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DECAY OF LIVING WESTERN REDCEDAR: A LITERATURE REVIEW Sturrock, R.N., Braybrooks, A.V., Reece, P.F.

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Decay of Living Western Redcedar: A Literature Review

Rona N. Sturrock¹, Ann V. Braybrooks², and Pamela F. Reece³

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¹Rona N. Sturrock - Research Scientist (retired), Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC ²Ann V. Braybrooks - Science Writer, Victoria, BC

³Pamela F. Reece - Currently Aquatic Scientist, Stantec, Victoria, BC

Natural Resources Canada Canadian Forest Service Pacific Forestry Centre 506 West Burnside Road Victoria, British Columbia V8Z 1M5 Tel.: 250-363-0600

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Abstract

An overview of literature relevant to decay in living western redcedar is provided. Despite the species' reputation for decay resistant heartwood, living western redcedar trees frequently have extensive decay. This overview has several sections, starting with background information on western redcedar distribution, attributes and inventory. This is followed by an introduction to decay, which covers decay fungi occurring on living western redcedar, host defences, and microbial succession in living western redcedar trees. Factors affecting decay such as age and site conditions are covered as are indicators and detection of decay in living western redcedar. The final sections of the overview present information about managing decay in living western redcedar and about future research needs. Also included is a summary about decay fungi affecting western redcedar wood products. Western redcedar has significant economic, cultural and ecological value throughout its natural range in western North America; better understanding of its interactions with decay fungi will enhance these values.

Keywords: Thuja plicata, decay fungi, decay resistance, heartwood extractives

Résumé

Survol de la littérature pertinente sur la pourriture du thuya géant vivant. Malgré la réputation de l'espèce dont le bois parfait résisterait à la pourriture, le thuya géant vivant accuse souvent une pourriture étendue. Ce survol se divise en plusieurs parties. Il donne d'abord des renseignements généraux sur la répartition, les attributs et les stocks du thuya géant. Ensuite vient l'explication de ce qu'est la pourriture : champignons décomposeurs présents, défenses de l'hôte et succession microbienne dans le thuya géant vivant. Les facteurs jouant sur la pourriture comme l'âge et les conditions du site sont abordés, comme aussi les indicateurs et la détection de la pourriture dans l'arbre. Les dernières parties présentent des renseignements sur la lutte contre la pourriture du thuya géant vivant et expliquent les futurs besoins de recherche. Le survol comprend aussi un sommaire des champignons décomposeurs qui attaquent les produits du bois de thuya géant. Le thuya géant a une importante valeur économique, culturelle et écologique dans toute son aire de répartition naturelle dans l'ouest de l'Amérique du Nord; mieux comprendre ses interactions avec les champignons décomposeurs permettra de rehausser cette valeur.

Mots-clés: Thuja plicata, champignons décomposeurs, matières extractibles du bois parfait, résistant à la pourriture

Executive Summary

Western redcedar (WRC; *Thuja plicata*) has significant economic, cultural and ecological value in the forests of the Pacific Northwest. British Columbia (BC) has the world's largest standing stocks of WRC; total revenues generated by WRC products in BC were recently estimated to be over one billion dollars per year. Despite WRCs renowned natural durability, which is associated with the presence of heartwood extractives, live WRC trees often have extensive decay. Decay is a primary cause of cull in WRC and results in increased harvesting costs and often, volumes reduced by around 30%. Improved understanding of decay dynamics is critical to reducing WRC losses to decay. This review synthesizes existing knowledge and applicable research about decay in living WRC to inform professionals involved in genetic selection programs and the full suite of stand management activities for this important species.

Wood decay is a deterioration of wood tissues caused primarily by the enzymatic activities of microorganisms, especially fungi. Decay fungi can be classified by the type of decay they cause — either 'white rot' or 'brown rot'. White rot fungi break down lignin, cellulose, and hemicellulose. Brown rot fungi break down only cellulose and hemicellulose. Basal wounds and fire scars appear to be the most important entry points for decay-causing microbes in living WRC. While more than 25 different species of decay-causing fungi have been found in living WRC, to date only around six of these species, namely *Obba rivulosa, Perenniporia subacida, Phellinus weirii, Porodaedalea pini, Postia balsamea* and *Postia sericeomollis* are considered to have notable incidence and impact on living WRC. Brief descriptions of what is known about the decay dynamics of the six fungi are provided in this review.

Decay in WRC involves a succession of microorganisms that invade the heartwood. Initial pioneer species are non-decay fungi that alter the chemistry of some heartwood extractives, rendering the extractives non-toxic to subsequent decay fungi. More than 20 different extractives have been identified in WRC heartwood, including terpene tropolones, terpenes, and lignans, but their roles in conferring heartwood decay resistance and durability in WRC still are not fully understood. It has been suggested that "*it is not possible to focus on a single heart-wood extractive measurement...to understand the natural durability of...wood, especially if one is considering the resistance of the wood to multiple biodeterioration agents.*"

Factors thought to affect decay in living WRC include tree age and site attributes such as location and elevation. In general, heartwood decay increases with tree age as the relative proportion of heartwood increases, wound-healing slows, and extractives degrade over time. Decay incidence and volume in WRC may be affected by silviculture and harvest practices. For example, individual WRC trees regenerated by layering are considered more susceptible to fungal colonization than those regenerated from seed. It is not clear if the practice of retaining WRC residuals (also known as advanced regeneration trees) at harvest to give the next rotation a head start is necessarily beneficial.

Detection of wood decay in living and dead trees is critical for both accurate timber valuations as well as hazard and wildlife tree assessments. Detection is enhanced by the presence of indicators of decay such as fruiting bodies while wounds and scars indicate potential infection courts for decay fungi. It has been suggested that scars and wounds, especially on the bole or roots, are reliable external indicators of decay in WRC. Although fruiting bodies occur but are seen rarely on WRC, they can help to detect and quantify decay in this species. Images and some general identification information about the fruiting bodies of the six major decay fungi affecting living WRC are provided in this review. Other methods that may possibly be used to detect, identify, and quantify decay in WRC, including biomolecular methods, are discussed.

While there is currently little information specific to **managing** decay in living WRC, research has been initiated to begin addressing this knowledge gap. The principle areas of investigation are focused on how tree breeding (including genomic selection) along with silvicultural activities might be used alone or together to reduce decay/improve WRC durability. Other important research questions and proposed approaches relevant to improving our understanding of decay in living WRC are summarized in this review. Because volume and value losses associated with decay, waste and breakage of WRC across its natural range are substantive there is an urgent need to update and better quantify impact data for WRC losses to decay fungi.

Although this review focuses on decay fungi occurring on living WRC, it also provides an introduction to decay and the decay fungi affecting WRC wood products. The review also presents several 'side bars' of information that delve into topics related to WRC and/or to decay in this species. Side-bar topics range from 'The peculiar stem form of WRC', to 'Armillaria assists other decay fungi affecting WRC?' to 'Climate change and WRC decay'.

1. Introduction

Western redcedar (WRC) (*Thuja plicata* Donn ex D. Don) is one of the most ecologically, economically, and culturally important tree species in the Pacific Northwest (Gonzalez 2004). WRC wood products are highly valued for their resistance to decay (Sowder 1929; Cartwright 1941; Scheffer 1957; van der Kamp 1986; Freitag and Morrell 2001; Laks et al. 2008). This natural durability is associated with the presence of fungitoxic heartwood extractives, including terpenoids (e.g., the thujaplicins (Rennerfelt 1948)), in combination with fungistatic lignans (Roff and Atkinson 1954) (e.g., plicatic acid and some of its derivatives) and their powerful antioxidant properties (Schultz and Nicholas 2000; Stirling and Morris 2015).

Despite the fungitoxic properties of the extractives present in the heartwood of WRC, live trees frequently have extensive decay, especially in old-growth forests (BC Forest Service 1957; van der Kamp 1975, 1986). The activities of wood decay fungi can result in loss of wood strength and reduced fibre yield, increased susceptibility to insect invasion and damage, stem breakage of live trees, and in some cases tree mortality. In the context of timber supply, decay is a primary cause of cull in WRC and results in increased harvesting costs and often, significantly reduced net volumes (Buckland 1946; Kimmey 1956; Dobie and Kasper 1975; Renzie and Han 2001). For example, data from a 1957 forest inventory conducted in BC indicated that the amount of decay expressed as a percentage of the total gross volume of wood was greater for WRC (32%) than for any other major conifer (average 12%) (BC Forest Service 1957). More recent data for volume losses to decay in WRC have been collected in BC but not yet summarized. In Alaska today, stem decay results in an estimated 30% old-growth timber volume loss of WRC, western hemlock (Tsuga heterophylla (Raf.) Sarg.), and Sitka spruce (Picea sitchensis (Bong.) Carr.) (USDA 2012).

It is important to also acknowledge that decay fungi are integral components of many forest ecosystems (Maser and Trappe 1984; Hansen and Goheen 2000), where they contribute to carbon and nutrient retention and cycling (Matsuzaki et al. 2012), the creation of canopy gaps (Hennon 1995; Worrall et al. 2005) and subsequent species succession, and the provision of wildlife habitat. For example, stem decay fungi soften wood, making it an attractive substrate for excavation by cavity nesters (Hennon and Mulvey 2014). The cores of long-lived and durable WRC snags hollowed out by decay fungi can serve as dens or shelters for hibernating bears and smaller mammals and amphibians. Due to its broad scale importance, many aspects of WRC have been well studied throughout its range, and much of this information is summarized in review papers and reports. For example, Minore (1983) provides a review of WRC abundance, associated plant species, morphology, products, diseases, pests, genetics, physiology and ecology, and silviculture. He also provides management recommendations and an extensive list of references. Gonzalez (2004) provides a BC-focused summary of WRC growth, properties, and uses. A more recent literature review on WRC by Klinka and Brisco (2009) was written for the BC Ministry of Forests and Range Forest Science Program to summarize information related to the establishment and growth of WRC in the coastal region of BC. Proceedings from A Tale of Two Cedars: International Symposium on Western Redcedar and Yellow–Cedar (USDA 2010) provides a summary of research and knowledge on both WRC and vellow-cedar (Callitropsis nootkatensis (D. Don) Little) that was current at the time.

Nevertheless, there is limited information specific to decay dynamics in living WRC; improved understanding of these dynamics is critical to reducing WRC losses to decay. Thus, this review aims to synthesize existing knowledge and applicable research about decay in living WRC to inform professionals involved in genetic selection programs and the full suite of stand management activities for this important species.

2. Background

2.1. Distribution

WRC grows in the Pacific Cordillera region of western North America, extending along the Pacific coast from California (40°N) to southeastern Alaska (57°N) (Hennon et al. 2016), and along the interior wet belt from McGregor,



Figure 1—The natural range of western redcedar in North America. https://esp.cr.usgs.gov/data/little/

BC (56°N) to western Montana and northern Idaho (45°N) (Minore 1983; Klinka and Brisco 2009). It appears that WRC range is slowly migrating north (O'Connell et al. 2008) in response to climate change but there is no research to indicate if decay fungi are keeping pace with this migration. The larger coastal distribution of WRC is essentially isolated from the smaller interior distribution (Figure 1) (Klinka et al. 1999) and is generally confined to regions with abundant precipitation and humidity, cool summers, and mild winters. The region currently optimal for WRC growth is in the Puget Sound area of Washington State (USDA 1990).

Western redcedar colonized its current range from refugia following retreat of the most recent glacial episode—the Wisconsin glaciation (O'Connell et al. 2008) 80,000—18,000 years ago (Dyke and Prest 1987 cited in O'Connell et al. 2008). Using genetic evidence, O'Connell et al. (2008) showed that the current distribution of WRC resulted from its northward migration from one major refugium located south of the glacial maximum. Some of the decay fungi with broad host ranges might have already been present in the current range, but host specific decay or other fungi would have needed to migrate with WRC. they grow very slowly (Krajina 1969; Neiland 1971, and Lennon et al. 2002, cited in D'Amore et al. 2009). A typical WRC tree can live for 800-1000 years, but some have been dated as old as 3000 years (Parker 1986, cited in Gonzalez 2004).

Western redcedar trees are typically 45-60 m tall with a long, narrow conical crown. The branches droop, sometimes contacting the ground, and turn up at the ends. A branch that contacts the ground can develop its own root system and transform into a new, potentially independent stem. This 'branch layering' also occurs when still living, fallen trees form roots from their branch and stem tissues in contact with the ground. Anecdotal evidence suggests that WRC saplings produced by layering are more abundant than seedlings regenerated from seed in mature forests in both Idaho (Parker 1979, cited in USDA Forest Service 2011) and BC (Lewis 1992). The WRC butt is often fluted, flared and broadly buttressed, especially in opengrown or released trees (Farrar 1995) though the degree of fluting varies widely. The bark is thin, rarely more than 2.5 cm, contrasting sharply with Douglas-fir bark which can be more than 30 cm thick (Gonzalez 2004).

2.2. Attributes

Western redcedar usually occurs in mixed stands and is extremely shade-tolerant in all stages of forest succession (Gonzalez 2004). In coastal areas WRC is associated with Sitka spruce; western hemlock; Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco); grand fir (Abies grandis (Dougl. ex D. Don) Lindl.); amabilis fir (Abies amabilis (Dougl. ex Loud.) Dougl. ex J. Forbes); Pacific yew (Taxus brevifolia Nutt.); red alder (Alnus rubra Bong.); black cottonwood (Populus trichocarpa Torr. & A. Gray); and bigleaf maple (Acer macrophyllum Pursh). In the interior WRC grows primarily with western larch (Larix occidentalis Nutt.); western white pine (Pinus monticola Dougl. ex D. Don); western hemlock; Douglas-fir; grand fir; and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). Western redcedar has adapted to varying climatic conditions with majestic, towering trees in areas of high precipitation and humidity but also wind-swept bushes in cold, mountainous areas in the interior (Collingwood and Brush 1947, cited in Hepting 1971). Western redcedar tolerates a wide range of soils including sandy, loamy, clay, swampy, and rocky types (Minore 1983; Symmetree et al. 2008). Western redcedar reaches its largest size as individual trees on well-drained soil, but is most common on the margins of bogs and other poorly drained soils with low nitrogen availability where



The peculiar stem form of WRC

Western redcedar trees often have a rapidly tapering stem, highly fluted lower bole and branches that persist in the lower crown (Nystrom 1980; Oliver at al. 1988). There are several, as yet unproven, theories about how and why WRC tends to have this 'peculiar' stem form. Minore (1983) states that WRC taper, and stem form is "profoundly influenced by stand density." Oliver et al. (1988) suggest that several physiological and morphological characteristics of WRC lead to its variation in stem form. They suggest that WRC's tapering stem may result when the high shade tolerant lower crown retains branches that contribute photosynthate downward from the stem thus allowing higher radial stem growth than species that do not frequently retain lower by branches. However, they also note that even WRCs

grown in pure stands at narrow spacings (i.e., conditions that usually encourage self-pruning of branches) "seem to have a tapered stem up to about five feet above the ground after which the stem becomes relatively untapered" and that butt swell in WRC "is probably inherent in the species...".

Western redcedars can also develop a buttressed or fluted lower bole (Sudworth 1908; McBride 1959, both cited in Minore 1979); a similar phenomenon occurs in western hemlock growing in southeastern Alaska (Julin 1988). Fluting is the "development of longitudinal grooves and ridges on the lower bole, resulting from uneven radial growth. For unknown reasons, radial growth stops at one or more locations around the circumference of the stem while the rest of the stem continues to grow at the same or higher rates" (Klinka and Brisco 2009). Oliver et al. (1988) proposed that there is a relationship between the location of dead and dying branches on the lower bole, uneven photosynthate allocations, and the development of flutes. While DeBell and Gartner (1997) found no such relationship they did detect minor flutes developing from the base of all the WRCs they studied. The flutes appeared to



be aligned with the spaces that occur between major roots, suggesting that fluting may develop as a response to mechanical stresses affecting stems (Klinka and Brisco 2009). The incidence and severity of fluting appears to increase with decreasing stand density (Nystrom 1980; Oliver et al. 1988) and with higher growth rates (DeBell and Gartner 1997; Singleton et al. 2003).

