot fungus *Stereum sanguinolentum* (Alb. & Schwein.)

Fr. was isolated from those trees, while *E. tinctorium* was associated with heart rot only in trees over 150 years of age. Although there were singular cases when true heart rot fungi (*Fomitopsis pinicola* (Sw.) P. Karst. and *Phellinus chrysoloma* (Fr.) Donk) were observed or isolated from logging and bark stripping damaged spruce (Vasiliauskas, 1989; Vasiliauskas and Stenlid, 1998a), it is likely that the trees were entered through natural infection courts; no other true (or root and butt) heart rots of spruce have been found associated with superficial sapwood wounds. Furthermore, the true heart rots of oak *F. robusta* and *Laetiporus sulphureus* s.l. were reported as dominant in over-mature stands (Sunhede and Vasiliauskas, 1996), but they were never observed in middle-aged stands suffering from bark stripping (Vasiliauskas, 1998c). In birch stands in north Europe, none of the dominant decayers of mature forest, such as *Fomes fomentarius* (L.) J. Kickx f., *Inonotus obliquus* (Ach. ex Pers.) Pilát, *Phellinus igniarius* s.l. and *Piptoporus betulinus* (Bull.) P. Karst. (Niemelä, 1975; Roll-Hansen, 1981), were detected in discolorations resulting from broken branches and logging wounds in managed younger stands (Hallaksela and Niemistö, 1998; Vasaitis *et al.*, 2012a). Similarly, in beech forests in south Germany, true heart rot *F. fomentarius* was reported to be the most common fungus in virgin forests and strict forest reserves, but was almost missing in stands with a high management intensity (Müller *et al.*, 2007).

Thus, true heart rots are a characteristic feature of old forest ecosystems, which, as a rule, are now under a protection regime. Consequently, this group of fungi should nowadays be viewed from the perspective of nature conservation rather than forest pathology. In contrast, wound heart rots are already introduced to young stands by management activities, and are a characteristic feature of forests under anthropogenic pressure.

### 10.1.4 Impact

#### *True heart rots and root and butt heart rots*

In individual stems, the volume of decay and losses in wood production caused by these

heart rots vary among fungal and tree species, but are usually significant (Berry and Lombard, 1978). Consequently, heart rots in forest stands were traditionally referred to as the most damaging of all types of tree disease, and much more important in mature and over-mature stands than in young stands (Tainter and Baker, 1996). It is assumed that losses due to decay increase with increasing tree age and are usually insignificant in trees less than 90 years old (Hansen and Lewis, 1997). According to graphs developed by Hepting and Hedgcock (1937), cull percentage in natural stands of oaks (northern red oak, *Q. rubra* L.; black oak, *Q. velutina* Lam.; white oak, *Q. alba* L.; and chestnut oak, *Q. prinus* L.) and tulip tree (*Liriodendron tulipifera* L.) would consistently increase with increasing percentage of trees with basal fire scars and stem diameter. Then, provided that 100% of trees possess fire scars: in a stand with an average tree diameter of 30 cm, the percentage cull would typically consist of 10–15%; in a stand of average tree diameter 50 cm, it would be 15–20%; and in a stand of average tree diameter of 75 cm, it would be 20–25%. In old-growth stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the US Pacific Northwest, the volume of cull caused by *Porodaedalea pini* (Brot.) Murrill, *Fomitopsis officinalis* (Vill.) Bondartsev & Singer, *F. cajanderi* (P. Karst.) Kotl. & Pouzar and *Phaeolus schweinitzii* (Fr.) Pat. was reported to comprise only 4% in 80–120 year old stands, but 34–85% in 160–200 year old and older stands (Tainter and Baker, 1996). Notably, the first three species of the true heart rot fungi just listed (as well as others) are now being used (and by forest pathologists themselves) for artificial inoculations of Douglas-fir and other conifers in the region so as to promote stem decay in trees to be subsequently used as wildlife habitats (Filip *et al.*, 2011). Consequently, the impacts of these disease agents currently clearly fall outside the range of forest pathology.

Moreover, as old-growth forests disappear or are being excluded from harvesting, there is simultaneously a decrease in losses caused by true heart rot fungi. For example, in the early 1900s in the USA, heart rot in the southern pines averaged about 20% of

the volume of the harvested timber for sawn timber production, but in the late 1900s losses were less than 1% (Tainter and Baker, 1996). In Europe, heart-rotting fungi of old natural (often montane) habitats have also previously been considered to be important forest pathogens. In a book by Černý (1989), for instance, *P. pini*, *P. schweinitzii*, *Onnia triquetra* (Pers.) Imazeki, *Phellinus vorax* (Harkn.) Černý and *Laetiporus montanus* Černý ex Tomšovský & Jankovský are the only heart rot fungi attributed to pine (*Pinus* spp.), and it is even implied that forests should be protected against these fungi. Conversely, current understanding would suggest that the occurrence of each of those fungi in a forest stand is a good indicator for the habitat to be considered for nature conservation (Nitare, 2000).

Apart from the impact of true heart rot fungi on and their beneficial roles in wildlife and habitat conservation, there is an increasing understanding of their relevance in natural stand development. Certain studies suggest that the role of these fungi in forest dynamics is more important than that of fire. Lewis and Lindgren (1999) investigated the importance of decay fungi as agents of gap formation and facilitators of uneven-aged stand structure in sub-boreal forests of British Columbia. The results indicated that decay fungi, in particular *E. tinctorium*, play an important role in removing fir from the overstorey and in enabling spruce recruitment. In pristine boreal forests of Europe, *Coniophora* spp., *P. chrysoloma*, *F. pinicola* and *Inonotus leporinus* (Fr.) Gilb. & Ryvar den were the main mortality agents of spruce, playing a key role in forest succession (Lännenpää *et al.*, 2008). *F. pinicola* has been reported as a mortality agent of old-growth spruce in pristine northern forests of Europe (Kotiranta and Niemelä, 1981; Renvall *et al.*, 1991), China (Dai, 1996) and Alaska (Holsten *et al.*, 2001). Also, fallen trunks provide habitats for many organisms (e.g. decay fungi inhabiting wood at late decomposition stages) and serve as nurse logs for subsequent forest regeneration (Vasiliauskas *et al.*, 2004).

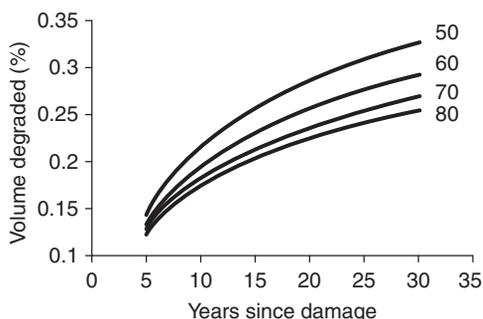
Among the true heart rots of economic importance, the most notorious is *Phellinus tremulae* (Bondartsev) Bondartsev & P.N. Borisov, which often almost totally destroys the timber

harvest in aspen (*Populus* spp.) stands that are already aged 40–50 years, which are distributed over large areas of the whole northern hemisphere (Niemelä, 1974; Tainter and Baker, 1996; Kuzmichev *et al.*, 2004; Dai *et al.*, 2007). In contrast, no heart rots were detected in 30 year old stands of birch, and the observed discolorations of heartwood, although common, were restricted and had no effect on wood quality (Hallaksela and Niemistö, 1998). For other tree species, a recent study in north-eastern Europe showed that a large proportion (75% on average) of trees in mature and over-mature stands of European (black) alder (*Alnus glutinosa* (L.) Gaertn.) is damaged by a heart rot, and that the principal agent is *Mensularia radiata* (Sowerby) Lázaro Ibiza. Decay columns of an average length of 7.7 m long develop in stems, and 4.2 m of this comprises the advanced (spongy) stages of rot (Arhipova *et al.*, 2012). This implies that the yield loss for a fully stocked 80 year old European alder stand would comprise 49.2% of the total stand volume, while the losses from advanced spongy rot would be 30.5%. According to a heart rot study in grey alder (*A. incana* (L.) Moench), the cull volume would be 32 m<sup>3</sup> ha<sup>-1</sup> at stand age of 45–50 years and 60 m<sup>3</sup> ha<sup>-1</sup> at age 60–65 years, corresponding to about 10% and 20% of the standing volume of a pure fully stocked stand (Arhipova *et al.*, 2011b). However, as the principal fungus isolated from decay columns was *Chondrostereum purpureum* (Pers.) Pouzar, it is unlikely that the observed heart rots were true heart rots.