Explanations for WRC fluting were also suggested by earlier researchers: Jackson and Knapp (1914) felt that bole buttresses indicated the number of principal roots in a WRC tree. Buckland (1946), after conducting his survey of decay in interior and coastal BC WRCs, suggested that the "well-known infolded or fluted base of cedars appears to be chiefly the result of numerous healed basal wounds" and he substantiated this by noting that in the absence of basal wounds, WRC stems were somewhat 'swell-butted' but did not have deep infolding or fluting. The factors responsible for WRC's peculiar stem form remain to be confirmed.

Western redcedar has a very strong, characteristically extensive and shallow root system (Gonzalez 2004) although root systems appear to be deeper and more extensive in drier soils and shallower and less extensive in wet soils (Hepting 1971; Minore 1983). In well drained soils, WRC trees form dense, profuse mats of fine roots with poorly defined or non-existent taproots (BC Ministry of Forests, Lands and Natural Resource Operations (MFLNRO) 2015). Smith (1964) found WRC roots to be shallower than Douglas-fir roots and deeper than western hemlock roots, but Eis (1974) found little difference in root depth between WRC and these species. Root grafting is more frequent in WRC than in Douglas-fir or western hemlock (Eis 1972).

Western redcedar wood is soft, brittle, reddish to dark brown, aromatic, light in density, and durable (Hepting 1971). The xylem is composed of distinct regions

of darker-coloured heartwood and lighter-coloured sapwood (Figure 2). Heartwood is made up of layers of non-living cells and increases in volume in mature trees. Heartwood contains no reserve food materials and serves largely as structural support. Western redcedar heartwood is relatively impermeable and highly variable in colour ranging from strawcoloured to pink to red to deep brown. van der Kamp (1986) described the distinct

colour zones of mature WRC heartwood as "irregularly shaped nesting The occurrence of discoloured wood in any tree can be indicative of both an injury and activity by decay organisms. For WRC especially, the distinction between wood discoloured as a result of injury and normal heartwood is important because 'healthy' heartwood has high economic value whereas heartwood darkened by injury and/or decay organisms is often weak and much less valuable.

2.3. Inventory

IBritish Columbia has the world's largest standing stocks of WRC (Gregory et al. 2017). Looking back to the late 1980s, the standing volume of mature (aged 121 years or more) WRC in the province was estimated at 824 million m³ (Quenet and Magdanz 1988). Of this volume, 81% was in the Coastal Western Hemlock (CWH) biogeoclimatic zone; the remaining 19% was in the Interior Cedar-Hemlock (ICH) zone, the Coastal Douglas-fir zone, lower elevations in the Mountain Hemlock zone, and the wetter

parts of the Montane Spruce zone. In 2011, the standing volume of WRC and yellow-cedar

in BC was estimated at 750 million m³ (BC Ministry of Natural Resource Operations (MNRO) and BC Ministry of Forests, Mines and Lands (MFML) 2011), 83% of which was coastal and 17% interior. Nearly 75% of WRC and yellow-cedar growing stock is old-growth, i.e., more than 250 years old (BCMNRO and BCMFML 2011).

The harvest of WRC in BC in 1995 was over 7.0 million m³ (10% of BC's total harvest). In 2010 the value of WRC lumber exported from Canada was \$465 million (Poon 2011). Even though the WRC harvest declined to

in 2014, the value was estimated to be

more than \$600 million (BCMFLNRO

Figure 2—Decay-free 'cookie' cut from western redcedar tree. 4.3 million m³ (7% of BC's total harvest) http://www.msacomputer.com/bc/Tree/Tree.html

cones with sides that are roughly parallel to the cambium in longitudinal but not in transverse section." Western redcedar sapwood is narrow, generally 25 cm or less wide and almost white in colour with a yellowish hue. It is relatively permeable, with over four times the moisture content of heartwood (Nielson et al. 1985, cited in Gonzalez 2004).

Mature WRC heartwood typically contains secondary metabolites and defensive compounds known as extractives, many of which can be toxic or detrimental to the growth of the microbes associated with wood decay. Extractives can break down over time, making older heartwood more vulnerable to decay. Some of the same extractives that occur in WRC heartwood are also present in WRC sapwood but in much smaller concentrations. Extractives account for the distinctive colour and aroma of WRC trees.

1995-2014, cited in Gregory et al. 2017). Total revenues generated by WRC products in BC including lumber, raw logs, shakes and shingles and siding were recently estimated to be over one billion dollars per year (Gregory et al. 2017).

By comparison, in the late 1980s the total standing volume of WRC in coastal Alaska, Washington, and Oregon was estimated at 228 million m³, about 40% of which was in western Washington (Gedney and Oswald 1988). In Alaska in 2011, about 43,300 m³ of WRC were harvested, which represented 10.5% of the total harvest that year (Berg et al. 2014). Revenue data for WRC wood products originating in the USA are not readily available.

3. Introduction to Decay

Wood decay is a deterioration of wood tissues caused primarily by the enzymatic activities of microorganisms. Most wood decay is carried out by fungi that belong to the Basidiomycota, a group of fungi that produce their sexual spores (basidiospores) on specialized structures (basidia) of fruiting bodies (e.g., conks and mushrooms, also known as sporophores). The basidiospores of stem decay fungi often gain entry into trees through wounds to stem and root tissues. Root and butt rot fungi can enter roots directly by the enzymatic action of their vegetative mycelia, which spread from infected to healthy roots at points of root contact in the soil. The incidence and extent of decay in trees is quite variable and depends on many factors such as tree species and host vigour, location and size of wounds, season of injury, and the species and virulence of invading microorganisms.

Decay fungi can be classified by the type of decay they cause — either 'white rot' or 'brown rot'. White rot fungi



down lignin, cellulose, and hemicellulose, leaving behind decayed wood which ranges in colour from whitish to

break

Figure 3—Pitted and laminar decay of western redcedar wood caused by a white rot fungus.

yellowish, spongy to stringy, and laminate to pitted (Figure 3). In advanced stages of decay, the residue can be brittle, soft, spongy, stringy, or laminated (Eriksson et al. 1990). White rot fungi decay wood completely and the residual material is not stable in forest soils (Ryvarden 2001).

Brown rot fungi break down only cellulose and hemicellulose, leaving behind wood containing modified lignin with a brown discolouration that cracks into roughly cubical pieces (Figure 4). This material resists further deterioration, and is an important and relatively stable component in forest soils (Gilbertson and Ryvarden 1986).



Figure 4—Brown cubical decay of western redcedar wood caused by a brown rot fungus.

Decay fungi can also be categorized as either 'true heart rot' fungi or 'wound parasites' depending on their most common mode of infection. True heart rot fungi, which attack and are usually confined to heartwood cells of living trees, rarely rely on wounds as their major infection courts (Hunt and Etheridge 1995; BC Ministry of Forests (MOF) 1997; Zeglen 1997). Instead, they enter through natural openings such as branch stubs. True heart rot fungi typically produce fruiting bodies on living trees, although for unknown reasons fruiting bodies are rare for most decay fungi occurring on living WRC (Patton 1942).

By contrast, 'wound parasites' include both heartwoodand sapwood-rotting fungi that usually invade living trees through wounds such as mechanical injuries, broken tops, or fire scars. While most wound parasites are secondary invaders that require wood already colonized by other microorganisms, some are pioneer fungi or primary pathogens that are able to colonize living tissues. Many wound parasites may also attack slash or continue as saprobes on dead trees or on wood in service (Etheridge 1973).

Buckland (1946) found that basal wounds and fire scars were the most important entry points for decay-causing microbes in living WRC, accounting for over 90% of initial infections. Other common defects he identified included

branch stubs, 'dry-side', and injured roots, but only injured roots were found to be important decay entry sites, especially

in young

Dead tops

stands.



Figure 5—Early (incipient) decay (see arrow) associated with white rot infection of western redcedar root.

or 'stag-heads' are also frequent in WRC but what causes

them and whether or not they are infection courts for decay fungi is not known; such top kill of conifers can result from water stress when drought or freezing conditions injure roots.

In the early or incipient stage of the decay process (Figure 5) affected wood is typically discoloured and firm, but may be soft and weak. Western redcedar wood with incipient decay may be used for low grades of lumber as it is not usually used for structural applications. While of no use in the manufacture of products, wood in an advanced or typical stage of decay may offer a potential feedstock for bioenergy plants as this industry (Howard 1988) develops in the Pacific Northwest of North America.

Damage caused by stem decay, and root and butt rot decay fungi can include weakened stems, loss of timber volume from culled wood, and mortality associated with stem and/or root breakage. Damage to trees by decay fungi often ultimately results in the creation of small gaps in the forest canopy or larger disease centers consisting of clumped/grouped, dead and dying trees (Hennon 1995; Worrall et al. 2005; Hennon and Mulvey 2014). Many of these fungi can also live saprophytically in dead roots and/ or stems for years (Etheridge 1973) or decades. An extensive review of tree wounding, host response, decay fungi, stem decay from wounding, and stand management strategies to prevent wounding is provided by Zeglen (1997).



— by 500 years of age, over 80% of tree volume was considered cull (Figure 6). Despite directly quantifying similar WRC volume losses over time, Buckland (1946) calculated that, for the coast and interior sites he sampled, losses to decay in stands aged 50 to 450 years never exceeded growth increment. Important to note here is that Buckland acknowledged that "the limited data upon which [his] computations were made may have distorted the true results, but it seems probable that such an observation on western red cedar may be true for the age period studied."

Volume and value losses with decay, waste and breakage of WRC across its natural range are substantive and there is an urgent need to update and better quantify impact data for WRC losses to decay fungi.

determined from the ground to a 4-inch top. Numbers of stems assessed are indicated beside

data points on graph. Graph and text adapted from Kimmey (1956).

6

3.1. Decay Fungi on Living Western Redcedar

In general, decay fungi occurring in living WRC cause either stem decay or root and butt rot and almost all belong to the Basidiomycota. Decay fungi identified from living WRC in western North America have been documented almost exclusively from two sources: Buckland's 1946 study conducted in BC using 615 coastal and 110 interior WRC trees aged 50 to 450 years, and Kimmey's 1956 study conducted in southeastern Alaska using 98 WRC trees aged 50 to 750 years. While more than 25 different species of decay-causing Basidiomycota have been found in living WRC, only around six of these species are considered by both studies to have notable incidence and impact on living WRC (Table 1). Summaries of fungi occurring on both living and dead WRC are provided in several other publications and sources, including Hepting (1971), Isenberg et al. (1980), Minore (1983), and Allen et al. (1996).

The white rot fungi are believed to cause relatively greater timber volume loss than brown rot fungi (Buckland 1946). The four white and two brown rot fungi having the greatest impact and frequency of occurrence on living WRC in the Pacific Northwest are described below. Pictures of the fruiting bodies of these six fungi are provided in section 5 of this publication.

NB: Fungal synonyms are listed alphabetically; coniferous hosts are listed alphabetically by common names; primary hosts are bolded.

	PATHOGEN AND DISEASE NAME	SYNONYMS	MODE(S) OF SPREAD IN STANDS (P: proposed; C: confirmed)
TS	 Obba rivulosa (Berk. & M.A. Curtis) Miett. & Rajchenb., white butt rot; white laminated rot most important white rot on coast; on living and dead trees, and on wood in service; incipient decay caused by <i>O. rivulosa</i> similar to that caused by <i>P. weirii</i> 	Ceriporiopsis rivulosa, Physisporinus rivulosus, Polyporus rivulosus, Poria albipellucida, Poria rivulosa	Spores (P); mycelial spread via root contact (P)
WHITE RO	 Perenniporia subacida (Peck) Donk, stringy butt rot on living and dead trees, and on wood in service 	Poria subacida	Spores (P); mycelial spread via root contact (C)
	 Phellinus weirii (Murrill) Gilb., cedar laminated root and butt rot most important white rot in interior; specific to cedar on living and dead trees, and on wood in service 	Phellinidium weirii, Poria weirii	Spores (P); mycelial spread via root contact (P)
	 Porodaedalea pini (Brot.) Murrill, red ring rot on living and dead trees; rarely on wood in service 	Fomes pini, Phellinus pini	Spores (C)
OTS	 Postia balsamea (Peck) Jülich, brown cubical butt rot on living trees 	Oligoporus balsameus, Polyporus balsameus	Spores (P)
BROWN R	 Postia sericeomollis (Romell) Jülich, brown cubical butt and pocket rot most important/damaging brown rot on coast and in interior on living and dead trees, and on wood in service 	Oligoporus sericeomollis, Polyporus sericeomollis, Poria asiatica, Poria sericeomollis	Spores (P)

Table 1. Principal decay fungi impacting living western redcedar

Obba rivulosa (White Butt Rot; White Laminated Rot)

Synonyms: Ceriporiopsis rivulosa, Physisporinus rivulosus, Polyporus rivulosus, Poria albipellucida, Poria rivulosa

Coniferous hosts include: amabilis fir, Douglas-fir, redwood, Sitka spruce, western hemlock, **WRC**, white spruce

Obba rivulosa is classified as a wound parasite (Zeglen 1997) that causes white ring rot (Figure 7). It is considered to be the most important butt rot of mature WRC in coastal BC (Allen et al. 1996) and one of three important decay fungi on WRC in Alaska (USDA 2012). While Buckland (1946) saw little evidence of *O. rivulosa* attacking living trees in the interior region of BC, Lewis (1992) found it on living WRC in BC's northern ICH zone, albeit at very low levels (0.7%).



Figure 7—Laminate decay in western redcedar caused by Obba rivulosa.

The yellow-brown stain characteristic of incipient decay caused by *O. rivulosa* appears similar to that caused by *P. weirii.* In more advanced stages of decay when infected wood separates along annual rings as laminations, *O. rivulosa* decay shows conspicuous white mycelial flecks between the lamina and the decay is crumbly. In contrast, *P. weirii* decay develops dark brown setal hyphae between the laminations and shows long striations of white cellulose-like material.

Perenniporia subacida (Stringy Butt Rot; Yellow Root Rot)

Synonyms: Poria subacida

Coniferous hosts include: **amabilis fir,** Douglas-fir, **Engelmann spruce, grand fir,** lodgepole pine, Scots pine, **Sitka spruce, subalpine fir** (*Abies lasiocarpa* (Hook.) Nutt.), western larch, **western hemlock, WRC**, western white pine, **white spruce** Perenniporia subacida (Figure 8) is classified as a wound parasite that causes a white stringy butt rot (Zeglen 1997). It has a wide range of hosts and is most common on mature trees that are suppressed or weakened (Hadfield et al. 1986). Infection has been associated with basal wounds and injured roots, and may also spread through contact with infected roots (Hadfield et al. 1986). At a site near Maple Ridge BC, P. subacida caused extensive butt rot in pole-sized WRC trees where the primary inoculum source of the fungus was proposed to be stumps infected after thinning (van der Kamp 1988), presumably by spores but this was not confirmed. In addition, Buckland (1946) identified P. subacida as one of four important and significant white rot decay fungi on WRC in localized areas, and identified coastal WRC as its most important host. Perenniporia subacida is also known to cause a spongy rot of eastern white cedar (Thuja occidentalis L.) and a feather rot of balsam fir (Abies balsamea (L.) Mill.) in forests of northeastern North America (Buckland 1946).

Perenniporia subacida can be reliably identified by the presence of fruiting bodies which can form on living WRC trees, but more typically occur on the underside of decayed logs (Allen et al. 1996). While Allen et al. (1996) state that "the presence of fruiting bodies on living trees indicates up to 3-4 m of defect; on dead trees fruiting bodies indicate almost total cull", it is not known if this is true for WRC. Advanced decay by *P. subacida* can be mistaken for cedar laminated root and butt rot but can be differentiated from it by the presence of small black flecks (Hadfield et al. 1986). Moreover, the yellow colour of mycelial mats is characteristic of *P.* subacida. The fungus can cause significant volume losses by predisposing infected trees to wind throw (Allen et al. 1996), but this kind of damage has not been specifically quantified for WRC.