#### Wound heart rots

Wound heart rot is a problem of intensively managed forest. Typical examples are European forests, where trees commonly suffer mechanical injuries inflicted during various types of selective harvesting, and bark stripping by deer and moose. In regions where shelterwood forestry is combined with game management (as is traditional in central and northern Europe), the proportion of wounded stems in the total growing stock could reach 20–50%, or even 60–90% (Vasiliauskas, 2001; Vasaitis *et al.*, 2012b). The pathological impacts of wound heart rots

have been reviewed by Vasiliauskas (2001), and it has been demonstrated that yield losses can be significant, depending on the number of wounded trees, the time since the damage occurred, stand age and forest productivity. For example, in a productive fully stocked 80 year old stand of spruce with 100% of stems wounded 30 years previously, cull volume would comprise 25% of the total standing volume (Fig. 10.2), while in a 70 year old stand of oak and a 100 year old stand of ash, the proportions of cull volume would comprise 10% and 60%, respectively. Note that, as tree growth exceeds heart rot spread, the proportion of cull volume decreases in older stands, although because the most valuable butt log is affected, the financial losses have been reported to increase with time (Vasiliauskas, 2001). Also more recent studies have shown that bark stripping and subsequent rot has decreased the financial value of 30 year old stems of fir and ash by 22.5% and 25.7%, respectively, and that the losses tend to increase in older trees (Barszcz and Jamroz, 2001). In this respect, birch seems to be an exception, as wound heart rot does not usually develop beyond its logging wounds, and discoloration is mainly restricted to the damaged portion of a stem (Shigo, 1966; Vasaitis *et al.*, 2012a). Consequently, the associated loss of wood production is reported to remain low during about 10 years after the damage has occurred.



**Fig. 10.2.** Percentage of cull volume comprising wound heart rot in fully stocked *Picea abies* (L.) Karst. stands containing 1% of stems with logging and/or bark stripping wounds in relation to stand age (50, 60, 70 and 80 years) and years since the damage (reprinted from Vasiliauskas, 2001).

The overall large impact of wound heart rots on forestry has been known for a long time. Thus, in Austria in 1961–1970, production loss due to logging damage has been estimated to comprise 30 million m<sup>3</sup> (Schimitschek, 1975). The situation with bark stripping damage is more complex and the losses cannot be expressed solely by decayed wood volume. Because, as a rule, the injury is located at a stem height of around 1.5 m, decay development makes such stems prone to wind and snow damage at a premature age. This leads to the destruction of middle-aged stands by wind and snow, and young forest has to be clear-felled and replanted.

## 10.2 Diagnosis

The presence of fruiting bodies and injuries are the symptoms that a tree is infected by a heart rot fungus, and the fruiting bodies also provide information on the identity of the fungus. Correlations between the presence of fruiting bodies (even their number and size) with the extent of heart rot in a stem were analysed by Boyce (1961). The analysis reflects data from different tree species and pathogens, but mainly true heart rots in mature and over-mature natural forests, and generally indicates that fruiting bodies of true heart rot fungi are formed after the tree stem has been extensively colonized. The presence of fruiting bodies of true heart rot fungi therefore implies that the larger part or entire trunk of the tree has already been transformed to cull status (Allen *et al.*, 1996). For example, the stems of firs and aspens bearing several fruiting bodies of *E. tinctorium*, *P. tremulae* and *P. pini* from a wood yield point of view are referred to as a total loss (Tainter and Baker, 1996). Conversely, the presence of fruiting bodies of root and butt heart rot fungi in most cases indicates that the decay column is restricted to the butt region (Phillips and Burdekin, 1982; Allen *et al.*, 1996). However, one should keep in mind that intact trees infected by true heart rot usually show neither fruiting bodies nor other external symptoms (Hansen and Lewis, 1997).

Logging, bark stripping and other similar wounds are indicators of wound heart rot.

Fruiting bodies of wound heart rot fungi are seldom produced on a surface of exposed sapwood, and the main value in wound heart rot diagnostics is not the presence of fruiting bodies, but the size (exposed sapwood area) and age of the injury. The pathological consequences of the mechanical wounding of a number of forest trees and decay agents have been reviewed by Vasiliauskas (2001). This review demonstrates that the majority of sapwood wounds have already been entered by stain or decay fungi by 2 years after injury, and that decay columns develop during subsequent years. For example, over 80% of logging and bark stripping wounds on spruce are colonized by decay fungi, which in 10–25 years spread over the heartwood and by 3–5 m longitudinally; the length of heart rot correlates positively with the wound dimensions. Bark stripping wounds on oak are typically associated with over 1 m long decay columns (Vasiliauskas, 1998c), and on fir with 2–3 m long decay columns (Barszcz and Jamroz, 2001; Pach, 2005), while in ash they result in 8–9 m long heartwood discolorations (Vasiliauskas and Stenlid, 1998b). In comparison, in stems of birch, discoloration associated with logging damage is largely confined to the limits of the wound (Shigo, 1966; Vasaitis *et al.*, 2012a), and the same applies to beech (Schumann and Dimitri, 1993). In addition, the studies cited above indicate that following wound closure, decay development in spruce, fir and oak is confined. Moreover, a recent study by Vasaitis *et al.* (2012b) demonstrated that spruce wounds of initial width <4 cm will usually occlude without being infected by decay, while no wounds that are initially 15 cm wide will occlude during 20 years (Fig. 10.3). Apart from wound decay diagnostics, the probability of wound occlusion brings into any plan certain disease management implications that are discussed later.

For the identification of all types of heart rots in the absence of fruiting bodies, samples of decayed wood need to be taken from a tree, followed by fungal isolation into pure culture and identification either by culture morphological characteristics (e.g. Stalpers, 1978; Vasiliauskas *et al.*, 1998), or by culture analysis using molecular methods (e.g. Lygis *et al.*, 2005;



**Fig. 10.3.** Occlusion of *Picea abies* (L.) Karst. stem wounds. (A)–(F), 19 year old wounds: occluded of 1 × 15 (A), 2 × 15 (B), 3 × 15 (C) and 4 × 15 (E) cm initial size, and open of 3 × 15 (D) and 5 × 15 (F) cm initial size; G–J, 20 year old wounds of 15 × 20 cm initial size: nearly occluded (G), occluding (H), and non-occluding (I) and (J); size of paper sheet 5 × 5 cm. Note the exit holes of siricid woodwasps in (F) and (J), indicating that the trees are decayed by *Amylostereum* wound heart rot, and that the pathogens were introduced to trees by the insects. Credits: Vaidotas Lygis.

Nicolotti *et al.*, 2010). Recently, molecular methods have been developed for detection of the latent presence of decay fungi directly from environmental samples taken from

visually healthy trees (Nicolotti *et al.*, 2010; Parfitt *et al.*, 2010), although these methods are laborious and too costly to be applied in practical forestry.

### 10.3 Infection Biology and Epidemiology

#### 10.3.1 Courts of infection

##### *True heart rots in intact trees*

Traditionally, it has been assumed that the entry point of heart rot to an otherwise intact stem has to be via a branch stub large enough to connect the heartwood with the outside environment (Boyce, 1961). This assumption was based on the simple fact that the fruiting body of a heart rot fungus is typically formed on or in the vicinity of a branch stub. However, some early studies have already indicated different modes of the establishment of heart rot fungi in intact trees. For example, Basham (1966) reported that while *P. pini* was the most common fungus isolated from heart rot columns of pine, it was only occasionally detected in branch stubs, and only in those encased by decayed heart rot, so that it had evidently entered the stubs from established rot and not *vice versa*. Haddow (1938a) reported that *P. pini* infects pines at young age through dead twigs (of only a few millimetres in diameter) and weevil-killed leaders. Furthermore, it was shown that another heart rot fungus, *E. tinctorium*, establishes in hemlock branchlets 0.5–1.5 mm in diameter and remains dormant until it is embedded by heartwood at some point in the future. Significant heart rot develops later, after the infected trees become old and are stressed through wounding or other factors (Etheridge and Craig, 1976; Holsten *et al.*, 2001). Moreover, dwarf mistletoe (*Arceuthobium* spp.) and fir broom rust (*Melampsorella caryophyllacearum* (DC.) J. Schröt.) infections were reported to serve as entry points for *Phellinus hartigii* (Allesch. & Schnabl) Pat. to stems of fir (Gilbertson and Ryvarden, 1987; Černý, 1989), and small twigs were demonstrated to be infection foci of *P. tremulae* for stems of aspen (Holmer *et al.*, 1994). On old-growth oaks, fruiting bodies of *F. robusta* were commonly observed on intact living branches 5–30 cm thick (Sunhede and Vasiliauskas, 2002). Hence, the question of whether branch stubs serve both as an entry and exit point for a fungus, or only as an exit point following a

substantial period of latent establishment in a living tree, has remained open (Rayner and Boddy, 1988).