Figure 8—Advanced decay in western redcedar caused by *Perenniporia subacida*.

Phellinus weirii (Cedar Laminated Root and Butt Rot)

Synonyms: Phellinidium weirii, Poria weirii

Coniferous hosts include: WRC, yellow-cedar

In North America, *Phellinus weirii* causes laminated root and butt rot of WRC (Figure 9) and is the only major fungal pathogen on WRC that specializes on some members of the Cupressaceae family of conifers. It is considered



Figure 9—Root and butt rot decay of western redcedar caused by *Phellinus weirii*. USDA Forest Service, Bugwood.org

the most important white rot in the interior of BC and in southeastern Alaska and Idaho (Figure 10) (Buckland 1946; Lewis 1992; Allen et al. 1996; Hagle 2006b). The fungus



Figure 10—Map of western North America showing sites where *Phellinus weirii* has been confirmed causing decay of western redcedar and yellow-cedar trees.

has occasionally been found causing limited damage in coastal BC, and has been observed on yellow-cedar at higher elevations (Allen et al. 1996). van der Kamp (1988) commented on the extensive decay caused by P. weirii in the lower bole of young WRC trees and on the severe losses associated with interior WRCs exhibiting the 'archery target' pat-



Figure 11—Cross-section of western redcedar showing the 'archery target' pattern colour variation found in some interior areas of BC and the northwestern United States. (Disk supplied by Pope & Talbot, Grand Forks, BC. Text and image sourced from Gonzalez 2004).

tern of colour variation in wood (Figure 11). This pattern consists of "alternate concentric bands of light and browncoloured wood when viewed on the cross-section" (Gonzalez 2004). The light-coloured bands resemble sapwood and so are often referred to as 'included sapwood'. The included sapwood in WRC is chemically more similar to sapwood than to heartwood (MacLean and Gardner 1956).

Most old-growth interior WRC has some *P. weirii*-caused butt rot, which weakens infected trees and increases susceptibility to stem breakage (Figure 12). Decay increases with tree age and is particularly common in mature trees

aged at least 100 years (Hagle 2006b). Although wounds do not appear to be necessary for P. weirii infection, they can expand decay by aerating the heartwood. The presence of basal wounds may indicate cull in stands with P. weirii; however, this is not always reliable as trees with no evidence of wounding may have extensive decay. In trees with old infections, roots and the lower stem may become hollow. Decay typically extends 2–3 m up from the butt, but oc-



Figure 12—Stem breakage of a western redcedar tree due to butt rot caused by *Phellinus weirii*.

casionally extends 10 m or more (Hagle 2006b). Although moderately resistant to WRC extractives, *P. weirii* rarely kills living WRC trees (Buckland 1946; Larsen et al. 1994; Hagle 2006b).

Limited information exists about the dispersal and infection biology of *P. weirii* on WRC. Nonetheless, Larsen et al. (1994) describe its "unique substrate colonization strategy in a live host", with mycelia progressively colonizing and decaying bark tissues up to 5 m above ground and positioning itself for access to woody tissues after stem breakage occurs. Larsen et al. (1994) observed that the fungus can grow through upper organic soil layers and will fruit without causing visible decay of western hemlock, western larch, and Douglas-fir root buttresses. This suggests that P. weirii can live on root tissues of non-cedar species to support fruiting body formation. As a result, the authors suggest that bark-inhabiting *P. weirii* mycelia may be more important than basidiospores for colonization but caution should be taken in interpreting the presence of *P. weirii* as an indicator of host susceptibility.

Preliminary data from field inoculation trials imply that *P. weirii* may infect WRC roots similar to the way that *Phellinus sulphurascens* Pilát infects Douglas-fir roots (Sturrock and Pellow 2013): *P. sulphurascens* spreads from infected tree roots and colonizes new roots as ectotrophic (surface) mycelia. It then penetrates the roots through the bark, killing phloem and cambium and causing decay in the xylem tissues (Wallis and Reynolds 1965). *Phellinus sulphurascens* (formerly called *P. weirii* - Douglas-fir form) is closely related to *P. weirii* (Lim et al. 2005b) and causes laminated root rot of mainly Douglas-fir and other commercially important coniferous species (Thies and Sturrock 1995). Seedling inoculation trials recently started by researchers at NRCan, CFS, Pacific Forestry Centre in a greenhouse setting should confirm the infection dynamics of *P. weirii* on WRC.

Porodaedalea pini (Red Ring Rot; Pocket Rot)

Synonyms: Fomes pini; Phellinus pini

Coniferous hosts include: most conifers



Figure 13—Advanced decay in a conifer stem caused by *Porodaedalea pini; P. pini* fruiting body adjacent to decay is evident on left hand side of cut stem. Image provided by Todd Manning, SRS Avimetrics, Victoria, BC.

Porodaedalea pini (Figure 13) is a widely distributed and destructive stem and butt decay fungus affecting many living coniferous species. While *P. pini* occurs in WRC, it is more prevalent in other hosts. Its importance in WRC is limited to localized areas in the interior (Buckland 1946) and to very old stands (DeNitto 2005). In Douglas-fir, western hemlock and western white pine, *P. pini* has been found to increase with stand age, slope incline, and in shallow soils (Aho 1982).

Porodaedalea pini is considered a true heart rot fungus (Hunt and Etheridge 1995) but details of its infection process are unclear (Zeglen 1997). The fungus has been confirmed to enter live hosts through small branches or leader stubs (Zeglen 1997), and also through wounds such as felling scars or broken tops. Conks at branch stubs and knots, and swollen knots ('punk knots') are external indicators of decay, and conk size, location, and tree age are used to estimate cull in host trees (Aho 1982). It is not known if external fruiting bodies of *P. pini* are an effective indicator of decay in WRC. Porodaedalea pini decay can progress from heartwood to sapwood and may cause tree death in many conifer species. The fungus can continue to grow on downed trees, but rarely in manufactured wood (Partridge and Miller 1974). Research is needed to determine if these decay dynamics also apply to WRC.

Postia balsamea (Brown Cubical Root and Butt Rot)

Synonyms: Oligoporus balsameus, Polyporus balsameus

Coniferous hosts include: balsam fir, other species of *Abies* and *Picea*, WRC

Buckland (1946) observed *Postia balsamea* (brown cubical butt rot) in relatively low abundance and in localized areas in the North Thompson and Revelstoke regions in interior BC. Although the fungus was rarely obtained from decay due to an abundance of secondary organisms in infected wood, Buckland proposed that if *P. balsamea* exhibits typical butt rot characteristics, it may have been responsible for many of the butt rot infections inspected. He suggested that a further study using fresh samples might better determine the relative importance of *P. balsamea* as a brown rot of cedar.

Postia sericeomollis (Brown Cubical Butt and Pocket Rot; Redcedar Pencil Rot)

Synonyms: Oligoporus sericeomollis, Polyporus sericeomollis, Poria asiatica, Poria sericeomollis

Coniferous hosts include: most conifers but mainly WRC

Postia sericeomollis is a major brown heart rot fungus on living WRC (Buckland 1946; Hagle 2006a) that has

been found to be commonly associated with the major white rot fungi affecting WRC (Buckland 1946). The fungus causes significant WRC volume losses in both coastal and interior regions of the Pacific Northwest yet it rarely infects live trees other than WRC (Hagle 2006a). Buckland (1946) asserted that P. sericeomollis was responsible for the greatest loss due to fungal decay in living WRC. Hagle (2006a) rates P. sericeomollis second



Figure 14—Brown cubical rot in western redcedar caused by Postia sericeomollis.

only to P. weirii in amount of decay volumes in living WRC in the interior of the western USA, and Partridge and Miller (1974) state that it can reduce stand volumes up to 40%.

The infection biology of P. sericeomollis is not well understood. Even though Zeglen (1997) lists it as a wound para-

site, Hagle (2006a) states that wounds are not necessary for establishment of P. sericeomollis on living WRC although wounds can promote decay by aerating the heartwood. Hagle (2006a) suggests that because the greatest proportion of advanced decay commonly occurs in the butt of P. sericeomollis-infected WRC trees (Figure 14), root infection is a likely mode of entry for the fungus. Pockets of P. sericeomollis decay are initially small and isolated in the heartwood but may eventual-

ly merge to form larger pockets of brown, cubically cracked

Rhizina root rot different from the others

decayed wood. The fungus often decays the entire heartwood of the lower stem (Figure 14). In WRC, P. sericeomollis can develop at any height in the stem, making scaling for brown cubical butt and pocket rot difficult. There are no external indicators of this fungus on live WRC trees; fruiting bodies form only on dead logs and slash of a wide variety of tree species. Although P. sericeomollis decay



Figure 15—Living western redcedar tree with cavities created by woodpeckers and sapsuckers and used by many other cavity-nesting birds and animals.

can be confused with the brown cubical rot caused by Phaeolus schweinitzii (Fr.) Pat. (Schweinitzii butt rot) (Allen et al. 1996), the fruiting bodies of these two fungi are very different. Old age and stem wounding increase the severity of cedar brown pocket rot in living WRC (Hagle 2006a). Woodpeckers and sapsuckers commonly develop nest sites in living WRC trees with P. sericeomollis decay (Parks et al. 1997) (Figure 15).

Complete summaries of the decay-causing Rot as a resource Basidiomycota that have been found in living The lignin residue of WRC are provided in Appendix 1 (white rot **Postia sericeomollis** fungi) and Appendix 2 (brown rot fungi). These butt rot in WRC has summaries include several unclassified and been used as a filler unidentified decay-causing Basidiomycota, and extender in which were isolated during a series of studies plywood glues on decay in WRC conducted at the University of Idaho in the 1930s and 40s. These included Gardner 1953). studies on two unclassified heart rots (Aust

1932), heart rots in northern Idaho (Sellers 1940), and

Rhizing undulata causing Rhizing root rot is the only non-Basidiomycota fungus found to cause root rot in living WRC (Allen et al. 1996; Burleigh et al. 2014); it belongs to the fungal group Ascomycota. Rhizina root rot is primarily a disease on young conifer seedlings on sites that have been burned to expose mineral soil within two years prior to regeneration. Disease occurrence is minimal on sites that have been lightly or severely burned, so R. undulata is likely more important on sites with intermediate to high burn intensity. The optimum temperature for spore germination is 35–45°C (95–113°F), so spores may lie dormant in the soil for up to two years until fire creates conditions suitable for the germination of ascospores (Hardison 1976). In acidic soil, the hyphae from germinating ascospores may colonize roots of fresh or living coniferous stumps, live seedlings, and trees. The fungus can penetrate and attack the inner bark and cambial zone where necrosis occurs (Hansen et al. 2017). Rhizina root rot is prevalent throughout BC, particularly in the CWH and ICH biogeoclimatic zones (Burleigh et al. 2014). Damage to any species affected by Rhizina may be reduced by delayed planting on burned, high risk sites (Klinka and Brisco 2009).

(MacLean and

brown cubical heart rots produced in culture (Southam 1941, cited in Patton 1942). Two of the brown rot fungi were suspected to be P. sericeomollis and Phaeolus schweinitzii (Patton 1942), but this was not confirmed. Appendix 3 lists sap rots, canker diseases, and conifer needle diseases documented to occur on living WRC, although they are not discussed in this report.

3.2. Western Redcedar Defenses – Induced Mechanical Responses

Conifers have a range of protective defenses against damaging agents such as pathogens. These defenses, which can be classified as either induced or constitutive (pre-existing), act together to try to limit damage in living trees. The induced defense system in conifers used against damaging agents such as pathogens often involves activation of many different chemicals and changes in anatomical structures to limit pathogen colonization and contain affected tissues. Western redcedar exhibits a significant ability to be induced to both heal wounds and respond to fungal infection. For example, Buckland (1946) observed complete healing in several WRC trees in which more than half the circumference of the cambium had been killed. Nearly all healed wounds inspected, however, had signs of decay. Cleary and Holmes (2011) and Cleary et al. (2012a, b) documented the response of roots of 20- to 30-year-old WRCs to both wounding and Armillaria ostoyae (Romagn.) Herink infection and found that WRC responded using three different and successive mechanical defenses. First, WRC efficiently formed a necrophylactic periderm (NP) to contain infections in the bark. Second, WRC exhibited a hypersensitive-type response consisting of rhytidome (cork) formation in the area of initial fungus penetration. Third, WRC formed traumatic phloem resin ducts (TPRDs) to further restrict entry by A. ostoyae. The latter two of these responses were newly described for WRC. The intensity of the TPRD formation was higher in roots inoculated with A. ostoyae than in roots that were wounded (Cleary and Holmes 2011). TPRDs were initiated at the time of phellogen restoration and formation of NP around the primary wounded tissue. This combination of host responses allowed most WRC roots to limit the cambial invasion and/or girdling of roots by A. ostoyae. By

contrast, in Douglas-fir and western hemlock A. ostoyae infection interfered with the formation of mechanical barriers, which were often breached and resulted in hosts having significantly lower resistance to the fungus (Cleary et al. 2012b). It is unknown if WRC responds to infection by other decay pathogens in the same way. Cleary et al. (2012a) remark that the "significance of the multitude of structural responses as defence mechanisms... in western redcedar, is complex and warrants further investigation."

3.3 Western Redcedar Defenses – Heartwood Extractives

Constitutive (pre-existing) defense mechanisms in WRC include heartwood extractives, which make up a portion of the non-structural compounds occurring in trees (Bennett and Wallsgrove 1994; Taylor et al. 2002). To date, most of the research on decay resistance in WRC has focused on these compounds. More than 20 different extractives have been identified in WRC heartwood, including terpene tropolones, terpenes, and lignans (Rennerfelt 1948; MacLean and Gardner 1956; Roff and Whittaker 1959; Nault 1988: Daniels and Russell 2007: Russell and Daniels 2010: Morris and Stirling 2012). Concentrations of thujaplicins, thujic acid and other extractives in WRC generally increase radially from the pith to the outer heartwood and longitudinally from crown to lower bole. Even though overall extractives content in WRC sapwood is low, using a modified soil block method, Eslvn and Highlev (1976) rated WRC sapwood as moderately resistant to white rot attack but susceptible to brown rot attack. While distribution of extractives in radial and longitudinal directions of wood tissues is reasonably well understood, micro-distribution within tracheids remains unclear (Stirling and Morris 2015). Overall extractive concentrations in WRC heartwood increase with tree age (Nault 1988; Daniels and Russell 2007). Although several extractives have been shown to be toxic to fungi (DeBell et al. 1999) and many are thought to confer some measure of heartwood decay resistance in WRC (Rennerfelt 1948: MacLean and Gardner 1956: Roff and Whittaker 1959: Nault 1988: Daniels and Russell 2007; Russell and Daniels 2010), their roles in conferring heartwood decay resistance and durability in WRC still are not fully understood.

WRC extractives – what's what (modified from Morris and Stirling 2012)

Nearly two-dozen extractives have been identified in WRC heartwood, and there are many others yet to be identified (Gardner and Barton 1958a,b; Gardner 1963; Stirling and Morris 2011). Five of the known extractives are terpene tropolones, including alpha-, beta-, and gamma-thujaplicin, beta-thujaplicinol, and beta-dolabrin. Another five are other terpenes of which thujic acid and methyl thujate are present in substantial amounts. The remaining three terpenes, nezukone, carvacrol methyl ether, and thujin, are only reported in trace amounts (Barton and MacDonald 1971; Jin et al. 1988b). The eleven other extractives reported in WRC heartwood are lignans. These include plicatic acid, plicatin (Gardner et al. 1959, 1960, 1966; Stirling and Morris 2015), thujaplicatin and thujaplicatin methyl ether (MacLean and Murakami 1966), and seven other compounds reported to be present in very low quantities (Barton and MacDonald 1971; MacDonald and Barton 1970, 1973). It is thought that most of the extractives in WRC heartwood are formed from precursors occurring at the heartwoodsapwood boundary (Swan et al. 1969).

Armillaria assists other decay fungi affecting WRC?

Armillaria ostoyae is the primary pathogen causing Armillaria root disease of conifers throughout the range of WRC in western North America. While this fungus girdles and quickly kills young WRCs (Buckland 1946; van der Kamp 1988) anecdotal evidence suggests that older WRC trees may be more tolerant of *A. ostoyae* than other conifers (Morrison 1988; van der Kamp 1988; Morrison et al. 2000, 2014). Buckland (1946) for example, describes *A. ostoyae* as being unimportant on WRC. In a study of the histology of *A. ostoyae* infection in different conifer species, Cleary (2007; 2010) and Cleary et al. (2012b) documented a combination of host-mediated defence mechanisms that reduced lesion spread of *A. ostoyae* in WRC as compared to spread in Douglas-fir and western hemlock. Based on this evidence Cleary (2010) proposed that inclusion of a high proportion of WRC when regenerating *A. ostoyae*-infested stands might be a good practice for management of the disease, particularly in the southern interior of BC.

Despite this apparently somewhat 'friendly' relationship between WRC and *A. ostoyae*, there is evidence that suggests that the fungus might play a role in facilitating entry of other pathogenic decay fungi that are commonly associated with butt rot in WRC. For example, in his 1946 report on investigations of decay in WRC in BC, Buckland stated that:

"In certain of the drier areas on the coast, fire scars were of considerable importance in exposing heartwood to infection, while basal wounds caused by other mechanical decorticating agencies were very frequent generally. In nearly all the localities inspected, but particularly the moister regions of the Interior, basal wounds of doubtful origin were found. These wounds appeared externally as depressed areas in the bark, limited to a small fraction of the circumference to cases of almost complete girdling. On examination it was found that the cambium had been killed beneath the bark. **No correlation was found with any natural causative factor**."

Is it possible that *A. ostoyae*, by way of its continuous initiation of minor infections of WRC roots and root collars, was the causal agent of Buckland's "*basal wounds of doubtful origin*"? Did Buckland examine the 'wounds' closely enough to determine if there was evidence of *Armillaria*?

The following description by van der Kamp (1988) of *A. ostoyae* infection of older WRCs closely resembles that of Buckland:

"The fungus often causes cat faces, killing a triangular area of bark at the base of the stem directly above the affected root. In such cases the bark remains attached and the damage does not become obvious until several years later when a sunken area of bark overlying a pocket of decay develops."

Additional evidence that *Armillaria* species likely play a predisposing role in the infection biology of other root and butt rot fungi was provided by Barrett and Greig's investigations of *P. schweinitzii* affecting *P. sitchensis* trees aged 10–19 years in southern Britain (1984). When they examined root systems of 300 of these trees Barrett and Greig found that a high proportion had been attacked by *A. ostoyae*, particularly the sinker roots in the taproot region rather than the secondary, lateral roots. They concluded from this field study and some laboratory studies conducted around the same time that:

"<u>P. schweinitzii</u> is not a primary pathogen, but requires some pre-disposing factor to by-pass the defence mechanisms of roots and enter the tree to cause decay. In crops of <u>P. sitchensis</u> in Britain, damage by <u>Armillaria</u> may be the crucial factor. Such an association provides a rational explanation for the occurrence of the disease on old broadleaved sites, commonly rich in <u>Armillaria</u> species."

More recently, CWFC and CFS researchers found evidence on 48-year-old WRCs of non *A. ostoyae*-decay associated with lesions caused by *A. ostoyae* that had healed (Mike Cruickshank, Canadian Wood Fibre Centre, Victoria BC, personal communication, July 8, 2015).

More research is needed to investigate the role that *A. ostoyae* and possibly other species of *Armillaria* have in the overall decay process on living WRCs, particularly the role they might play in facilitating the entry of other decay organisms from root lesions not visible aboveground.

WRC decay resistance multifactorial

Using gas chromatography and soil block assays of heartwood plugs from eleven WRCs aged 90–100 years, DeBell et al. (1997) found that decay resistance was highly variable at low concentrations of tropolones, but was consistently high at concentrations over 0.25%. The authors suggest that tropolone content might be a useful indicator of decay resistance in living WRC. However, since several samples with low concentrations of tropolones were resistant to decay it is likely not the only factor in decay resistance. Daniels and Russell (2007) made similar observations in their study of concentrations of extractives in second-growth and coastal BC WRC trees where they also saw significant variation in heartwood extractives both within and between trees aged 40-125 years. Trees with visible decay had dramatically lower concentrations of extractives within and adjacent to decayed tissues. In comparison to coastal trees, interior WRC trees had considerably more decay in the heartwood, which these authors suggest might be attributed to lower levels of β -thujaplicin.

Taylor et al. (2006) found high variability and weak positive correlation between decay resistance and total methanol-soluble extractives in WRC and yellow-cedar and stated that their observations "suggest that it is not possible to focus on a single heartwood extractive measurement in order to understand the natural durability of the wood, especially if one is considering the resistance of the wood to multiple biodeterioration agents."

Recent research suggests that while WRC lignans such as plicatic acid and plicatin appear to have little direct fungal toxicity they may contribute indirectly to decay resistance via their antioxidant/radical scavenging and metal chelating properties (Stirling et al. 2007; Stirling and Morris 2015). This association between extractives in wood and decay resistance was first put forward by Schultz and Nicholas (2000, 2002). Further studies are needed to better understand how extractives content in living WRC trees correlate with susceptibility to decay organisms.

3.4 Microbial Succession in Western Redcedar

Despite the prevalence and diversity of extractives in the heartwood of living WRC trees, decay fungi commonly occur there and can cause significant decay. How do decay fungi and other microbes, be they primary or secondary invaders, tolerate WRC's fungistatic and toxic heartwood compounds?

van der Kamp (1975) hypothesized that in old-growth coastal WRC, decay "involves a succession of microorganisms such that the first fungi to invade toxic heartwood destroy the natural toxins, rendering the wood subject to decay." These pioneer invaders do not cause decay but do alter the protective chemicals found in WRC heartwood (Barton and MacDonald 1971; van der Kamp 1986). This allows invasion by microorganisms into the reactive zone (a protective boundary zone between fully functional sapwood and decaying heartwood), further promoting the succession of decay fungi (van der Kamp 1975). How and when pioneer fungi initially enter into the tree and begin detoxification activities, and why decay fungi do not appear to progress into the sapwood of living WRCs are questions yet to be answered.

In his 1975 study, van der Kamp also sampled and cultured microbes from several differently coloured zones in the heartwood of six decayed and stained old-growth WRC trees; he found a consistent pattern of microbe distribution (Figure 16). Generally, the centralized decay column (Zone

1) was inhabited by numerous filamentous fungi, as well as bacteria, yeasts, insects, and plant roots. Obba rivulosa was isolated from this central decay column and from a narrow area (Zone 2) that was the edge of the sound heartwood. Zone 2 also hosted a small suite of diverse microorganisms. In the next zone (Zone 3), which consisted of brown-stained heartwood, van der Kamp found three fungi, two of which he identified as a Cylindrocephalum



Figure 16—Diagram showing crosssection of decayed, old-growth western redcedar stem and typical zones of discolouration as described by van der Kamp (1975). Zone 1: central column of decayed wood; Zone 2: inner edge of wound heartwood; Zone 2: inner edge of wound heartwood; Zone 4: red-stained heartwood; Zone 5: outer, straw-coloured heartwood; Zone 6: white-coloured sapwood.

sp. (likely the same fungus Jin et al. (1988a) later referred to as *Sporothrix* sp.) and *Kirschteiniella thujina*. The third fungus was probably a *Phialophora* sp., as later identified by Jin et al. (1988a). The red-stained heartwood (Zone 4) outside the brown-stained zone hosted only *Cylindrocephalum* sp. and the last of the heartwood zones (Zone 5) was straw-coloured and free of microorganisms. van der Kamp did not sample the sapwood (Zone 6) of the WRCs he assessed. These results are in agreement with earlier studies by Eades and Alexander (1934) and Findlay and Pettifor (1941) who found that the lighter coloured areas of WRC heartwood were largely free of microorganisms whereas the dark-coloured core often hosted many. van der Kamp (1975) noted an absence of bacteria in the early stages of microbe succession in living WRC. In contrast, Shigo (1967) detected bacteria as primary invaders of hardwoods following wounding. van der Kamp suggested that bacteria may be passively transported through hardwood xylem, whereas such movement is restricted in conifers by the structure of the bordered pits present in their tracheids. In addition, bacteria may be inhibited by high acidity levels of WRC heartwood (van der Kamp 1975).

In 1986 van der Kamp reported the effects of fungi on extractive content in WRC heartwood. Blocks of heartwood from both a mature (300+ years) and a young (80 years) WRC tree were inoculated with *Cylindrocephalum* spp., *K. thujina*, and *O. rivulosa*. The content of thujaplicin — a major fungitoxic extractive, as well as hot water solubility and decay resistance of test blocks — were subsequently measured. From this study van der Kamp concluded that:

"the non-decay fungi tentatively identified as Cylindrocephalum sp. and K. thujina, which commonly inhabit the inner, sound but stained heartwood of western redcedar, have the ability to invade sterile heartwood containing high levels of thujaplicin. Once established, these fungi degrade or somehow alter the thujaplicins, and reduce the hot water solubility of the wood [i.e., reduce the content and/or concentration of other, fungicidal phenolics], resulting in considerable reductions in the natural decay resistance of test blocks with initial high levels of thujaplicin. Nevertheless, a similar loss of decay resistance of stained wood with low thujaplicin levels from a living tree could not be demonstrated. Some other mechanisms of decay resistance may be involved. Low levels of thujaplicin in stained western redcedar heartwood do not necessarily imply low decay resistance."

Jin et al. (1988a) corroborated van der Kamp's 1975 and 1986 results: they found that a Sporothrix sp. (likely what van der Kamp referred to as Cylindrocephalum sp.), Kirschteiniella thujina, and a Phialophora sp., render the thujaplicins in living WRC non-toxic to the pioneers. The decrease in heartwood decay resistance allows a succession of fungi to subsequently invade heartwood (Shigo and Hillis 1973; Jin et al. 1988a) and cause changes from a very light straw-colour, to red, to various shades of brown discolouration in these tissues. Jin et al. (1988a) proposed that fungal succession in WRC originates at the centre and base of an affected tree and moves up the bole and outwards toward the heartwood-sapwood border. Sporothrix sp. invades first, followed by K. thujina and finally by *Phialophora* sp.: *Sporothrix* sp. biodegrades thujaplicins to the lactone thujin, which was found only in the outer edges of discoloured heartwood sampled from living trees (Jin et al. 1988a). A bioassay conducted in the laboratory by Jin et al. (1988a) supported their hypothesis: when blocks cut from the light-coloured outer heartwood of living WRC

trees were exposed to the three fungi in petri dishes, thujin was only detected in blocks exposed to a *Sporothrix* isolate. In a study of sugar maples infected with the decay fungus *Coltricia focicola* (Berk. & M.A. Curtis) Murrill (syn. *Fomes connatus* (Weinm.) Gillet, Tattar et al. (1971) documented results similar to those of Jin et al. (1988a) and van der Kamp (1975): i.e., central columns of decayed tissues surrounded by intact, discoloured tissues, which are bounded by clear-coloured wood. Total content of extractives in sugar maples was lower in decayed and discoloured tissues than in clear wood. Clear wood was essentially sterile while a succession of microorganisms including bacteria, nondecay fungi, and nematodes were isolated from decayed and discoloured tissues in advance of *C. focicola*.

4. Factors Affecting Decay in Living Western Redcedar

4.1 Age

In general, heartwood decay increases with tree age as the relative proportion of heartwood increases, wound-healing slows, and extractives degrade over time (Wagener and Davidson 1954). Western redcedars live longer than their associates so may accumulate more wounds, and decay fungi affecting them have a long time to advance. Not surprisingly then, hollow, old-growth WRCs are common (Daubenmire and Daubenmire 1968, cited in Minore 1983). Both Buckland (1946) in BC and Kimmey (1956) in



Figure 17—Relationship of the occurrence of decay to age in western redcedar. Buckland (1946) investigated decay in a total of 615 coastal and 110 interior western redcedar trees in BC. Numbers of trees assessed at ages in 50 year increments are indicated beside data points on graph. Graph and text adapted from Buckland (1946).



Figure 18—Relationship of the occurrence of decay to age in western redcedar, western hemlock, and Sitka spruce trees containing measurable amounts of decay. Kimmey (1956) investigated decay in a total of 98 western redcedar trees, 230 western hemlock trees and 232 Sitka spruce trees in southeast Alaska. Numbers of trees assessed at ages in 100 year increments are indicated beside data points on graph. Graph and text adapted from Kimmey (1956).

southeast Alaska found that the occurrence of decay in WRC trees was highly correlated with tree age (Figures 17 and 18).

In fact, the occurrence and impact of decay in young WRC is not well-documented and should receive more attention (Antos et al. 2016). While acknowledging that his study focussed on decay in old-growth WRC, even Buckland (1946) indicated that "young cedars are apparently quite susceptible to attack by several important heart rotting organisms. Until a careful study is made of the conditions existing in these young trees, no conclusions can be drawn concerning the significance of decay in its effect on the silviculture and management of red cedar. Observational evidence would indicate that decay in young cedars is of importance and should be studied carefully in relation to the management of the species."

4.2 Location and Elevation

Stand location may also influence the incidence of decay in WRC. In 2007, Daniels and Russell evaluated heartwood extractives from a total of 26 second-growth WRC trees ranging in age from 40 to 125 years old from two southern Vancouver Island (coastal) populations and from two interior BC populations. They detected a higher incidence of heartwood decay in interior trees than in coastal trees, which they suggested might be related to lower levels of β -thujaplicin in interior trees.

When Buckland (1946) examined decay in coastal and interior WRC trees in BC, he found yet could not explain an observed higher incidence and impact of decay in interior WRC trees (Figure 19). Patterns of heartwood discolouration also appear to differ between coastal and interior WRC but this is not well-documented in the literature. A type of colour variation found in WRC heartwood called the archery target pattern is described

In both studies the percentage of WRC trees with decay increased sharply from about the age of 50 years until 300-450 years at which time all the trees had some decay. However, this is not to



Figure 19—Average percentage loss in volume and length in merchantable pole-sized western redcedar trees infected by four principal decay fungi occurring in the coastal and interior forests of BC. Buckland (1946) included a total of 103 is just incidental in young WRC. and shown in Figure 11 on page 9 of this report. This type of heartwood colour variation is relatively common in some parts of BC and the northwest USA interior.

In addition to geographical location, elevation may be related to incidence and volume of WRC decay. Kimmey (1956) found no relationship between WRC decay volume and elevation in southeast Alaska, but Hobbs and Partridge (1979) found that over 80% of the trees infected by *P. sericeomollis* and *P. weirii* in northern Idaho were WRC, and these infected trees were restricted to stands below 1500 m; they did not look at decay volumes. In a study of the incidence of decay in WRC in two biogeoclimatic regions in BC's ICH, Robison (2000) also found that decay volume was inversely related to elevation.

4.3 Site

There is evidence that some site factors also affect decay incidence and/or volumes in trees but results across species are quite variable. For example, Bouslimi et al. (2013) looked at both site and between and within tree variation effects on brown rot decay in eastern white cedar (*T. occidentalis*). Decay incidence increased with stand age and site moisture and as heartwood volume increased, so did brown rot decay; as sapwood volume increased, decay decreased. In living trees, decay was limited to the heartwood; in non-living trees decay was in both heartwood and sapwood. In contrast to Buckland's finding for young WRC, Bouslimi et al. (2013) observed no serious decay in trees younger than 80 years old.

Hofmeyer et al. (2009) looked at the influence of soil site class, which ranged from Site Class 1 (well drained soils) to Site Class 5 (very poorly drained soils) and light exposure on growth and decay of northern white cedar (*T. occidentalis*), balsam fir, and red spruce (*Picea rubens* Sarg.) in Maine. They found that "*incidence of decay in outwardly sound northern white-cedar*... was highest on well-drained mineral soils, and mean proportion of basal area decayed at breast height increased in outwardly sound northern white-cedar as drainage improved from poorly drained to well-drained soils."