Currently, the evidence is increasingly accumulating on the latent presence of decay fungi in the functional sapwood of intact trees, and such data is summarized in Table 10.2. Apart from the true heart rot agents that have already been discussed, *F. fomentarius*, *F. pinicola* and *M. radiata* were consistently detected in sound wood (and *F. pinicola* also in healthy phloem) of living trees, either by isolations or molecular methods. It should be noted that for those heart rot fungi the main infection court was traditionally thought to be stem injuries and large wounds on which fruiting bodies formed (Schwarze *et al.*, 2000). In the case of *F. fomentarius* though (for example), neither stem dissection nor rot column analysis could trace infections to stem wounds in beech (Skov and Thomsen, 2003). It is, therefore, likely that a period of latent establishment precedes the development of active decay in true heart rots, thus complying with the Haddow–Etheridge concept, although the pathways followed by most of these are unknown. A study by Oses *et al.* (2008) demonstrated the presence of fungal hyphae attached to the inner cell surface of healthy living tree xylem before the induction of wood degradation. Thin periderm, lenticels, scars on twigs, leaves and buds were all considered as infection courts for the latent establishment of propagules of decay fungi (Baum *et al.*, 2003; Parfitt *et al.*, 2010).

Notably, in order to be able to develop subsequent active decay, except for homothallic fungi, at least two spores of opposite mating types must penetrate, come in contact with each other and form a stable heterokaryon inside the xylem of a living tree. For example, heterokaryons of *P. betulinus* were regularly detected in intact birch, and there were no cases where the same genotype was obtained from more than one tree, suggesting that genetically diverse basidiospores act as infective agents (Adams, 1982). One possible scenario could then be the airborne arrival of basidiospores, which land on the tree surface, germinate and colonize certain areas of the surface by vegetative spread of homokaryotic mycelium; this is

**Table 10.2.** Decay fungi detected as latent in visually healthy intact trees.

Fungus	Tree species	Substrate	Reference	Remarks
<b>1. True heart rots of intact tree stems</b>				
<i>Echinodontium tinctorium</i> (Ellis & Everh.) Ellis & Everh.	<i>Tsuga heterophylla</i> (Raf.) Sarg.	Dead 1 mm diameter branchlets	Etheridge and Craig, 1976	The branchlets are subsequently encased by healthy stemwood
<i>Fomes fomentarius</i> (L.) J. Kickx f.	<i>Acer campestre</i> L., <i>Betula</i> spp., <i>Fraxinus excelsior</i> L., <i>Malus domestica</i> Borkh., <i>Quercus robur</i> L., <i>Salix</i> spp. <i>Fagus sylvatica</i> L.	Healthy xylem/ functional sapwood of branches and stems Healthy xylem	Parfitt <i>et al.</i> , 2010  Baum <i>et al.</i> , 2003; Parfitt <i>et al.</i> , 2010	Also rot of intact <i>Alnus incana</i> and <i>A. glutinosa</i> stems (Arhipova <i>et al.</i> , 2011a, 2012)
<i>Fomitopsis pinicola</i> (Sw.) P. Karst.	<i>Picea abies</i> (L.) Karst.  <i>Alnus glutinosa</i> (L.) Gaertn.	Sound wood of intact stems Intact stem phloem Sound wood of intact stems	Vasiliauskas <i>et al.</i> , 2001 R. Vasaitis <i>et al.</i> , 2012, unpublished results Arhipova <i>et al.</i> , 2012	Also rot of intact <i>A. glutinosa</i> and <i>A. incana</i> (Arhipova <i>et al.</i> , 2011a, 2012), <i>Betula</i> <i>pendula</i> (Lygis <i>et al.</i> , 2004a), <i>P. abies</i> (Cleary <i>et al.</i> , 2013) stems and wounded <i>P. abies</i> stems (Vasiliauskas and Stenlid, 1998a)
<i>Mensularia radiata</i> (Sowerby) Lázaro Ibiza	<i>Alnus glutinosa</i>	Sound wood of intact stems	Arhipova <i>et al.</i> , 2012	Also rot of intact <i>A. glutinosa</i> , <i>A. incana</i> (Arhipova <i>et al.</i> , 2011a, 2012) and <i>B. pendula</i> (Lygis <i>et al.</i> , 2004a) stems
<i>Phellinus tremulae</i> (Bondartsev) Bondartsev & P.N. Borisov	<i>Populus tremula</i> L.	Healthy-looking twigs	Holmer <i>et al.</i> , 1994	Entering stem via twigs
<i>Porodaedalea pini</i> s.l. (Brot.) Murrill	<i>Pinus strobus</i> L.	Twig stubs, 0.2–1.3 cm diameter	Haddow, 1938a,b	The twig stubs are subsequently encased by healthy stemwood
<b>2. True heart rots associated with heartwood-exposing natural injury (broken branches and tops, stem cracks, fire scars)</b>				
<i>Stereum gausapatum</i> (Fr.) Fr.	<i>Acer campestre</i> , <i>Fagus</i> <i>sylvatica</i> , <i>Fraxinus</i> <i>excelsior</i> , <i>Quercus robur</i> , <i>Salix</i> spp.	Functional sapwood of branches and stems	Parfitt <i>et al.</i> , 2010	Associated with heartwood-exposing injuries (Berry and Lombard, 1978)
<b>3. Wound heart rots associated with artificial mechanical damage (logging, bark stripping, pruning wounds)</b>				
<i>Coniophora puteana</i> (Schumach.) P. Karst.	<i>Fagus sylvatica</i>  <i>Picea abies</i>	Xylem of intact twigs, branches and stems Intact stem phloem	Chapela and Boddy, 1988; Hendry <i>et al.</i> , 2002; Baum <i>et al.</i> , 2003 R. Vasaitis <i>et al.</i> , 2012, unpublished results	Also rot of intact (Cleary <i>et al.</i> , 2013) and wounded (Vasiliauskas, 1998b) <i>P. abies</i> stems, and wounded <i>F. excelsior</i> stems (Lygis <i>et al.</i> , 2005); fruiting bodies on stem wounds of <i>Q. robur</i> (Vasiliauskas, 1998c)