In a study designed to develop a method to predict decay volume and round-wood end use volume for a hardwood species — trembling aspen (*Populus tremuloides* Michx.) — Schneider et al. (2008) found that stand origin (fire versus clearcut) and location (ecological region), along with tree age, height, quality, and presence of decay fungi contributed to the presence and proportion of decayed merchantable volume. However, Thor et al. (2005) emphasize that, in general, relationships between site factors and tree decay remain unclear.

Mycorrhizal fungi occurring in forest soils form mutually beneficial root associations with many plant species. Western redcedar trees have arbuscular mycorrhizae (AM) associated with the exterior of their fine root sheaths (Minore 1979). Beese (1987) found that WRC nursery stock was generally not mycorrhizal until after planting, although inoculation trials with AM indicate that they are important to the growth of both containergrown (Kough et al. 1985) and bareroot seedlings (Berch et al. 1991). It is not known if AM play a role, protective or otherwise, in the presence and extent of decay in living WRCs.



4.4 Silviculture

Decay incidence and volume in WRC may be affected by silviculture and harvest practices. For example, individual WRC trees regenerated by layering are considered more susceptible to fungal colonization than those regenerated from seed (Klinka and Chourmouzis 2005). Apparently, the original branch that gives rise to the 'new' tree usually dies and decays as the new tree becomes established. Decay associated with the new tree may then spread up the root collar and into the lower bole resulting in butt rot (Paul Hennon, USDA Forest Service, Alaska, personal communication, February 24, 2015). It is also possible that some causal pathogens move through root contact and may readily attack clumped, layered, or root-connected trees (Robin Mulvey, USDA Forest Service, Alaska, personal communication, March 4, 2015).

Koenigs (1969) compared the incidence of root disease on 100 year-old WRCs in paired thinned and un-thinned stands in Idaho and observed more root rot caused by *Armillaria ostoyae* and other fungal species in thinned stands. For example, *A. ostoyae* was isolated from 41% of WRCs in thinned plots versus only 12% in un-thinned plots. Koenigs (1969) speculated that this result might be due to increased inoculum potential of *A. ostoyae* associated with infected stumps of thinned trees.

It is not clear if the practice of retaining WRC residuals (also known as advanced regeneration trees) at harvest to give the next rotation a head start is necessarily beneficial. Residual trees may have internal decay that is not indicated on stems and so may not be good crop trees (BCMOF 1997). Also, stumps of harvested WRC trees harboring decay fungi could experience a build-up of fungal inoculum, which could lead to increased decay problems for remaining crop trees. When Lewis (1992) found decay in 30–60% of advanced regeneration WRCs sampled across several sites in northern BC and isolated *P. weirii* from almost 30% of these trees, she cautioned that "the high incidence of decay in cedar is of concern regarding

Climate change & WRC decay

Climate has always shaped the world's forests (Bhatti et al. 2006), but the world's climate has become warmer and will continue to change at an unprecedented rate (Hepting 1963; IPCC 2007; Kurz et al. 2008). Climate change generally will lead to reductions in tree health and increases in tree mortality, and will improve conditions for several forest pathogens (Hepting 1963; Ayres and Lombardero 2000; Desprez-Loustau et al. 2006, 2007; van Mantgem et al. 2009; Daniels et al. 2011; Chakraborty 2013; Allen et al. 2015). Decay of wood is heavily dependent on moisture and temperature; therefore, decay rates will likely increase with warmer and wetter conditions and decrease with warmer and drier conditions (Boland et al. 2004; Dukes et al. 2009; Sturrock et al. 2011). Conversely, the future incidence and impact of root and butt decay fungi such as *A. ostoyae*, and even *A. sinapina* associated with stressed trees (Cleary et al. 2012c), are predicted to increase under warmer and drier conditions. This is due to the more direct effect that drought has on inciting water stress in trees, which renders them more susceptible to primary and secondary pathogens (Desprez-Loustau et al. 2006; Kliejunas et al. 2009; Lowther 2010). The fate of WRC and its suite of decay-causing organisms under climate change are clearly uncertain.

To date we are aware of one study that has specifically looked at climate change and a forest pathogen affecting WRC. Gray et al. (2013) modelled cedar leaf blight (CLB, caused by *Didymascella thujina* (E.J. Durand) Maire) disease risk under observed climate (2003 to 2008) and multiple future climate scenarios for the 2020s, 2050s, and 2080s. They found that the majority of future climate scenarios predict coastal environments will continue to favour occurrence of the disease. Eventually, however, with projected reductions of available summer climate moisture during times of ascospore discharge and germination, CLB intensity is predicted to decrease towards the 2080s. Regardless, the authors recommended that current reforestation efforts deploy CLB resistant WRC seedlots in high risk environments to avoid significant mortality and growth reduction due to the disease.

the selection of advanced regeneration as crop trees". While a retrospective study of advanced regeneration WRC in southern BC (DeLong 1997) indicated that advance cedar has a good potential for release in the subzones sampled, the study results also acknowledged that because "decay incidence was lower than expected in the harvested openings" more research is needed to "look at decay in advanced cedar that has been released longer, as well as the relationship that advanced cedar has with <u>Armillaria ostoyae</u>."

5. Indicators and Detection of Decay in Trees

Detection of wood decay in living and dead trees is critical for both accurate timber valuations as well as hazard and wildlife tree assessments. Detection is enhanced by the presence of indicators of decay such as fruiting bodies and punky or swollen knots while wounds and scars (e.g., mechanical scars, fire scars, cracks in the main bole, and cankers) indicate potential infection courts for decay fungi. These indicators, along with tree size, site variables, and tree age have been used to indicate and quantify decay in many living hardwood and softwood species (Farr et al. 1976; Aho 1982).

Kimmey (1956) proposed that reliable external indicators of decay in WRC should include scars and wounds (especially on the bole or roots), dry-side, 'sucker limbs' of the 'bayonet type', and rotten burls on the main bole.

WRC decay in BC's very wet cool ICH zone

The role of climate in the growth of WRC is poorly understood in BC's inland temperate rainforest (ITR). Conflicting future predictions for the ITR under climate change scenarios and the potential ongoing harvest of individual ancient WRCs (Coxson et al. 2012) make the ITR an area of special concern for research, management, and conservation. In a study to quantify the sensitivity of WRC to climate variables in the ICH, Konchalski (2015) set out to sample WRC and analyze the annual growth increments, and to guantify relationships between WRC, western hemlock looper (Lambdina fiscellaria lugubrosa Hulst), and climate (Kathy Lewis, University of Northern BC, Prince George, BC, personal communication, Fall 2014). However, Konchalski found it difficult to find sound trees free of decay for dendrochronology analysis. Almost all of the 260 WRC trees sampled along transects from lower to higher elevation and on north- and southfacing slopes had some heart rot. Many more WRCs could not be used in the study due to extensive heart rot limiting their utility to yield growth ring data. Although the study was not designed to quantitatively assess decay incidence or decay volume, these observations will help to identify the extent of decay in WRC in the BC interior and may help to focus future research in the area.

Manning (2001) found stem damage to be the most common indicator of decay on WRC. In interior and coastal WRC, LeMay (1993) determined that measurement of decayed wood area at breast (1.3 m) and stump (0.3 m) height, along with tree size and tree age, yielded more accurate estimates of percent decay than the presence of external decay indicators. External signs that do not appear to indicate appreciable amounts of cull in WRC include dead spike tops, broken tops, forked tops, and sound burls (Buckland 1946; Kimmey 1956).

Although fruiting bodies occur but are seen rarely on WRC, they can help to detect and quantify decay in this species. In this report, we provide images and some general identification information about the fruiting bodies of the six major decay fungi affecting living WRC.

Obba rivulosa (white butt rot; white laminated rot): Fruiting bodies are annual, thin (up to 3 mm thick),



resupinate, poroid and white (Figure 20). They are rare and therefore not as useful for identification as are other signs of decay (Allen et al. 1996). They form primarily on slash.

Figure 20—Fruiting body of Obba rivulosa. http://cals.arizona.edu/classes/plp427L/ aphyllo.htm

Perenniporia subacida (stringy butt rot): Fruiting bodies

are perennial, resupinate, and leathery to crustlike (Figure 21) (Allen et al. 1996). They may form on living WRC, but are usually found on the underside of decayed logs or on the lower stems of dead standing trees



Figure 21—Fruiting body of Perenniporia subacida. http://farm3.static.flickr.com/2433/ 4062727910_84132ea182_z.jpg



Figure 22—Fruiting body of Phellinus weirii. under roots, in

Phellinus weirii (cedar laminated root and butt rot): Fruiting bodies are resupinate, perennial and typically dark in colour (Figure 22). They develop

basal scars, and on the undersides of logs (Aho 1982). Larsen et al. (1994) noted that the occurrence of P. weirii fruiting bodies at or near the ground on downed trees and on fluted and buttressed stems was common in riparian ecosystems in some areas of Idaho and Washington State; fruiting bodies were scarce to non-existent on drier sites in these same areas.



Figure 23—Fruiting body of Porodaedalea pini.

Postia sericeomol-

lis (brown cubical and pocket rot): Fruiting bodies are annual, resupinate, thin, and white (Allen et al. 1996) (Figure 24). They rarely form on living WRC (Harvey and Hessburg 1992) and are usually found on the ends of decayed logs or on slash.

Postia balsamea (brown cubical butt rot): Fruiting bodies of *P. balsamea*





Figure 24—Fruiting body of Postia sericeomollis. http://farm5. staticflickr.com/4066/4242132260 _953db1100c_z.jpg

have been described on *Crataegus* spp. but not on WRC.



Figure 25—Fruiting body of Postia balsamea. http://www.hlasek.com/ postia balsamea1en.html Postia balsamea_bo6089

Fruiting bodies are shelf-shaped with broad or constricted attachment, single or regularly overlapping, fairly tough when fresh, and chalky hard when dry (Ryvarden and Gilbertson 1993-1994) (Figure 25). The upper surface turns from cream-coloured to pale greyishbrown to mouse grey, darkening when drying.

5.1 Other Methods to Detect and/or Quantify Decay in Trees

Since biology (growth rate, infection process, etc.) differs among pathogens, early identification/diagnosis of the causative agent of decay allows for a better assessment of the risks of pathogen-caused tree failure. Traditional morphological and biochemical methods for the identification of decay pathogens require expert knowledge and can be time-consuming and unreliable. Morphological identification of fungi is typically based on fruiting bodies,



which are often ephemeral or absent (Nicolotti et al. 2009). The detection of decay fungi in wood is typically performed by isolating pure cultures on selective media. These isolated cultures are then inspected for macro- and microscopic features, and may be subjected to biochemical, chemical, and immunological tests. Immunological methods such as the ELISA (en-

zyme-linked immunosorbent assay) test use antibodies and colour change to identify decay pathogens. ELISA tests have been developed for *Armillaria* and *Ganoderma*. More recently, molecular genetic methods for identification have been developed, which can be efficient, rapid, and accurate, and may not require isolation of the fungi (Guglielmo et al. 2010).

Nicolotti et al. (2009) reviewed newly developed biomolecular methods to identify some of the most important and widespread decay fungi directly from wood. When a pathogen of interest is known and there are diagnostic markers for likely candidate pathogens, taxon-specific polymerase chain reaction (PCR) primers and PCR-RFLP (restriction fragment length polymorphism) are the most commonly used methods for identification due to their high reproducibility and relatively lower costs. Taxonspecific PCR primer sets may be used singly or in multiplex PCRs to accurately detect fungi in wood collected from decay-affected trees. When the causal agent of wood decay is unknown, universal PCR primers can be used to preferentially amplify just basidiomycota (Gardes and Bruns 1993) or all fungal ribosomal DNA (White et al. 1990). The DNA sequences of the amplified DNA can then be determined and compared to that of known fungi for positive identification in databases such as GenBank® or EMBL (European Molecular Biology Laboratory) using NCBI BLAST (National Center for Biotechnology Information Basic Local Alignment Search Tool). Advances in DNA-based diagnostic methods that can be used to survey fungal diversity and detect unknown fungi include pyrosequencing and other

next-generation sequencing platforms (e.g., Ovaskainen et al. 2010). An increasing amount of sequence information is becoming available, allowing more sequences from unknown isolates to be matched to that of verified taxa, and for use in the design of taxa-specific markers.

Guglielmo et al. (2008, 2010) and Gonthier et al. (2015) have developed multiplex PCR assays for detection of a suite of specific wood decay fungi in standing trees. These assays are independent of any signs or symptoms of decay. In addition, Gonthier et al. (2015) have developed a similar assay for the detection and identification of the 12 most hazardous and wide-spread decay fungi on conifers, including WRC, in the northern hemisphere. Wood and needle tissue of WRC is known to contain PCR-inhibiting compounds, but this challenge was overcome with the use of a DNA extraction kit designed by QIAGEN that removes PCR inhibitors. Test assays performed on wood samples and fruiting bodies confirmed the reliability of this multiplex PCR-based diagnostic method. The following fungi and fungal-related microbes were identified in WRC using the QIAGEN DNA extraction kit, followed by PCR (Matteo Garbelotto, University of California at Berkeley, personal communication, June 12, 2015):

Candida tropicalis (Castell.) Berkhout Malassezia restricta E. Guého, J. Guillot & Midgley Phaeolus schweinitzii Phialophora Pucciniomycetes sp. Sebacina grisea Bres. Septobasidium ramorum (Schwein.) Donk Xenopolyscytalum pinea Crous

PCR-based diagnostic methods hold promise for the future development of identification methods of important WRC decay fungi. Marker systems specific to some of the top six pathogens of WRC and for *Armillaria* species have already been designed: e.g., for *O. rivulosa* and *P. sericeomollis* (Adair et al. 2002); for *P. weirii* and *A. ostoyae* (Guglielmo et al. 2007; and others); for *P. subacida* (Tabata et al. 2009); and for *P. pini* (Gonthier et al. 2015). Moreover, in southeast Alaska, work has been initiated using pyrosequencing to identify key decay fungi from cedar wood samples, as well as several taxa-specific PCR primers (Robin Mulvey, USDA Forest Service, Alaska, personal communication, September 10, 2014).

Other non-molecular tools such as instruments using vibro-acoustical or electromagnetic radiation techniques have been developed to aid detection and quantification of incipient and advanced decay in standing trees (Ouis 2003). One such device, the Sound Impulse Hammer, is used to detect internal defects (Bethge et al. 1996). Both acoustic tomography and resistograph technology can be used to evaluate the extent of stem decay in living trees (USDA 2015). Bethge et al. (1996), Ouis (2003), and Leong et al. (2012) review the different tools and provide information on the capabilities and limitations of each.

Preliminary results from researchers at the CWFC and the CFS indicate that the Resistograph® is very effective in identifying the occurrence of decay in WRC trees, and likely also has application in quantifying this decay (Mike Cruickshank, Canadian Wood Fibre Centre, Victoria BC, personal communication, August 2015). While the abovementioned methods can detect and quantify wood decay in standing trees, they do not identify the causal agents.

6. Management of Decay in Living Western Redcedar

To date, there is little information specific to managing decay in living WRC. DeNitto (2006) outlines general considerations and methods for management of conifer stem decay. Zeglen (1997) and others (e.g., BCMOF 1997) describe some site management practices that can minimize decay incidence in forests though no one practice is specific to WRC. Below are some of the recommended practices:

- Harvest WRC trees sooner, i.e., before they reach the age of 'pathological rotation'.
- Do not practice partial cutting/use of residuals and larger retention trees after harvesting as both could be sources of inoculum of decay fungi. If residual trees are kept, avoid injuring them as wounds provide major courts for infection. Wounding can considerably accelerate the rate at which decay develops, even in young trees (Zeglen 1997).
- Plant seedlings and do not encourage vegetative regeneration as WRC trees regenerated by layering are considered to be more susceptible to decay (Symmetree et al. 2008).