<i>Resinicium bicolor</i> (Alb. & Schwein.) Parmasto	<i>Picea abies</i>	Intact stem phloem	R. Vasaitis <i>et al.</i> , 2012, unpublished results	Also rot of wounded <i>P. abies</i> stems (Vasiliauskas, 1998b)
<i>Sistotrema brinkmannii</i> (Bres.) J. Erikss.	<i>Alnus incana</i> (L.) Moench	Sound wood of intact stems	Arhipova <i>et al.</i> , 2011a	Also rot of wounded <i>P. abies</i> stems (Vasiliauskas <i>et al.</i> , 1996; Vasiliauskas, 1998b)
<b>4. Root and butt rots</b>				
<i>Ganoderma applanatum</i> (Pers.) Pat.	<i>Fraxinus excelsior</i>	Sound wood of intact stems	Lygis <i>et al.</i> , 2005	Living <i>F. excelsior</i> with dieback symptoms
<b>5. Decay fungi producing fruiting bodies on dead decomposed wood and generally considered as saprotrophs</b> (Eriksson and Ryvarden, 1976; Eriksson <i>et al.</i> , 1978, 1981, 1984; Breitenbach and Kränzlin, 1986; Jahn, 1990; Ryman and Holmåsén, 1992; Ryvarden and Gilbertson, 1993, 1994)				
<i>Bjerkandera adusta</i> (Willd.) P. Karst.	<i>Alnus glutinosa</i>	Sound wood of intact stems	Arhipova <i>et al.</i> , 2012	Rot of intact <i>A. glutinosa</i> , <i>A. incana</i> , <i>P. abies</i> (Arhipova <i>et al.</i> , 2011a,b, 2012) and <i>B. pendula</i> stems (Lygis <i>et al.</i> , 2004a); known decay agent of living trees (Phillips and Burdekin, 1982; Dai <i>et al.</i> , 2007)
	<i>Alnus incana</i>		Arhipova <i>et al.</i> , 2011a	
	<i>Fraxinus excelsior</i>		Lygis <i>et al.</i> , 2005	
<i>Coprinellus disseminatus</i> (Pers.) J.E. Lange	<i>Picea abies</i>	Sound wood of intact stems	N. Arhipova <i>et al.</i> , 2012, unpublished results	
		Intact stem phloem	R. Vasaitis <i>et al.</i> , 2012, unpublished results	
	<i>Alnus incana</i>	Sound wood of intact stems	Arhipova <i>et al.</i> , 2011a	Rot of intact <i>A. incana</i> and wounded <i>B. pendula</i> stems (Vasaitis <i>et al.</i> , 2012a)
<i>Gloeophyllum</i> sp.	<i>Fraxinus excelsior</i>		Lygis <i>et al.</i> , 2005	Living <i>F. excelsior</i> with dieback symptoms
	<i>Picea abies</i> , <i>Pinus sylvestris</i> L.		N. Arhipova <i>et al.</i> , 2012, unpublished results	In <i>P. sylvestris</i> determined to genus level
	<i>Picea abies</i>	Intact stem phloem	R. Vasaitis <i>et al.</i> , 2012, unpublished results	Rot of intact <i>P. abies</i> stems (Arhipova <i>et al.</i> , 2011b)
<i>Gymnopilus penetrans</i> (Fr.) Murrill	<i>Pinus sylvestris</i>	Sound wood of intact stems	N. Arhipova <i>et al.</i> , 2012, unpublished results	
<i>Merulius tremellosus</i> Schrad.	<i>Alnus incana</i>		Arhipova <i>et al.</i> , 2011a	Rot of intact <i>A. incana</i> stems (Arhipova <i>et al.</i> , 2011a)
<i>Mycocacia uda</i> (Fr.) Donk	<i>Pinus sylvestris</i>		Lygis <i>et al.</i> , 2004b	
	<i>Fraxinus excelsior</i>		Lygis <i>et al.</i> , 2005	<i>F. excelsior</i> with dieback symptoms, and stem wounds
<i>Oxyporus latemarginatus</i> (Durieu & Mont.) Donk	<i>Alnus incana</i>		Arhipova <i>et al.</i> , 2011a	
<i>Peniophora cinerea</i> (Pers.) Cooke	<i>Alnus glutinosa</i>		Arhipova <i>et al.</i> , 2012	Rot of intact <i>A. glutinosa</i> and <i>A. incana</i> stems (Arhipova <i>et al.</i> , 2011a, 2012), and wounded <i>F. excelsior</i> stems (Lygis <i>et al.</i> , 2005)
	<i>Alnus incana</i>		Arhipova <i>et al.</i> , 2011a	

Continued

**Table 10.2.** Continued.

Fungus	Tree species	Substrate	Reference	Remarks
<i>Peniophora limitata</i> (Chaillat ex Fr.) Cooke	<i>Fraxinus excelsior</i> <i>Fraxinus excelsior</i>		Lygis <i>et al.</i> , 2005 Lygis <i>et al.</i> , 2005	Living <i>F. excelsior</i> with dieback symptoms <i>F. excelsior</i> with dieback symptoms; fruiting bodies on <i>F. excelsior</i> wounds (Vasiliauskas and Stenlid, 1998b)
<i>Phanerochaete sordida</i> (P. Karst.) J. Erikss. & Ryvardeen	<i>Alnus glutinosa</i> <i>Alnus incana</i> <i>Picea abies</i> , <i>Pinus sylvestris</i>		Arhipova <i>et al.</i> , 2012 Arhipova <i>et al.</i> , 2011a N. Arhipova <i>et al.</i> , 2012, unpublished results	
<i>Phellinidium ferrugineofuscum</i> (P. Karst.) Fiasson & Niemelä	<i>Betula pendula</i> Roth		Lygis <i>et al.</i> , 2004a	Fruiting bodies on <i>Picea</i> spp.; in Europe, indicator of forest value for nature conservation (Nitare, 2000)
<i>Phlebia radiata</i> Fr.	<i>Fagus sylvatica</i> <i>Pinus sylvestris</i>	Healthy branch xylem Sound wood of intact stems	Baum <i>et al.</i> , 2003 Lygis <i>et al.</i> , 2004b	Rot of intact <i>P. abies</i> stems (Arhipova <i>et al.</i> , 2011b)
<i>Phlebia rufa</i> (Pers.) M.P. Christ.	<i>Fraxinus excelsior</i>	Sound wood of intact stems	Lygis <i>et al.</i> , 2005	Living <i>F. excelsior</i> with dieback symptoms
<i>Phlebiopsis gigantea</i> (Fr.) Jülich	<i>Pinus mugo</i> Turra		V. Lygis <i>et al.</i> , 2012, unpublished results	
<i>Pholiota highlandensis</i> (Peck) Singer	<i>Pinus mugo</i>		V. Lygis <i>et al.</i> , 2012, unpublished results	Fruiting bodies on burned wood (Ryman and Holmåsen, 1992)
<i>Piptoporus betulinus</i> (Bull.) P. Karst.	<i>Betula</i> spp.	Latent in intact trunks	Adams, 1982	Restricted to <i>Betula</i> spp.; reported also as sap rot and heart rot agent (Roll-Hansen, 1981; Butin, 1995; Kuzmichev <i>et al.</i> , 2004; Dai <i>et al.</i> , 2007)
<i>Stereum rugosum</i> Pers.	<i>Acer campestre</i> , <i>Betula</i> spp., <i>Fagus sylvatica</i> , <i>Fraxinus excelsior</i> , <i>Malus domestica</i> , <i>Quercus robur</i> , <i>Salix</i> spp.	Functional sapwood of branches and stems	Parfitt <i>et al.</i> , 2010	
<i>Trametes hirsuta</i> (Wulfen) Lloyd	<i>Fraxinus excelsior</i>	Sound wood of intact stems	Lygis <i>et al.</i> , 2005	Vigorous trees showing external <i>Armillaria</i> spp. rhizomorphs

later is fertilized by newly landing spores, resulting in formation of heterokaryons. In fact, mass production and efficient spore dispersal is a general feature of wood decay basidiomycetes. For example, a 1 mm<sup>2</sup> pore layer of *P. tremulae* fruiting body could produce over 100,000 basidiospores a day (Manion, 1991). Seasonal spore production from a single *F. pinicola* fruiting body was estimated to exceed 10<sup>11</sup> basidiospores a day (Nordén, 1997). Skov and Thomsen (2003) investigated spore spread of *F. fomentarius* in Denmark, and concluded that there are spores of *F. fomentarius* almost everywhere due to its immense spore production. Consequently, it is realistic to speculate that numerous genetically diverse basidiospores of true heart rot fungi would be normally present on trees in forest stands. However, the infection venues of true heart rot fungi in intact trees, the mechanisms of their symptomless persistence and the factors triggering decay development are mostly unknown to date, and much remains to be explored under the Haddow–Etheridge infection concept.

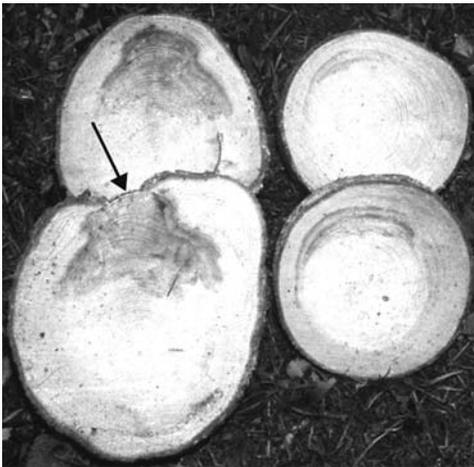
#### *True heart rots associated with natural injury*

From this category, only *Stereum gausapatum* (Fr.) Fr. was detected in functional sapwood of intact trees (Table 10.2). Apart from five different forest tree species (hedge maple, *Acer campestre* L.; European beech, *Fagus sylvatica* L.; European ash, *Fraxinus excelsior* L.; English oak; and willows, *Salix* spp.) the study, based on direct molecular analyses of intact xylem, consistently revealed the latent presence of the fungus in elder (*Sambucus nigra* L.) and hazel (*Corylus avellana* L., also known as common filbert) (Parfitt *et al.*, 2010). This, besides demonstrating *S. gausapatum* as one of the currently known most efficient colonizers of intact woody plants, also puts under serious doubt the categorization of the species as true heart rot associated with natural injury. The basis for this was that some other representatives of the genus are typical wound pathogens, and that the fungus commonly occurs in oaks with broken tops and fire scars (Berry and Lombard, 1978), although the suggested venues might in fact well be the exit points.

The same study also noted the common association of *S. gausapatum* with dead and sound branch stubs, and in Europe the fungus was reported to be one of the most common pathogens of old-growth oaks (Aufsess, 1973), typically producing fruiting bodies on branches that are still attached (Eriksson *et al.*, 1984). Therefore, it seems likely that the fungus does comply with the Haddow–Etheridge infection concept, and could be put under true heart rots of intact trees. Notably, none of the rest of fungi from true heart rots associated with natural injury has been so far detected in intact trees, so seemingly are able to enter trees only through damage that exposes heartwood, so complying with the Hartig infection concept. These findings explicitly demonstrate that while infecting trees true heart rots principally exhibit different entrance modes and strategies.

#### *Wound heart rots*

Logging and bark stripping wounds represent injury in which bark is knocked or ripped off the stem, exposing the underlying dead sapwood. While in the living stem, functional sapwood is more resistant to decay than heartwood, following the death of a tree the situation reverses, and sapwood becomes the most susceptible (Rayner and Boddy, 1988). When bark is ripped off from a certain part of a living stem, as typically occurs during logging and bark stripping damage, this results in rapid death of the exposed portion of the underlying sapwood, which, due to desiccation and loss of physiological reactions, becomes accessible to growth over long distances by the hyphae of decay fungi (Metzler *et al.*, 2012). Certain fungal species (e.g. *Stereum*, *Amylostereum* and *Postia* spp.) by means of such dead sapwood acting as a bridge, grow into the heartwood and cause heart rot in mechanically wounded, but otherwise vigorous, trees (Vasiliauskas, 1998a, 2001 and references therein). As noted by Shigo (1966), such an infection pattern apparently involves fungal colonization, competition and succession in exposed dead sapwood, while newly formed functional sapwood remains decay free (Fig. 10.4; Plate 12). This pattern of infection presumes colonization of the exposed wound surface by airborne spores.



**Fig. 10.4.** Cross-section of *Picea abies* (L.) Karst. stem with logging wound. The arrow indicates the surface of the wound (exposed non-functional sapwood) through which *Stereum sanguinolentum* (Alb. & Schwein.) Fr. invades the heartwood and starts heart rot formation. The injured tree sustains growth and the layer of newly formed functional sapwood remains free of decay. Credits: Vytautas Bardauskas.

Among wound heart rot fungi, three species, i.e. *Coniophora puteana* (Schumach.) P. Karst., *Resinicium bicolor* (Alb. & Schwein.) Parmasto and *Sistotrema brinkmannii* (Bres.) J. Erikss., were also either isolated from intact stems or detected in healthy phloem using molecular methods (Table 10.2), thus apparently not complying with airborne arrival to the wound surface and participation in fungal succession. Although each of those fungi were demonstrated to develop distinct decay columns in wounded Norway spruce (*Picea abies* (L.) Karst.) (Vasiliauskas, 1998b), and *C. puteana* was reported to fruit occasionally on stem wounds of oak (Vasiliauskas, 1998c) and ash (Vasiliauskas and Stenlid, 1998b), once again the question is whether wounds for those fungi served as entry points. Moreover, the fungus was isolated from heart rot of pine as well (Basham, 1966). So, as *C. puteana* is also known as a heart rot and mortality agent in pristine old-growth boreal forests (Holsten *et al.*, 2001; Lännpää *et al.*, 2008), it could probably be classified as a true heart rot of intact stems, while *R. bicolor* and *S. brinkmannii*

could be classified as saprotrophs that are both able to establish latently in living trees and able to cause limited decay following wounding. None of the rest of the wound heart rots has been so far detected in intact trees, so presumably they are able to enter living trees only by hyphal growth through dead exposed sapwood (Metzler *et al.*, 2012).

Apparently, true heart rots on dead exposed sapwood are unable to participate in succession and compete with numerous saprotrophs, in particular with heartwood-accessing wound heart rot fungi, which otherwise are normally typical saprobic decomposers of various types of woody debris in forest ecosystems. Although some true heart rot fungi were occasionally observed or isolated from logging and bark stripping wounds, as for instance *F. pinicola* and *P. chrysoloma* on Norway spruce (Vasiliauskas, 1989; Vasiliauskas and Stenlid, 1998a), in those instances mechanical wounds were apparently used by the fungi as exit and dispersal points. Therefore, one might conclude that wound heart rots and true heart rots seemingly possess mutually exclusive routes of infection.

#### Root and butt heart rots

Of those fungi listed in Table 10.1, only *Ganoderma applanatum* (Pers.) Pat. has been detected as latent in the healthy wood of intact tree stems (Table 10.2). It is known that the fungus infects trees through injuries of the largest roots (<7.5 cm diameter) (Ross, 1976), and so in the cases that have been observed, it could have entered the apparently intact stems through root damage in the subsoil. Similarly, observed infections of the fungus in urban trees were in most cases associated with roots (Terho, 2009). Interestingly, the study by Parfitt *et al.* (2010) mentioned above detected the latent presence of *Hericiium* spp. in intact sapwood of ash, beech, hazel and maple, and discussed the possible relationship of the detected fungus to *H. erinaceus* (Bull.) Pers., which is known to cause butt heart rot of oak and poplar (*Populus* spp.) in North America (Berry and Lombard, 1978; Tainter and Baker, 1996). Of this ecological group, *Grifola frondosa* (Dicks.) Gray typically causes butt heart rot in oaks with no sign

of stem injuries, apparently penetrating into the stem via the heartwood of large dead or injured roots (Schwarze *et al.*, 2000). Moreover, soil infestations of basidiospores are reported as a potential source of infection to tree roots by *P. schweinitzii* (Barrett and Uscuplic, 1971), and a similar mode of infection has also been considered for *Pseudoinonotus dryadeus* (Pers.) T. Wagner & M. Fisch. (Schwarze *et al.*, 2000), *Climacocystis borealis* (Fr.) Kotl. & Pouzar and *I. leporinus*; for the latter species, tree-to-tree infections via root contacts have been discussed too (Černý, 1989). Despite rather limited knowledge on the entry courts of listed root rot and butt rot fungi to living trees, it is obvious that this ecological group of pathogens possess very specific infection pathways, in this respect clearly distinguishing them from the rest of the heart rot fungi.

#### *Saprotrophs or sap rots*

Traditionally, it was assumed that following the death of a tree (or a certain part of that tree, e.g. a branch), the substrate immediately becomes subject to colonization by abundant basidiospores representing high diversity of fungal species and genotypes. This assumption is generally confirmed by observations of numerous fungal individuals on the surface of woody substrates, and of their competition and succession (Cooke and Rayner, 1984; Rayner and Boddy, 1988). Such a mode of colonization would generally resemble the infection pattern occurring on dead sapwood exposed on living stems during the initial stages of its colonization by wound heart rot and other fungi. However, recent studies are increasingly revealing the latent presence in intact trees of wood decay fungi generally known as saprotrophs (Table 10.2). This situation provides them with a colonization advantage over those wood fungi that arrive at the substrate by means of airborne spores following the death of a tree. Hence, those saprotrophic fungi might have developed infection courts and strategies that are characteristic of true heart rots in intact trees. Although, in contrast to the latter, they are not able to decay the heartwood of a living tree, they quickly initiate sap rots in trees subjected to stress, e.g. attack by insects and/or pathogens.

In addition, insects themselves are also being considered as potential direct vectors of sap rot. Five such common and widely distributed decomposers of dead wood as *F. pinicola*, *S. sanguinolentum*, *Bjerkandera adusta* (Willd.) P. Karst., *Phlebiopsis gigantea* (Fr.) Jülich and *Trichaptum abietinum* (Dicks.) Ryvarden have been occasionally detected on hibernating individuals of the bark beetle *Ips typographus* (Linnaeus) (Persson *et al.*, 2009). Two of these five fungi (*F. pinicola* and *S. sanguinolentum*) are listed in Table 10.1 as important rots, while three of them have been also reported to be latent inhabitants of intact trees and are listed in Table 10.2 (*F. pinicola*, *B. adusta* and *P. gigantea*), putting into question whether they have been beetle-introduced to trees, or acquired by the beetles while attacking the trees.