Fortunately, research has been initiated to begin addressing the knowledge gaps around managing decay in WRC. We know that WRC durability is strongly, though not solely, linked to the **overall** presence of heartwood extractives, also referred to as secondary metabolites (Morris and Stirling 2012). We also know that variation in decay resistance among and within tree species is significant (Zabel and Morrell 1992, cited in Yu et al. 2003) and likely attributable to both environmental and genetic factors (Yu et al. 2003; Bush et al. 2011; Partanen et al. 2011). Thus, it makes sense to investigate how tree breeding (including genomic selection) along with silvicultural activities might be used alone or together to reduce decay and improve WRC durability through enhanced accumulation of secondary extractives (Russell and Yanchuk 2012).

Starting in the late 1990s, a WRC breeding and related research program was established in BC to support sustainable reforestation and harvest of the species. Initial efforts to improve the WRC population focused on tree growth and adaptability as well as heartwood durability (Russell and Yanchuk 2012). Investigation of extractives suggested that tropolones, while present in relatively

small concentrations in heartwood of living trees, were toxic to many decay fungi occurring there (Daniels and Russell 2007). Lignans, although not as fungitoxic as tropolones, occurred in higher concentrations in heartwood, an attribute especially critical to the durability of WRC heartwood products (Morris and Stirling 2012). Both groups of extractives



were determined to generally have moderate to high heritabilities in WRC (Daniels and Russell 2007; Russell and Daniels 2010); heritability is used for estimating the degree of genetic control of a specific trait in a population.

The WRC breeding program in BC subsequently evolved to incorporate screening results for WRC resistance to browsing by black-tailed deer (Odocoileus hemionus columbianus) and to cedar leaf blight caused by Didymascella thujina. These biotic agents have increasingly caused WRC plantation failures and reduced growth. Black-tailed deer were shown to avoid browsing trees that are high in volatile foliage monoterpenes (Vourch et al. 2002; Kimball et al. 2012). Similar to heartwood secondary extractives, foliage monoterpenes in WRC have moderate to high heritabilities. Also, there is significant genetic variation in resistance to CLB across moderately to heavily infected sites (Russell et al. 2007) and this variation is strongly correlated to population-origin climate with parents from wetter, milder sites having greater resistance. Importantly, there is little evidence of a trade-off between growth and secondary extractives in both WRC foliage and heartwood (Russell and Yanchuk 2012).

Today, the WRC breeding program is moving towards using genomic selection to incorporate multiple traits in one durable advanced generation breeding population that is resilient to multiple biotic and abiotic stressors (Russell and Yanchuk 2012). This approach, which is intended to reduce breeding cycle costs and times, will involve the use of genomics based techniques such as assembling reference transcriptomes, DNA and gene sequencing, genotype and phenotype characterization, gene expression studies, and development of predictive models for genomic selection (John Russell, BCMFLNRO, personal communication, March 9, 2016). Promising results to date include identification of genes in WRC foliar terpenoid defenses (Foster et al. 2013) and first time characterization of a gymnosperm cytochrome P450 gene involved in the biosynthesis of a foliar terpene-thujone in WRC (Gesell et al. 2015).

7. Decay Fungi on Western Redcedar Wood Products

Although the focus of this report is on decay fungi occurring on living WRC, we provide here an introduction to decay and the decay fungi affecting WRC 'wood in service'. Readers can find more in-depth information on decay of WRC wood products in several reports and journal publications (e.g., Scheffer 1957; Cabrera Orozco 2008, 2011; Chedgy et al. 2009; Morris and Stirling 2012; Morris et al. 2016). A tabular summary of the fungi causing decay of WRC wood products will be provided in a review of the subject expected to be published in 2017 (Rod Stirling, FPInnovations, Vancouver, BC, personal communication, October 11, 2016).

Western redcedar is one of more than two dozen tree species from around the world listed in the USDA Forest Products Lab Wood Handbook (Clausen 2010; see also Scheffer



and Morrell 1998) and similar directories in Europe and Australia (Rod Stirling, FPInnovations, Vancouver, BC, personal communication, October 23, 2016) as having heartwood classified as 'resistant to decay'. Global markets for such naturally durable wood generally continue to expand due in part to increasing restrictions on the use of wood preservatives such as chromated copper arsenate (Kirker et al. 2013). Western redcedar

wood is used for a wide range of products including shakes, shingles, and sawn siding as well as home decking, boat hull planking, log homes, doors and window frames, utility poles, fence panels and posts, crates, and caskets (Klinka and Brisco 2009).

Despite the presence of extractives that inhibit fungal colonization in WRC heartwood, decay fungi (predominantly brown rots) are still a major factor in product failure in wood in service (Lim et al. 2005a; Kirker et al. 2013). Research groups have identified these decay fungi mostly from WRC utility poles (Scheffer et al. 1984; Freitag and Morrell 2001), shakes and shingles (Smith and Swann 1976), and from fence material (Lim et al. 2005a). As is the case for identification of decay organisms associated with living WRC, the speed and accuracy of identifying decay organisms associated with WRC wood products has been greatly increased by combining molecular techniques with traditional morphological techniques (Lim et al. 2005a).

In addition to determining which fungi and other microbes are responsible for decay of WRC wood in service, forest products researchers are also interested in understanding which extractive(s) are most responsible for product durability, what their mode(s) of action are and what factors affect the durability they confer. Experts generally do this testing under a variety of laboratory and field settings using natural or treated stakes or blocks of WRC heartwood exposed to one or more in-situ or standard-test microbes (e.g., *Coniophora puteana* (Schumach.) P. Karst., brown cubical trunk rot and *Rhodonia placenta* (Fr.) Niemelä, K.H. Larss. & Schigel (formerly *Postia placenta*)).

For example, field tests on WRC shingles have shown that extractives are rapidly depleted after a few years and are largely absent after 25 years (Johnson and Cserjesi 1980; Stirling 2010). Depletion is a combination of leaching and biodegradation; leaching causes the depletion of major heartwood extractives, leaving the wood susceptible to fungal invasion (Southam and Ehrlich 1943). Chedgy et al. (2009) looked at the effect of extractive leaching on decay resistance in WRC products. They found that, in general, extractive leaching resulted in a greater incidence and severity of decay. Because of the high variability in fungal resistance to WRC extractives, even a small amount of leaching can result in significant decay and reduced product service life (Chedgy et al. 2009).

Earlier concern that the durability of products made from heartwood of second-growth WRC trees was less than that of old-growth heartwood has generally been allayed (Morris et al. 2016). While research by Nault (1988) had indicated that thujaplicin content and thus decay resistance was less in young (fast-growing) versus old-growth (slow-growing) trees, Scheffer (1957) and Freitag and Morrell (2001) found no correlation between decay resistance and several factors, including tree age. These authors concluded that the durability of second-growth wood in WRC wood in service is the same, on average, as that of old-growth wood.

The WRC wood industry would ideally like to standardize their products and prescribe recommendations on predicted service life and performance (Evans 2003) but this continues to be extremely challenging given the variability in extractive content both within and between trees (Scheffer and Cowling 1966). Methods to quickly assess WRC heartwood durability are also needed to identify breeding stock that will ultimately yield trees with durable wood when harvested (Stirling et al. 2015).

8. Future Research

Western redcedar is one of North America's most valuable commercial coniferous species despite the occurrence of an average 30% volume loss to decay in old-growth stems, and possibly lesser but significant volume losses in secondgrowth trees. Western redcedar trees are important to the ecology of coastal and interior forests, serving as long-lived agents critical to both carbon sequestration and carbon cycling. Western redcedar is also of tremendous cultural importance to First Nations. Imagine the gains for use of the species if the incidence and impact of decay in WRC could be reduced.

While this literature review provides a comprehensive synthesis of what we currently know about decay in living WRC there remain many information gaps. Table 2 lists several research questions that fall under the general themes of Survey & Biology, Genetics & Extractives, and Silviculture & Disease Management. Research efforts focussed on these questions will enable forest professionals and others to better understand decay dynamics in WRC and better inform their decision making around tree breeding and stand management activities to reduce the incidence and impact of decay on WRC. Table 2. Summary of research questions and approaches relevant to improving understanding of decay in living western redcedar

to answer questions
Field studies
 assess stands of different ages, regeneration history/origin, geographic location, etc. for decay presence and incidence; sample WRC trees and take detailed measurements of growth, defect, etc. collect performance data from WRCs in existing and newly established monitoring plots in 'new' coastal and interior WRC ranges; conduct requ-
lar surveys for forest health agents including fungi and insects.
Lab &/or greenhouse studies
 culture wood samples collected &/or use ge- nomics tools (e.g., DNA & gene sequencing) to identify decay-associated organisms.
 conduct inoculation trials with pertinent decay- associated organisms to simulate potential infection dynamics.
Lab &/or greenhouse studies
 conduct inoculation trials using pertinent decay-associated organisms and genetically diverse seedlings/families. conduct drought tolerance trials using geneti- cally diverse seedlings/families. use chemical tests (e.g., analyses of wood extractives; high performance liquid chroma- tography (HPLC)), genomics and related tools
to assess chemical, &/or molecular &/or genetic bases of decay resistance &/or tolerance.
Field studies
 collect decay incidence data from existing and newly established monitoring plots &/or remediation treatment plots; conduct detailed destructive sampling of decay in individual trees over a range of stands and regions over time. conduct financial/economic analyses

9. Literature Cited

Adair, S.; Kim, S.H.; Breuil, C. 2002. A molecular approach for early monitoring of decay basidiomycetes in wood chips. FEMS Microbiol. Lett. 211:117-122.

Aho, P.E. 1982. Indicators of cull in western Oregon conifers. Gen. Tech. Rep. PNW-GTR-144. United States Department of Agriculture (USDA), Forest Service, Pacific Northwest Forest and Range Experiment Station: Portland, OR. 17 p. <u>http://www.treesearch.fs.fed.us/pubs/7552</u>

Allen, C.D.; Breshears, D.D.; McDowell, N.G. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6(8):129. <u>http://dx.doi.org/10.1890/ES15-00203.1</u>

Allen, E.; Morrison, D.J.; Wallis, G. 1996. Common tree diseases of British Columbia. 3rd ed. Natural Resources Canada (NRCan), Canadian Forest Service (CFS), Pacific Forestry Centre, Victoria, BC. 178 p.

Aust, P.W. 1932. A study of two unclassified heart rots of western red cedar. MSc. Thesis. University of Idaho: Moscow, ID. 15 p.

Antos, J.A.; Filipescu, C.N.; Negrave, R.W. 2016. Ecology of western redcedar (*Thuja plicata*): implications for management of a high-value multiple-use resource. Forest Ecol. Manag. 375:211-222.

Ayres, M.P.; Lombardero, M.J., 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Sci. Total Environ. 262:263–286. doi:10.1016/S0048-9697(00)00528-3

Barrett, D.K.; Greig, B.J.W. 1984. Investigations into the infection biology of *Phaeolus schweinitzii*. Pages 95-103 *in* G.A. Kile, ed. Proceedings of the 6th International Conference on Root and Butt Rots of Forest Trees, International Union of Forest Research Organizations (IUFRO) Working Party S2-06-0I. Commonwealth Scientific and Industrial Research Organization (CSIRO): Melbourne, Australia.

Barton, G.M.; MacDonald, B.F. 1971. The chemistry and utilization of western redcedar. Review. Publ. 1023. CFS, Department of Fisheries and Forestry: Ottawa, ON.

Beese, W.J. 1987. Effects of prescribed burning on VAM and ectomycorrhiza inoculums potential. MacMillan Bloedel Ltd.: Nanaimo, BC. Unpublished report.

Bennett, R.N.; Wallsgrove, R.M. 1994. Secondary metabolites in plant defence mechanisms. New Phytol. 127:617–633. doi:10.1111/j.1469-8137.1994.tb02968.x

Berch, S.M.; Deom, E.; Willingdon, T. 1991. Western red cedar growth and vesicular-arbuscular mycorrhizal colonization in fumigated and nonfumigated nursery beds. Tree Planters' Notes 42:14-16.

Berg, E.C.; Gale, C.B.; Morgan, T.A.; Brackley, A.M.; Keegan, C.E.; Alexander, S.J.; Christensen, G.A.; McIver, C.P.; Scudder, M.G. 2014. Alaska's timber harvest and forest products industry, 2011. Gen. Tech. Rep. PNW-GTR-903. USDA, Forest Service, Pacific Northwest Research Station: Portland, OR: 39 p.

Bethge, K.; Mattheck, C.; Hunger, E. 1996. Equipment for detection and evaluation of incipient decay in trees. Arboric. J. 20(1):13–37. doi:10.1080/03071375.1996.9747095

Bhatti, J.S.; Lal, R.; Apps, M.J.; Price, M.A.; 2006. Climate and managed ecosystems. CRC Press: Boca Raton, FL. 445 p.

Boland, G.J.; Melzer, M.S.; Hopkin, A.; Higgins, V.; Nassuth, A. 2004. Climate change and plant diseases in Ontario. Can. J. Plant Pathol. 26(3):335–350.

Bouslimi, B.; Koubaa, A.; Bergerson, Y. 2013. Variation of brown rot decay in eastern white cedar (*Thuja occidentalis* L.). BioResources 8(3):4735-4755.

British Columbia (BC) Forest Service. 1957. Continuous forest inventory of British Columbia, 1957. Department of Lands and Forests: Victoria, BC.

(BCMOF) British Columbia Ministry of Forest. 1997. Forest Practices Code: Tree wounding and decay guidebook. <u>https://www.for.gov.bc.ca/tasb/legsregs/fpc/fpcguide/Decay/tw-toc.htm</u>

(BCMNRO) British Columbia Ministry of Natural Resource Operations and (BCMFML) British Columbia Ministry of Forests, Mines, and Lands (MFML). 2011. Summary of cedar management considerations for coastal British Columbia. Discussion Draft. 13 p.

(BCMFLNRO) British Columbia Ministry of Forests, Lands and Natural Resource Operations. 2015. Tree species compendium – western red cedar. http://www.for.gov.bc.ca/hfp/silviculture/compendium/WesternRedcedar.htm.

Buckland, D.C. 1946. Investigations of decay in western red cedar in British Columbia. Can. J. Res. 24(5):158–181.

Burleigh, J.; Ebata, T.; White, K.J.; Rusch, D.; Kope, H. eds. 2014. Field guide to forest damage in British Columbia (Joint publication, ISSN 0843-4719; no. 17). 355 p. ISBN 978-0-7726-6819-6.

Bush, D.; McCarthy, K.; Meder, R. 2011. Genetic variation of natural durability traits in *Eucalyptus cladocalyx* (sugar gum). Ann. For. Sci. 68:1057-1066.

Cabrera Orozco, Y. 2008. Improving the durability of second growth timbers of naturally durable species. MSc. Thesis. Department of Wood Science and Engineering, Oregon State University: Corvallis, OR. 89 p. <u>http://ir.library.oregonstate.edu/xmlui/handle/1957/8226</u>

Cabrera Orozco, Y. 2011. Effects of biocide treatment on durability and fungal colonization of teak, western redcedar, and redwood. PhD. Thesis. Department of Wood Science and Engineering, Oregon State University: Corvallis, OR. 162 p. <u>http://ir.library.oregonstate.edu/xmlui/handle/1957/18108</u>

Cartwright, K. St G. 1941. The variability in resistance to decay of the heartwood of home-grown western red cedar (*Thuja plicata* D. Don.) and its relation to position in the log. Forestry 15(1):65–75.

Chakraborty, S. 2013. Migrate or evolve: options for plant pathogens under climate change. Global Change Biol. 19:1985–2000. doi: 10.1111/gcb.12205

Chedgy, R.J.; Lim, Y.W.; Breuil, C. 2009. Effects of leaching on fungal growth and decay of western redcedar. Can. J. Microbiol. 55(5):578–586. doi:10.1139/w08-161

Clausen, C.A. 2010. Biodeterioration of wood. Gen. Tech. Rep. FPL-GTR-190. Pages 14.1-14.6 *in* Wood handbook: wood as an engineering material. Centennial ed. USDA, Forest Service, Forest Products Laboratory: Madison, WI.

Cleary, M. 2007. Host responses in Douglas-fir, western hemlock and western redcedar to infection by *Armillaria ostoyae* and *Armillaria sinapina* in the southern interior of British Columbia. PhD. Thesis. Faculty of Forestry, University of British Columbia: Vancouver, BC.