### 10.3.2 Access to host

#### *True heart rots*

In living intact trunks, the opportunities for infection by heart rot fungi could be limited, and allow extensive establishment of only a limited number of genotypes (Rayner and Boddy, 1988). Thus, in living stems of aspen and oak, each examined for heart rot columns of *P. tremulae*, *F. robusta*, *Inonotus dryophilus* (Berk.) Murrill and *Laetiporus sulphureus* (Bull.) Murrill, the heart rot fungus constituted a single fungal individual, or genet (Holmer *et al.*, 1994; Sunhede and Vasiliauskas, 2002, 2003a; Vasiliauskas *et al.*, 2003). This demonstrates that every observed infection to each entry point was accomplished by a single heterokaryotic mycelium, and that subsequently the same court was not reused by any other mycelium of the same or another pathogen. Moreover, due to the apparently limited amount of natural entry points per tree, a heart rot infected stem typically harbours one or a few genets of the pathogen. For example, the studies cited above report one to four genets per tree (mostly one) for *P. tremulae* and *F. robusta*, and exclusively one per tree for *I. dryophilus* and *L. sulphureus*.

In the case of *L. sulphureus*, this was rather surprising as the extensive decay columns in

the oaks examined were associated with heartwood-exposing butt cracks over 1 m long, obviously accessible to multiple infections by genetically diverse airborne basidiospores. Yet, despite a presumably high infection pressure, only a single genotype of the fungus has established as an extensive decay column in each tree examined, so selection must be rigorous. An interesting parallel could be drawn here to the root-infecting heart rot fungus *Heterobasidion annosum* (Fr.) Bref. *s.l.* Infections by the basidiospores of this pathogen result in numerous genets on stump surfaces (Swedjemark and Stenlid, 2001), but very few of those genets possess the ability for further growth into the roots. As a result, root systems and groups of trees over a discrete territory around the centre of multiple infections (basidiospore-infected stumps) are typically colonized by a single fungal genet (Vasiliauskas and Stenlid, 1998d; Lygis *et al.*, 2004a; see Gonthier and Thor, Chapter 7, this volume). Therefore, while high diversity of the pathogen was observed on the court of infection exposed to the environment, only single genotypes were present in the heartwood of infected trees. This might also apply to true heart rot fungi entering the tree through heartwood-exposing injuries, as with *L. sulphureus*, although their mycelial interactions, early colonization patterns and mechanisms of genotypic selection during the initial phases of infection remain largely unknown. Even less is known about root and butt heart rot fungi. Nevertheless, distinct genotypes of *P. schweinitzii* were detected in different trees in the same plantation, and always as a single genet per tree, thereby implying individual infection by just one heterokaryotic mycelium from soil that is otherwise infested with genetically diverse basidiospores (Barrett and Uscuplic, 1971).

#### *Wound heart rots*

Artificial bark wounds exposing sapwood are readily colonized by numerous fungi and multiple infections occur. For example, wood samples just 6–8 cm long and of 0.5 cm diameter taken from decay columns above mechanical stem wounds normally showed the presence of three to five different fungal

species (Vasiliauskas *et al.*, 1996; Vasiliauskas and Stenlid, 1998a,b). Moreover, some such samples were infected by two or even three different genets of the wound heart rot fungus *S. sanguinolentum* (Vasiliauskas and Stenlid, 1998c). These observations clearly demonstrate that the dead sapwood on a living stem is easily accessible to multiple colonization by wood-inhabiting fungi, including wound heart rot pathogens. In this respect, a parallel could be drawn with the sapwood of a dead trunk exposed to airborne infections by sap rot fungi. Apparently, large amounts of airborne spores land on the wound surface and germinate, and numerous individual mycelia grow into the functionally dead wood of an injured tree stem. As the mycelia of wound heart rot fungi are competitive with the mycelia of strictly saprotrophic fungi, they grow into the heartwood and initiate heart rot. However, more detailed studies on how many wound heart rot genets form decay columns in individual stems are lacking.

### 10.3.3 Stem colonization

#### *True heart rots*

According to their ecological traits, fungi are categorized as combative (establishing and persisting in a substrate), stress tolerant (growing under stress conditions) and ruderal (early arrival, reproduction and replacement) (Cooke and Rayner, 1984). During the colonization of a tree, wood decay fungi typically combine more than one of those traits, but in different sequences. Thus, true heart rots of intact trees exhibit stress-tolerant traits, while latently establishing in intact xylem and then, during subsequent growth under stressful conditions, establish rot inside intact stems. Yet, following the death of a tree, they switch to combative mode, and are able to persist on dead wood for decades. For example, field observations of *F. robusta* showed that its fruiting body continued development after 25 years of growth on a standing oak, producing annual growth layers on the fallen trunk for over 12 years, and was still living when collected (Sunhede and Vasiliauskas, 2002). In contrast, true heart rots associated

with heartwood exposure must apparently also be combative during the initial stages of infection in order to replace earlier arrived ruderal fungi or other heart rot fungi. Then, like the fungi from previous group (true heart rots of intact trees), they switch to stress-tolerant growth while developing heart rot inside living stems, and, again to combative mode while continuing to decompose and produce fruiting bodies on dead trees for many years. Little is known about whether root and butt heart rots infect subsoil roots under stress-tolerant or combative conditions, but following infection they follow the strategies of true heart rots described above.

#### *Wound heart rots*

Following establishment in the heartwood, all wound heart rot fungi exhibit stress tolerance as heart rots in living stems, followed by exhibiting combative mode as sap rots on dead wood. Yet, they possess notably different strategies during the initial infection of exposed sapwood. Thus, *C. purpureum* and *S. sanguinolentum* during the infection phase combine ruderal and combative traits: rapid arrival, establishment and defending captured wood from competitors. *Pleurotus* spp. and *Postia* spp. behave differently; they are combative species, replacing less combative (ruderal) fungi in exposed sapwood. Such modes of infection can be also characterized, respectively, as primary and secondary resource capture (*sensu* Cooke and Rayner, 1984). *Amylostereum* spp. also exhibit a combative strategy during the initial colonization of wounded trees, yet those fungi possess a unique infection pathway, as they are introduced to wounds by siricid woodwasps, inserted as heterokaryons during oviposition (Plate 12). In northern Europe, the spread of these wound heart rots is largely dependent on insects, as genetic diversity in fungal populations is low and fruiting bodies rare (Vasiliauskas *et al.*, 1998). For over 100 years, *Amylostereum* spp. have been known as an economically important cause of sap rot in plantations of southern pines, causing consistently increasing problems, particularly in the southern hemisphere (Slippers *et al.*, 2012). Following tree death, all wound heart rot

fungi are known to persist and regularly produce fruiting bodies on decomposing wood.

#### *Saprotrophs or sap rots*

Despite the general assumption that standing dead trunks become subject to massive colonization by airborne spores of ruderal and combative decay fungi, the evidence is increasingly accumulating on the latent presence of decay fungi in the sound xylem of living intact trees (Table 10.2). This implies a stress-tolerant condition during latent establishment in a living tree for these saprotrophic species too. Such a situation would provide the possibility for early-established combative fungi to rapidly colonize sapwood following death of a tree, thereby providing clear advantage over subsequently arriving competitors. Then, the combative saprotrophs would persist and produce fruiting bodies on decomposing substrate over the years, as is also the typical case for all heart rot fungi. A recent study on fungal succession in Norway spruce attacked by *I. typographus* (R. Vasaitis *et al.*, 2012, unpublished results) has demonstrated that a number of decay fungi invade the sapwood of dying trunks (with still green, but yellowing, crowns) within weeks of beetle attack, spreading in stems radially in succession after ophiostomatoid fungi (which are known to kill sapwood following beetle attack). Among these decay fungi, *F. pinicola*, *S. brinkmannii* and *Gloeophyllum sepiarium* (Wulfen) P. Karst. are species with known latent establishment in intact phloem and sapwood. Moreover, in the sapwood of dying spruce, the wound heart rot and sap rot agents *S. sanguinolentum*, *Amylostereum areolatum* (Chaillet ex Fr.) Boidin and *Schizophyllum commune* Fr. were also detected, and the first two of which could have been introduced to dying trees by insect attack as well as being present through latent establishment (Persson *et al.*, 2009; Slippers *et al.*, 2012).

Among the saprotrophs known for stress-tolerant latent establishment in intact visually healthy trees, *B. adusta*, *Coprinellus disseminatus* (Pers.) J.E. Lange, *Gloeophyllum* sp., *Merulius tremellosus* Schrad., *Peniophora cinerea* (Pers.) Cook, and *Phlebia radiata* Fr. have been previously isolated from heart rotten

but otherwise intact stems, and *Mycocacia uda* (Fr.) Donk and *Peniophora limitata* (Chaillet ex Fr.) Cooke have been isolated from wounded stems (Table 10.2). However, the possible roles of these fungi in heart rot formation remain unclear, and are probably negligible. Fruiting bodies of *P. betulinus* have been regularly observed on dying birch, and in some texts the fungus is pointed out as a pathogen, yet the question remains open as to whether the death of a tree activates decay and fruiting of the fungus on trunks, or vice versa (Rayner and Boddy, 1988). For others of the fungi in this group, any association with decay in living trees so far has not been reported. Therefore, one might generally conclude that all the sap rot fungi listed are indeed true saprotrophs, using a stress-tolerant mode of initial colonization of living trunks, followed by extensive spread in wood after the death of a tree, and persistence and the regular production of fruiting bodies on dead decomposing wood.

#### *Colonization strategies*

There are four types of strategies exhibited by wood decay fungi during the colonization of a living tree stem. These are formulated as: (i) unspecialized opportunism, (ii) specialized opportunism, (iii) heart rot and (iv) active pathogenesis. As the living tree consists of a heterogeneous assemblage of microenvironments, each posing distinctive constraints on growth, in order to successfully colonize a tree, individual fungi are typically capable of combining several strategies (Rayner and Boddy, 1988). During the initial colonization, true heart rot fungi exhibit specialized opportunism, combined with either stress tolerance (when entering intact trees), or combative behaviour (when colonizing exposed heartwood of selective tree taxa). Apart from heartwood colonization, true heart rots that enter intact trees often invade functional sapwood by mechanisms of active pathogenesis, developing distinct canker rots, e.g. *Fomitiporia*, *Phellinus* and *Porodeadalea* spp., and *E. tinctorium* and *I. obliquus*. Initial colonization by wound heart rot fungi typically includes unspecialized opportunism during the combative (primary or secondary) capture of exposed dead

sapwood, followed by sapwood colonization and spread inside the stem. Heart rot is a characteristic of all heart rot fungi. After entering the heartwood, all heart rots exhibit stress-tolerant growth, apparently overcoming the presence of fungitoxic compounds and the constraints of the gaseous regime, and developing a heart rot column, while functionally intact sapwood remains decay free (Rayner and Boddy, 1988; Plate 12).

#### **10.3.4 Development of fruiting bodies**

Following colonization of a tree, the life cycle of heart rot fungi is completed by fruiting body production and the abundant release to the environment of airborne spores that will subsequently cause tree infections. True heart rots have two distinct types of fruiting bodies: fleshy annual and hard perennial (conks). Fleshy annual fruiting bodies are characteristic of species that invade stems through natural heartwood-exposing injuries (except for *Fomitopsis cajanderi*, Table 10.1). Seemingly, those fungi in a colonized trunk have a permanent unrestricted access to the outer environment, which enables their fruiting (usually directly upon an injury) and the regular seasonal dispersal of basidiospores. Interestingly, true heart rot species that invade intact trees typically produce perennial conks. The situation for those fungi in tree stems is radically different, as the need to breach functionally intact sapwood becomes paramount if exit structures, notably fruiting bodies, are to be produced (Rayner and Boddy, 1988). Such venues are provided either by branch stubs originating from the heartwood, or by breaching the functional sapwood during active pathogenesis and canker formation. Consequently, perennial conks of the heart rots are typically produced on and around branch stubs and cankers. Thus, the formation of perennial fruiting bodies on a living tree could be regarded as the long-term investment of a fungus. For example, actively growing conks of the heart/sap rot fungus *F. robusta* on living oaks are known to exceed an age of 35 years (Sunhede and Vasiliauskas, 2002).

All wound heart rot fungi have access to the outer environment through dead colonized sapwood. The fruiting bodies of all wound heart rotting fungi are fleshy and annual, and are developed directly on the wound surface. Notably, this fruiting on the wound surface seldom occurs. In a study by Vasiliauskas (1989), more than 1000 Norway spruces with logging and bark stripping wounds were monitored over two vegetation seasons, and fruiting bodies were observed on only 79 of them (<10%). Only 6% of the bark stripping wounds examined on stems of ash and oak showed fruiting bodies of wood decay fungi (Vasiliauskas, 1998c; Vasiliauskas and Stenlid, 1998b). Apparently, wounds on a standing tree do not normally provide the appropriate microenvironment, in particular moisture, for the formation of fleshy annual fruiting bodies. One should bear in mind that in primeval forest ecosystems, these decay fungi evolved as pioneer combative wood decomposers of dead wood, and are adapted to fruit abundantly under increased moisture conditions, e.g. on downed decomposed woody debris. In contrast, wound heart rot fungi can be generally characterized by their relatively rapid reproduction rates, and produce fruiting bodies on wounds that are less than 10 years old. Such observations are available for *C. puteana*, *Stereum hirsutum* (Willd.) Pers. and *Trametes versicolor* (L.) Lloyd on birch, oak and ash (Shigo, 1966; Vasiliauskas, 1998c; Vasiliauskas and Stenlid, 1998b), and for *S. sanguinolentum* on Norway spruce (Vasiliauskas *et al.*, 1996).

### 10.3.5 Host range

#### *True heart rots of intact trees*

The ability to enter intact stems through natural courts of infection presumably requires adaptation to a certain host range. In order to be host specific, heart rot fungi must possess tolerance both to specific microenvironmental conditions and to variations in these conditions while entering and spreading inside a tree (Rayner and Boddy, 1988). Consequently, true heart rots that invade intact trees usually have one or few hosts on which they predominantly

occur, while being able occasionally to occur also on other tree species. In forest stands in Europe, typical examples of such host selectivity are *P. hartigii* on silver fir (*Abies alba* Mill.), *F. robusta* on oak, *P. chrysoloma* on Norway spruce, *P. pini* on pine, *Phellinus nigricans* (Fr.) P. Karst. on birch, and *P. tremulae* and *Phellinus populicola* Niemelä on aspen (Niemelä, 1974, 1975; Butin, 1995). Although *Phellinus igniarius* (L.) Quél. was traditionally considered to be a harmful pathogen of numerous woody species (Niemelä, 1975; Butin, 1995), recent studies based on molecular methods have demonstrated that the *P. igniarius* group in Europe consists of different species that are mostly host specific (Tomšovský *et al.*, 2010b). In North America, a broader host range was reported for true heart rots in intact stems. Thus, it was noted that *E. tinctorium* typically occurs on true firs, hemlock and spruce, but *P. pini* was usually considered as having an even broader host range and capable of causing heart rot in many tree species (Manion, 1991; Tainter and Baker, 1996; Hansen and Lewis, 1997). While the potential for cryptic species and host specificity in *E. tinctorium* has been not investigated, recent research on *P. pini* has demonstrated that in North America the fungus is indeed an aggregate of over ten different species that are mainly host specific (Fischer, 1996; Tomšovský *et al.*, 2010a). In this respect, the exceptions among invaders of intact trees could be *F. fomentarius* and *F. pinicola*, the fruiting bodies of which are frequently observed on the wood of numerous hosts (Ryvarden and Gilbertson, 1993). However, a recent study based on molecular methods has revealed the presence of cryptic species and a certain host selectivity in *F. fomentarius* (Judova *et al.*, 2012). In contrast, early studies had already demonstrated that specimens of *F. pinicola* collected from conifers and deciduous trees were interfertile (Mounce and Macrae, 1938), indicating that individuals of the fungus colonizing broad spectrum of hosts represent a single although highly versatile biological entity.

#### *True heart rots associated with natural injury*

Among the heart rots associated with natural injury, there are species with both a narrow

and a wide host range. *Fistulina hepatica* (Schaeff.) With., *Hapalopilus croceus* (Pers.) Donk, *I. dryophilus*, *S. gausapatum* and *Xylobolus frustulatus* (Pers.) Boidin are mostly found on oaks, while *F. cajanderi* causes rot in many coniferous species, although mainly in Douglas-fir. Traditionally, *L. sulphureus* was a classical example of a fungus that causes heart rot and decomposes the wood of many deciduous and conifers (Ryvarden and Gilbertson, 1993). Currently, at least seven distinct species are recognized in the *L. sulphureus* complex, some distributed over a distinct geographic range and some probably invasive, and most of them apparently possessing a certain host selectivity. Host specificity reported so far for root and butt heart rots is based on observations of fruiting bodies; some of them, such as *G. frondosa* or *I. leporinus*, are seemingly more host specific, while others, such as *Perenniporia subacida* (Peck) Donk and *P. schweinitzii*, are less host specific. For this group of fungi, the possible existence of cryptic species with certain host specificity has not been investigated and cannot be excluded.