Cleary, M.R. 2010. Traumatic resin duct formation in the phloem of western redcedar and other resistance mechanisms effective against Armillaria root disease. Pages 53-56 *in* C. Harrington, ed. Proceedings of A tale of Two Cedars—International Symposium on Western Redcedar and Yellow-cedar. 2010 May 24-28. University of Victoria, Victoria, BC. Gen. Tech. Rep. PNW-GTR-828. USDA, Forest Service, Pacific Northwest Research Station: Portland, OR.

Cleary, M.R.; Holmes, T. 2011. Formation of traumatic resin ducts in the phloem of western redcedar (*Thuja plicata*) roots following abiotic injury and pathogenic invasion by *Armillaria ostoyae*. IAWA J. 32(3):351–359. doi:<u>10.1163/22941932-90000063</u>

Cleary, M.R.; van der Kamp, B.J.; Morrison, D.J. 2012a. Effects of wounding and fungal infection with *Armillaria ostoyae* in three confer species. I. Host response to abiotic wounding in non-infected roots. For. Pathol. 42:100-108. doi:<u>10.1111/j.1439-0329.2011.00726.x</u>

Cleary, M.R.; van der Kamp, B.J.; Morrison, D.J. 2012b. Effects of wounding and fungal infection with *Armillaria ostoyae* in three confer species. II. Host response to the pathogen. For. Pathol. 42:109-123. doi: <u>10.1111/j.1439-0329.2011.00727.x</u>

Cleary, M.R.; van der Kamp, B.J.; Morrison, D.J. 2012c. Pathogenicity and virulence of *Armillaria sinapina* and host response to infection in Douglas-fir, western hemlock and western redcedar in the southern interior of British Columbia. For. Pathol. 42:481-491. doi:10.1111/j.1439-0329.2012.00782.x

Coxson, D.S.; Goward, T.; Connell, D.J. 2012. Analysis of ancient western redcedar stands in the upper Fraser River watershed and scenarios for protection. JEM 13(3):1-20.

D'Amore, D.V.; Hennon, P.E.; Schaberg, P.G.; Hawley, G.J. 2009. Adaptation to exploit nitrate in surface soils predisposes yellowcedar to climate-induced decline while enhancing the survival of western redcedar: a new hypothesis. Forest Ecol. Manag. 258:2261-2268.

Daniels, C.R.; Russells, J.H. 2007. Analysis of western redcedar (*Thuja plicata* Donn) heartwood components by HPLC as a possible screening tool for trees with enhanced natural durability. J. Chromatogr. Sci. 45:281-285. doi:10.1093/chromsci/45.5.281

Daniels, L.D.; Maertens, T.B.; Stan, A.B.; McCloskey, S.P.J.; Cochrane, J.D.; Gray, R.W. 2011. Direct and indirect impacts of climate change on forests: three case studies from British Columbia. J. Plant Pathol. 33(2):108-116. doi:10.1080/07060661.2011.563906

DeBell, J.D.; Gartner, B.L. 1997. Stem characteristics on the lower log of 35-year-old western redcedar grown at several spacings. West J. Appl. For. 12(1):9-14.

DeBell, J.D.; Morrell, J.J.; Gartner, B.L. 1997. Tropolone content of increment cores as an indicator of decay resistance in western redcedar. Wood Fiber Sci. 29(4):364-369. <u>http://hdl.handle.net/1957/14025</u>

DeBell, J.D.; Morrell, J.J.; Gartner, B.L. 1999. Within-stem variation in tropolone content and decay resistance of second-growth western redcedar. For. Sci. 45(1):101-107.

DeLong, D.L. 1997. A retrospective investigation of advanced western redcedar regeneration in the ICHwk1, ICHmw2, and ICHmw1 of the Nelson Forest Region—Experimental Project 1174. Working Paper 25. BCMOF (Canada), Research Branch: Victoria, BC.

DeNitto, G. 2005. Management guide for red ring rot. Report 13.3. USDA, Forest Service, Forest Health Protection and State Forestry Organizations. <u>http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5187541.pdf</u>

DeNitto, G. 2006. Management guide for stem decays. Report 13.0. USDA, Forest Service, Forest Health Protection and State Forestry Organizations. <u>http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5188054.pdf</u>

Desprez-Loustau, M-L.; Marçais, B.; Nageleisen, L-M.; Ouiym, D.; Vannini, A. 2006. Interactive effects of drought and pathogens in forest trees. Ann. For. Sci. 63:597–612. doi: <u>org/10.1051/forest:2006040</u>

Desprez-Loustau, M-L.; Robin, C.; Reynaud, G.; Déqué, M.; Badeau, V.; Piou, D.; Husson, C.; Marçais, B. 2007. Simulating the effects of a climate-change scenario on the geographical range and activity of forest-pathogenic fungi. Can. J. Plant Pathol. 29:101-120.

Dobie, J.; Kasper, J.B. 1975. Log values for hemlock and cedar from Northwestern British Columbia. Information Report VP-X-144. Environment Canada.

Dukes, J.S.; Pontius, J.; Orwig, D.; Garnas, J.R.; Rodgers, V.L.; Brazee, N.; Cooke, B.; Theoharides, K.A.; Stange, E.E.; Harrington, R.; Ehrenfeld, J.; Gurevitch, J.; Lerdau, M.; Stinson, K.; Wick, R.; Ayres, M. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: what can we predict? Can. J. For. Res. 39(2):231–248. doi:10.1139/X08-171

Eades, H.W.; Alexander, J.B. 1934. Western red cedar: significance of its heartwood colourations. Circ. 41. Forest Products Labs Canada.

Eis, S. 1972. Root grafts and their silvicultural implications. Can. J. For. Res. 2:111-120. doi:10.1139/x72-022

Eis, S. 1974. Root system morphology of western hemlock, western red cedar, and Douglas-fir. Can. J. For. Res. 4:28-38. doi:<u>10.1139/x74-005</u>

Eriksson, K-E. L.; Blanchette, R.A; Ander, P. 1990. Microbial and enzymatic degradation of wood and wood components. Berlin, Heidelberg: Springer.

Eslyn, W.E. 1970. Utility pole decay. Part II: basidiomycetes associated with decay in poles. Wood Sci. Technol. 4:97-103. doi:10.1007/ BF00365296

Eslyn, W.E.; Highley, T.L. 1976. Decay resistance and susceptibility of sapwood of fifteen tree species. Phytopathology 66:1010-1017.

Etheridge, D.E. 1973. Wound parasites causing tree decay in British Columbia. Forest Pest Leaflet No. 62. CFS, Pacific Forest Research Centre: Victoria, BC. 16 p.

Evans, P. 2003. Emerging technologies in wood protection. For. Prod. J. 53(1):14-22.

Farr, W.A.; LaBau, V.J.; Laurent, T.H. 1976. Estimation of decay in old-growth western hemlock and sitka spruce in southeast Alaska. Res. Pap. PNW-204. USDA, Forest Service, Pacific Northwest Forest and Range Experiment Station: Portland, OR. <u>http://babel.ha-thitrust.org/cgi/pt?id=umn.31951d02995120v;view=1up;seq=1</u>

Farrar, J.L. 1995. Trees in Canada. Fitzhenry and Whiteside Ltd. and CFS in cooperation with Canada Communication Group—Publishing, Supply and Services Canada. 502 p.

Findlay, W.P.K.; Pettifor, C.B. 1941. Dark coloration in western red cedar in relation to certain mechanical properties. Empire For. J. 20(1):64-72.

Foster, A.J.; Hall, D.E.; Mortimer, L.; Abercromby, S.; Gries, R.; Gries, G.; Bohlmann, J.; Russell, J.; Mattsson, J. 2013. Identification of genes in *Thuja plicata* foliar terpenoid defenses. Plant Physiol. 161:1993-2004.

Freitag, C.M.; Morrell, J.J. 2001. Durability of a changing western redcedar resource. Wood Fiber Sci. 33(1):69-75. <u>http://hdl.handle.net/1957/13699</u>

Gardes, M.; Bruns, T.D. 1993. ITS primers with enhanced specificity for basidomycetes – application to the identification of mycorrhizae and rusts. Mol. Ecol. 2:113-118.

Gardner, J.A.F. 1963. The chemistry and utilization of western red cedar. Publ. 1023. Canadian Department of Forestry: Ottawa, ON. 26 p.

Gardner, J.A.F.; Barton, G.M. 1958a. Occurrence of β-dolabrin (4-isopropenyltropolone) in western red cedar (*Thuja plicata* Donn). Can. J. Chem. 36:1612-1615.

Gardner, J.A.F.; Barton, G.M. 1958b. The extraneous components of western red cedar. Forest Prod. J. 8:189-192.

Gardner, J.A.F.; Barton, G.M.; MacLean, H. 1959. The polyoxyphenols of western red cedar (*Thuja plicata* Donn) I. Isolation and preliminary characterization of plicatic acid. Can. J. Chem. 37:1703–1709. doi:10.1139/v59-246

Gardner, J.A.F.; MacDonald, B.F; MacLean, H. 1960. The polyoxyphenols of western red cedar (*Thuja plicata* Donn). II. Degradation studies on plicatic acid, a possible lignan acid. Can. J. Chem. 38:2387-2394. doi:10.1139/v60-324

Gardner, J.A.F.; Swan, E.P.; Sutherland, S.A.; MacLean, H. 1966. The polyoxyphenols of western red cedar (*Thuja plicata* Donn). III. Structure of plicatic acid. Can. J. Chem. 44:52-58. doi:10.1139/v66-009

Gedney, D.R.; Oswald, D.D. 1988. The western redcedar resource in the United States. Pages 4-7 *in* N.J. Smith, ed. Proceedings of Western Red Cedar—Does it have a Future? 1987 Jul 13-14. University of British Columbia, Faculty of Forestry: Vancouver, BC.

Gesell, A.; Blaukopf, M.; Madilao, L.; Yuen, M.M.S.; Withers, S.G.; Mattsson, J.; Russell, J.H.; Bohlmann, J. 2015. The gymnosperm cytochrome P450 CYP750B1 catalyzes stereospecific monoterpene hydroxylation of (+)-sabinene in thujone biosynthesis in western redcedar. Plant Physiol. 168:94-106.

Gilbertson, R.L.; Ryvarden, L. 1986. North American polypores. Vol. 1. Fungiflora. Lubrecht and Cramer: Oslo. 433 p.

Gonthier, P.; Guglielmo, F.; Sillo, F.; Giordano, L.; Garbelotto, M. 2015. A molecular diagnostic assay for the detection and identification of wood decay fungi of conifers. Forest Pathol. 45(2):89-101. doi:10.1111/efp.12132

Gonzalez, J.S. 2004. Growth, properties and uses of western red cedar. Publ. SP-37R. ISSN 0824-2119.

Gray, L.; Russell, J.H.; Yanchuk, A.D.; Hawkins, B.J. 2013. Predicting the risk of cedar leaf blight (*Didymascella thujina*) in British Columbia under uncertain future climate change. Agr. For. Meteorol. 180:152-163. doi:10.1016/j.agrformet.2013.04.023

Gregory, C.; McBeath, A.; Filipescu, C. 2017. An economic impact assessment of the western redcedar industry in British Columbia. Information Report FI-X-017, NRCan, CFS, Canadian Wood Fibre Centre, Pacific Forestry Centre: Victoria, BC.

Guglielmo, F.; Bergemann, S.E.; Gonthier, P.; Nicolotti, G.; Garbelotto, M. 2007. A mutiplex PCR-based method for the detection and early identification of wood rotting fungi in standing trees. J. Appl. Microbiol. 102:1490-1507. PMID:17953560

Guglielmo, F.; Gonthier, P.; Garbelotto, M.; Nicolotti, G. 2008. A PCR-based method for the identification of important wood rotting fungal taxa within *Ganoderma, Inonotus* s.l. and *Phellinus* s.l. FEMS Microbiol. Lett. 282:228-237. doi:<u>10.1111/j.1574-6968.2008.01132.x</u>

Guglielmo, F.; Gonthier, P.; Garbelotto, M.; Nicolotti, G. 2010. Optimization of sampling procedures for DNA-based diagnosis of wood decay fungi in standing trees. Lett. Appl. Microbiol. 51(1):90–97. doi:10.1111/j.1472-765X.2010.02860.x

Hadfield, J.S.; Goheen, D.J.; Filip, G.M.; Schmitt, C.L.; Harvey, R.D. 1986. Root diseases in Oregon and Washington conifers. R6-FPM-250-86. USDA, Forest Service. <u>http://www.fs.usda.gov/detail/r6/forest-grasslandhealth/insects-diseases/?cid=fsbdev2_027376</u>

Hagle, S. 2006a. Management guide for cedar brown pocket rot. Publ. 13.4. USDA, Forest Service, Forest Health Protection and State Forestry Organizations.

Hagle, S. 2006b. Management guide for cedar laminated root and butt rot. Publ. 13.5. USDA, Forest Service, Forest Health Protection and State Forestry Organizations.

Hansen, E.M.; Goheen, E.M. 2000. *Phellinus weirii* and other native root pathogens as determinants of forest structure and process in western North America. Annu. Rev. Phytopathol. 38:515–539. doi:10.1146/annurev.phyto.38.1.515

Hansen, E.M.; Lewis, K.J., Chastagner, G., eds. 2017. Compendium of conifer diseases in forests and Christmas Trees, 2nd Edition. APS Press: St Paul MN.

Hardison, J.R. 1976. Fire and flame for plant disease control. Ann. Rev. Phytopathol. 14:355–379. doi:10.1146/annurev. py.14.090176.002035

Harvey, R.D.; Hessburg, P.F. 1992. Long range planning for developed sites: the context of hazard tree management. FPM-TP039-92. US Government Printing Office, Pacific Northwest Region.

Hennon, P.E. 1995. Are heart rot fungi major factors of disturbance in gap-dynamic forests? Northwest Sci. 69(4):284-293.

Hennon, P.E.; McKenzie, C.M.; D'Amore, D.V.; Wittwer, D.T.; Mulvey, R.L.; Lamb, M.S.; Biles, F.E.; Cronn, R.C. 2016. A climate adaptation strategy for conservation and management of yellow-cedar in Alaska. Gen. Tech. Rep. PNW-GTR-917. USDA, Forest Service, Pacific Northwest Research Station. 382 p. http://www.fs.fed.us/pnw/pubs/pnw_gtr917.pdf

Hennon, P.E.; Mulvey, R.L. 2014. Managing heart rot in live trees for wildlife habitat in young-growth forests of coastal Alaska. Gen. Tech. Rep. PNW-GTR-890. USDA, Forest Service, Pacific Northwest Research Station. 23 p. <u>http://www.fs.fed.us/pnw/pubs/pnw_gtr890.</u> pdf

Hepting, G.H. 1963. Climate and forest diseases. Annu. Rev. Phytopathol. 1:31-50. doi:10.1146/annurev.py.01.090163.000335

Hepting, G.H. 1971. Diseases of forest and shade trees of the United States. Agriculture Handbook No. 386. USDA, Forest Service. 658 p.

Hobbs, S.D.; Partridge, A.D. 1979. Wood decays, root rots, and stand composition along an elevation gradient. For. Sci. 25:31-42.

Hofmeyer, P.V.; Seymour, R.S.; Kenefic, L.S. 2009. Influence of soil site class on growth and decay of northern white-cedar and two associates in Maine. North. J. Appl. For. 26(2):68–75.

Howard, J.O. 1988. Energy values for whole trees and crowns of selected species. Res. Note PNW-RN-480. USDA, Forest Service, Pacific Northwest Research Station: Portland, OR. 8 p.

Hunt, R.S.; Etheridge, D.E. 1995. True heart-rots of the Pacific region. Forest Pest Leaflet No. 55. NRCan, CFS, Pacific Forestry Centre: Victoria, BC. 8 p. ISBN 0-662-23897-4 http://cfs.nrcan.gc.ca/publications?id=4202.pdf

Isenberg, I.H.; Harder, M.L.; Louden, L. 1980. Pulpwoods of the United States and Canada. 3rd ed. Georgia Institute of Technology. Institute of Paper Chemistry: Appleton, WI.