#### Wound heart rots

As wound heart rot fungi produce fruiting bodies on the decomposed wood of numerous tree species, in the mycological literature they are traditionally referred to as common and widely spread saprotrophic wood decomposers with a broad host range. It seems that while gaining access to living trees they are more specialized. *Amylostereum* and *Postia* spp., and *S. sanguinolentum*, are primarily reported as wound pathogens of Norway spruce and silver fir, with *C. purpureum* found on alder (*Alnus* spp.) and birch (Table 10.1; Vasiliauskas, 2001 and references therein). A special case among the wound heart rot fungi is *C. puteana*, a globally distributed generalist and versatile saprotroph on a wide variety of substrates and environments, growing in woody buildings, but also on dead and living trees in managed forest stands and in old-growth pristine forests. Yet the fungus also possesses certain features characteristic of true heart rots of intact stems, as it is capable of establishing latently in living trees and

is known to cause heart rot of over-mature trees. Interestingly, the presence of cryptic species with apparent hybridization has also been reported for *C. puteana* (Kausrud *et al.*, 2007).

## 10.4 Management Strategies and Tactics

### 10.4.1 True heart rots and root and butt rots

Certain silvicultural practices have been suggested to control true heart rots. Those include avoiding the planting of susceptible species on high hazard sites with high incidence of the pathogens, selective harvesting to promote a multiple aged stand and uneven canopy structure, and spacing to allow symmetrical crown development (Hansen and Lewis, 1997). Yet, as the losses significantly increase in mature and over-mature stands, the only realistic and economically feasible measure would be to shorten the rotation age or, in other words, to harvest trees before the losses become excessive (Boyce, 1961; Tainter and Baker, 1996; Hansen and Lewis, 1997; Holsten *et al.*, 2001). In particular, reducing the rotation age would be applicable to fast-growing forest plantations, e.g. of aspen and alder, where significant losses already occur at a relatively young age (Arhipova *et al.*, 2011a, 2012). Moreover, as aspen clones seem to differ in susceptibility to *P. tremulae*, breeding for resistance of this tree against the pathogen could be considered (Manion, 1991).

Some texts suggest the removal from forest stands of trees with fruiting bodies of heart rot fungi (Černý, 1989; Hansen and Lewis, 1997), which apparently contradicts currently ongoing programmes for their artificial inoculation (Filip *et al.*, 2011). Moreover, it has already been pointed out by Boyce (1961) that such an operation is unlikely to be economically feasible. Furthermore, the aim of reducing infection potential is unlikely to be achieved as the fruiting bodies typically hide up in the tree crowns and produce huge numbers of spores with a highly efficient airborne spread capacity (Sunhede and

Vasiliauskas, 2002). One should also keep in mind that nowadays the majority of true heart rots occur in over-mature old-growth forests, which become increasingly relevant for biodiversity and nature conservation, and to large extent are supposed to be under a protection regime. Indeed, surveys in such forests increasingly reveal the presence of rare and protected heart rot fungi, and point to the necessity for these sites to be put under protective status (Sunhede and Vasiliauskas, 2003b). In fact, this could currently be seen as an alternative management strategy for true heart rots and most butt heart rots. In fact, measures for the restoration of populations of certain fungal species (e.g. *H. croceus* in Europe) are presently being considered.

#### 10.4.2 Wound heart rots

The absence of artificial wounding would be a prerequisite for complete wound heart rot control in forest stands, but this is unrealistic. The aim should, therefore, be directed at avoiding and minimizing stand damage. Studies on how logging damage could be reduced by the planning of forest operations, the training and adequate supervision of workers, use of different harvesting methods and treatment of wounds have been reviewed, and a number of silvicultural and operational options discussed (Dimitri, 1983; Vasiliauskas, 2001). In addition to this, for broadleaves it has been pointed out that seedlings of seed origin generally contain less rot than trees of sprout origin; additionally, sprouts from small stumps (<10 cm and not >15 cm in diameter) should be favoured as crop trees; single sprouts are preferable to fused sprouts (Boyce, 1961; Tainter and Baker, 1996). Another option for wound heart rot management strategy would be the planting of trees less susceptible to logging damage, and in this respect, several tree species have been investigated. For example, in the USA, a higher proportion of residual trees was injured during thinning in a birch stand than in similar treatments in a mixed beech and oak stand (Ostrofsky *et al.*, 1986). In Europe, silver fir has been shown to suffer fewer injuries during harvesting operations than Norway spruce (Kohnle and

Kändler, 2007) and, what is more, wounds on silver fir were shown to be less susceptible to rot fungi (Metzler *et al.*, 2012). As a management implication, it was concluded that the economic risks in respect of wounding are expected to be lower in silver fir and, in particular, that timely removal of wounded silver fir is less critical than that of Norway spruce.

A recent study has provided criteria for the assignment of fresh mechanical stem wounds of Norway spruce either to decay risk or to non-risk categories, on which a decision could be based for retaining or removing spruce in damaged stands during selective felling (Vasaitis *et al.*, 2012b). The study demonstrated that in cases where 5 cm wide wounds were inflicted on stems of Norway spruce, the injuries were unlikely to occlude during two subsequent decades; neither did wounds of a 15 cm initial width occlude at all, and these were 100% invaded by decay (Figure 10.3). Consequently, in order to avoid yield losses, trees with such wounds should be considered for removal during any selective felling. The management of Norway spruce stands with old wounds in areas susceptible for bark stripping should primarily remove stems with old open wounds during any partial harvesting, while retaining trees with closed wounds (Vasaitis *et al.*, 2012b). For silver fir, it takes a much shorter time to occlude bark stripping wounds – 4–10 years for a 2 cm wide wound, and 6–12 years for a 5 cm wide wound (Pach, 2008), so on heavily damaged sites, trees with such injuries should be retained. In plantations of Sitka spruce (*Picea sitchensis* (Bong.) Carrière) all stem wounds with an initial size of <60 cm<sup>2</sup> were fully closed over a 15 year period, but none larger than 180 cm<sup>2</sup> were occluded (Welch *et al.*, 1997); this finding should also be considered during management decisions. Wounded oak, beech and birch, due to a low susceptibility to wound heart rot, should not be subject to any particular strategy in relation to other stems in a stand during forestry operations, while all viable ash, despite extensive wound heartwood discoloration due to the catastrophic epidemics of dieback currently devastating this tree species on a continental scale (Bakys *et al.*, 2009), must be retained in stands despite any mechanical wounding.

Among other measures for wound heart rot management, the shaping of irregular mechanical wounds by cutting off loose pieces of bark that have been knocked has been suggested to enhance callus formation and wound closure (Manion, 1991; Schumann and Dimitri, 1993). Recommendations for pruning suggest that the pruning cuts should be close but not injure the bark of the main stem, that tearing of the bark below the pruned branch should be avoided, and that loose bark should be removed from around the wound (Manion, 1991). In north Europe, the pruning of birch resulted in only limited development of discoloration in stems (Schatz *et al.*, 2008), as little as that developing from natural branch stubs (Raulo *et al.*, 1978), thereby implying that this tree species is as resistant to pruning wounds as to logging wounds (Vasaitis *et al.*, 2012a). According to studies in the USA, the incidence of discoloration in pruning wounds of birch is also low, and pruning of small trees with small branches was recommended (Solomon and

Shigo, 1976). In Norway spruce, the pruning of green branches proved to be excellent in this respect, as long as branch collar and bark injuries, and too long branch stubs were avoided (Metzler, 1997).

Finally, one should be aware that at least in central and north Europe, three of the most important forest diseases and pests are present, namely: (i) annosum root rot (*H. annosum s.l.*), (ii) the pine weevil (*Hylobius abietis* Linnaeus) and (iii) the big game (red deer and moose). Among other damages caused (e.g. the destruction of forest plantations and regeneration, travel accidents, etc.), the third pest category is one of the principal causes for wound heart rot and is incompatible with sustainable forest management (R. Vasaitis, 2012, unpublished results). However, in comparison with root rot and the pine weevil, this third category of the most destructive forest pests is the easiest one to physically eliminate or be sustained within game reserves. This would significantly improve the health condition of European forests.

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