IPCC (Intergovernmental Panel on Climate Change). 2007. Pachauri, R.K., Reisinger, A., eds. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change: Geneva, Switzerland. IPCC. 104 p.

Jackson, A.G.; Knapp, J.B. 1914. Forest characteristics of western red cedar. West Coast Lumberman. 25:34-40.

Jin, L.; van der Kamp, B.; Wilson, J.W.; Swan, E.P. 1988a. Biodegradation of thujaplicins in living western red cedar. Can. J. Forest Res. 18:782-786. doi:10.1139/x88-119.

Jin, L.; Wilson, J.W.; Swan, E.P. 1988b. Thujin, a novel lactone isolated from the discolored heartwood of *Thuja plicata* Donn. Can. J. Chem. 66:51-53. doi:10.1139/v88-007.

Johnson, E.L.; Cserjesi, A.J. 1980. Weathering effect of Thujaplicin concentration in western redcedar shakes. Forest. Prod. J. 60(4):353-356.

Julin, K.R. 1988. The fluted western hemlock of southeastern Alaska. PhD. Dissertation. University of Washington: Seattle. 137 p.

Kimball, B.A.; Russell, J.H.; Ott, P. 2012. Phytochemical variation within a single plant species influences foraging behavior of deer. Oikos 121: 743–751.

Kimmey, J.W. 1956. Cull factors for sitka spruce, western hemlock, and western redcedar in southeast Alaska. Station Pap. No. 6. USDA, Forest Service, Alaska Forest Research Center. 31 p.

Kirker, G.T.; Blodgett, A.B.; Aragno, R.A.; Lebow, P.K.; Clausen, CA. 2013. The role of extractives in naturally durable wood species. Int. Biodeter. Biodegr. 82:53-58. doi:10.1016/j.ibiod.2013.03.007

Kliejunas, J.T.; Geils, B.W.; Glaeser, J.M.; Goheen, E.M.; Hennon, P.; Kim, M-S.; Kope, H.; Stone, J.; Sturrock, R.; Frankel, S.J. 2009. Review of literature on climate change and forest diseases of western North America. Gen. Tech. Rep. PSW-GTR-225. USDA, Forest Service, Pacific Southwest Research Station: Albany, CA. 54 p. Klinka, K.; Brisco, D. 2009. Silvics and silviculture of coastal western redcedar: a literature review. Special Report Series 11. BC Ministry of Forests and Range (BCMOFR), Forest Science Program: Victoria, BC. ISBN 978-0-7726-6110-4 <u>https://www.for.gov.bc.ca/hfd/pubs/</u> Docs/Srs/Srs11.htm

Klinka, K.; Chourmouzis, C. 2005. Ecological and silvical characteristics of major tree species in British Columbia. Pages 326-347 *in* Watts, S.B.; Tolland, L., eds. Forestry handbook for British Columbia. Faculty of Forestry, University of British Columbia: Vancouver, BC.

Klinka, K.; Worrall, J.; Skoda, L.; Varga, P.; Chourmouzis, C. 1999. The distribution and synopsis of ecological and silvical characteristics of tree species of British Columbia's forests. Scientia Silvica Publ. ISSN 1209-952X, no. 10. <u>https://circle.ubc.ca/handle/2429/714</u>.

Koenigs, J.W. 1969. Root rot and chlorosis of released and thinned western redcedar. J. For. 67(5):312–315.

Konchalski, C. 2015. Sensitivity of western redcedar to climate and western hemlock looper in British Columbia's inland temperate rainforest. MSc. Thesis. Natural Resources and Environmental Studies, University of Northern British Columbia: Prince George, BC. 89 p.

Kough, J.L.; Molina, R.; Lindermann, R.G. 1985. Mycorrhizal responsiveness of *Thuja, Calocedrus, Sequoia,* and *Sequoiadendron* species of western North America. Can. J. Forest Res. 15:1049-1054.

Krajina, V.1969. Ecology of forest trees in British Columbia. Ecol. West. N. Amer. 2:1-146.

Kurz, W.A.; Dymond, C.C.; Stinson, G.; Rampley, G.J.; Neilson, E.T.; Carroll, A.L.; Ebata, T.; Safranyik, L. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature. 452:987–990.

Laks, P.E.; Morris, P.I.; Larkin, G.M.; Ingram, J.K. 2008. Field tests of naturally durable North American wood species. International Research Group on Wood Protection. Document No. IRG/WP/08-10675. 11 p.

Larsen, M.J.; Lombard, F.; Clarke, J.W. 1994. Phellinus sulphurascens and the closely related P. weirii in North America. Mycologia 86(1):121–130. doi:10.2307/3760727

LeMay, V.M. 1993. Percent decay estimation using decayed wood area at breast or stump height. Can. J. Forest Res. 23(2):307–312. doi:10.1139/x93-041

Lewis, K. 1992. Decay in advanced regeneration in the Northern Interior Cedar-Hemlock Biogeoclimatic Zone. Final Report. Industrial Forestry Service Ltd. 28 p.

Leong, E.; Burcham, D.C.; Fong, Y. 2012. A purposeful classification of tree decay detection tools. Arboric. J. 34(2):91–115. doi:10.108 0/03071375.2012.701430

Lim, Y.W.; Kim, J.; Chedgy, R.; Morris, P.I.; Breuil, C. 2005a. Fungal diversity from western redcedar fences and their resistance to β-thujaplicin. A. Van. Leeuw. J. Microb. 87:109–117. doi:<u>10.1007/s10482-004-1729-x</u>

Lim, Y.W.; Yeung, Y.C.A.; Sturrock, R.N.; Leal, I.; Breuil, C. 2005b. Differentiating the two closely related species, *Phellinus weirii* and *P. sulphurascens*. Forest Pathol. 35:305-314. doi:10.1111/j.1439-0329.2005.00410.x

Lowther, L. 2010. Assessment of climate change and impacts of *Armillaria* root disease in Alberta's boreal forest. MSc. Environment and Management Thesis. Royal Roads University: Victoria, BC. <u>http://hdl.handle.net/10170/435</u>

McBride, C. F.1959. Utilizing residues from western red cedar mills. For. Prod. J. 9(9):313-316.

MacDonald, B.F.; Barton, G.M. 1970. Lignans of western red cedar (*Thuja plicata* Donn). X. Gamma-Thujaplicatene. Can. J. Chem. 48(20):3144–3146. doi:<u>10.1139/v70-531</u>

MacDonald, B.F.; Barton, G.M. 1973. Lignans of western red cedar (*Thuja plicata* Donn). XI. Beta-Apoplicatitoxin. Can. J. Chem. 51(4):482–485. doi:10.1139/v73-074

MacLean, H.; Gardner, J.A.F. 1953. Some chemical and plastic properties of western red cedar butt rot. J. For. Prod. Res. Soc. 3(4):35-37, 72.

MacLean, H.; Gardner, J.A.F. 1956. Distribution of fungicidal extractives (thujaplicin and water-soluble phenols) in western red cedar heartwood. For. Prod. J. 6(12): 510-516.

MacLean, H.; Murakami, K. 1966. Lignans of western red cedar (*Thuja plicata* Donn). IV. Thujaplicatin and thujaplicatin methyl ether. Can. J. Chem. 44:1541-1545. doi:10.1139/v66-229

Manning, T. 2001. Dangerous tree report: British Columbia's dangerous tree assessment process: implications for worker safety. Destructive Sampling Field Project, Final Report. Prepared for IWA Canada-Forest Industry SAFER Council Weyerhaeuser-BC Coastal Group, BCMOF, Forest Practices Branch. 8 p.

Manning, T. 2007. Evaluation of the effects of heart rot fungi on live tree structural stability. Project No. 500755TVT040. Report submitted to BC Ministry of Forests and Range, Forest Practices Branch. 20 p.

Marshall, D.D.; DeBell, D.S. 2002. Stem characteristics and wood properties: essential considerations in sustainable multipurpose forestry regimes. Pages 145 -149 *in* Proceedings of the Wood Compatibility Initiative Workshop. 2001 Dec 4-7. Washington, USA. Gen. Tech. Rep. PNW-GTR-563. USDA, Forest Service, Pacific Northwest Research Station: Portland, OR.

Maser, C.; Trappe, J.M., tech. eds. 1984. The seen and unseen world of the fallen tree. Gen. Tech. Rep. PNW-164. USDA, Forest Service, Pacific Northwest Research Station: Portland, OR. 56 p.

Matsuzaki, E.; Sanborn, P.; Fredeen, A.L.; Shaw, C.H.; Hawkins, C. 2012. Carbon stocks in managed and unmanaged old-growth western redcedar and western hemlock stands of Canada's inland temperate rainforests. Forest Ecol. Manag. 297:108-119.

Minore D. 1979. Comparative autecological attributes of northwestern tree species—a literature review. Gen. Tech. Rep. PNW-87. USDA, Forest Service, Pacific Northwest Research Station: Portland, OR. 72 p.

Minore, D. 1983. Western redcedar: a literature review. Gen. Tech. Rep. GTR-PNW-150, USDA, Forest Service, Pacific Northwest Research Station: Portland, OR. 70 p.

Morris, P.I.; Laks, P.; Larkin, G.; Ingram, J.K.; Stirling, R. 2016. Above-ground decay resistance of selected Canadian softwoods at four test sites after ten years of exposure. For. Prod. J. 66(5-6):268-273.

Morris, P.I.; Stirling, R. 2012. Western red cedar extractives associated with durability in ground contact. Wood Sci. Technol. 46(5):991–1002. doi:10.1007/s00226-011-0459-2

Morrison, D.J.; Wallis, G.W.; Weir, L.C. 1988. Control of *Armillaria* and *Phellinus* root diseases: 20 year results from the Skimikin stump removal experiment. Information Report BC-X-302, CFS, Pacific Forest Research Centre: Victoria, BC. 16 p.

Morrison, D.J.; Cruickshank, M.G.; Lalumière, A. 2014. Control of laminated and Armillaria root diseases by stump removal and tree species mixtures: amount and cause of mortality and impact on yield after 40 years. Forest Ecol. Manag. 319:75-98.

Morrison, D.J.; Pellow, K.W.; Norris, D.J.; Nemec, A.F.L. 2000. Visible versus actual incidence of Armillaria root disease in juvenile coniferous stands in the southern interior of British Columbia. Can. J. Forest Res. 30:405-414. doi:10.1139/x99-222

Nault, J. 1988. Radial distribution of thujaplicins in old growth and second growth western red cedar (*Thuja plicata* Donn). Wood Sci. Technol. 22:73-80. doi:10.1007/BF00353230

Nicolotti, G.; Gonthier, P.; Guglielmo, F.; Garbelotto, M.M. 2009. A biomolecular method for the detection of wood decay fungi: a focus on tree stability assessment. Arboricul. Urban For. 35(1):14–19.

Nystrom, M.N. 1980. Reconstruction of pure, second-growth stands of western redcedar (*Thuja plicata* Donn.) in western Washington: the development and silvicultural implications. MSc. Thesis. University of Washington: Seattle, WA. 97 p.

O'Connell, L.M.; Ritland, K.; Thompson, S.L. 2008. Patterns of post-glacial colonization by western red cedar (*Thuja Plicata*, Cupressaceae) as revealed by microsatellite markers. Botany 86(2):194–203. doi:10.1139/B07-124

Oliver, C.D.; Nystrom, M.N.; DeBell, D.S. 1988. Coastal stand silvicultural potential for western redcedar. Pages 39-45 *in* N.J. Smith, ed. Proceedings of Western Red Cedar—Does it have a Future? 1987 Jul 13-14. University of British Columbia, Faculty of Forestry: Vancouver, BC.

Ouis, D. 2003. Non destructive techniques for detecting decay in standing trees. Arboricul. J. 27 (2):159–177. doi:10.1080/03071375.2 003.9747371

Ovaskainen, O.; Nokso-Koivisto, J.; Hottola, J.; Rajala, T.; Pennanen, T.; Ali-Kovero, H.; Miettinen, O.; Oinonen, P.; Auvinen, P.; Paulin, L.; Larsson, K-H.; Mäkipää, R. 2010. Identifying wood-inhabiting fungi with 454 sequencing—what is the probability that BLAST gives the correct species? Fungal Ecol. 3:274-283. doi:10.1016/j.funeco.2010.01.001

Parks, C.G.; Raley, C.M.; Aubry, K.B.; Gilbertson, R.L. 1997. Wood decay associated with pileated woodpecker roosts in western redcedar. Disease Notes 81(5):551. <u>http://dx.doi.org/10.1094/PDIS.1997.81.5.551C</u>

Partanen, J.; Harju, A.M.; Venäläinen, M.; Kärkkäinen, K. 2011. Highly heritable heartwood properties of Scots pine: possibilities for selective seed harvest in seed orchards. Can. J. Forest Res. 41:1993–2000. doi:<u>10.1139/x11-116</u>

Partridge, A.D.; Miller, D.L. 1974. Major wood decays in the inland Northwest. Idaho Research Foundation. Natural Resource Series No. 3. 125 p.

Patton, R.F. 1942. Isolation of fungi from brown cubical heart rots of western redcedar. Including preliminary tests of their saprogenicity and tolerance for heartwood extracts. MSc. Thesis. University of Idaho: Moscow, ID. 150 p.

Poon, J., 2011. Global wood product trade flows: 2011 Edition. FPInnovations report.

Quenet, R.V.; Magdanz, H.A. 1988. Western redcedar inventory of British Columbia. Pages 1-3 *in* N.J. Smith, ed. Proceedings of Western red cedar--does it have a future? Conference, 1987 Jul 13-14. University of British Columbia, Faculty of Forestry: Vancouver, BC.

Rennerfelt, E. 1948. Investigations of thujaplicin, a fungicidal substance in the heartwood of *Thuja plicata* D. Don. Physiol. Plant. 1(3):245-254. doi:10.1111/j.1399-3054.1948.tb07128.x

Renzie, C.D.; Han, H.-S. 2001. An operational comparison of partial cut and clearcut harvesting methods in old cedar-hemlock forests in central British Columbia, Robson Valley. Proceedings of Enhanced Forest Management Pilot Project (EFMPP) Information Session. 2001 Mar 15-16.

Robison, Z. 2000. The incidence of decay in western redcedar between two biogeoclimatic regions. BSc. Thesis. Natural Resources Management, College of Science and Management, University of Northern British Columbia: Prince George, BC. 25 p.

Roff, J.W.; Atkinson, J.M. 1954. Toxicity tests of a water-soluble phenolic fraction (thujaplicin-free) of western red cedar. Can. J. Bot. 32(1):308-309. doi:10.1139/b54-025

Roff, J.W.; Whittaker, E.I. 1959. Toxicity tests of a new tropolone, β -thujaplicinol (7-hydroxy-4-isopropyl tropolone) occurring in western red cedar. Can. J. Bot. 37(5):1132-1134. doi:10.1139/b59-089

Russell, J.H.; Daniels, B. 2010. Variation in western redcedar heartwood extractives. Pages 83-85 *in* C. Harrington, ed. Proceedings of A tale of two cedars—international symposium on western redcedar and yellow-cedar. 2010 May 24-28, University of Victoria, Victoria, BC, Canada. Gen. Tech. Rep. PNW-GTR-828. Forest Service, Pacific Northwest Research Station: Portland, OR.

Russell, J.H.; Yanchuk, A.D. 2012. Breeding for growth improvement and resistance to multiple pests in *Thuja plicata* under a changing climate. Pages 40-44 *in* R.A. Sniezko; A.D. Yanchuk; J.T. Kliejunas; K.M. Palmieri; J.M. Alexander; S.J. Frankel, tech. coords. Proceedings of the Fourth International Workshop on the Genetics of Host-Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees. 2011 July 31–August 5, Eugene, OR, USA. Gen. Tech. Rep. GTR-PSW-240. Pacific Southwest Research Station: Albany, CA.

Ryvarden, L.; Gilbertson, R.L. 1993-1994. European polypores 1-2. Fungiflora: Oslo. 743 p.

Ryvarden, L. 2001. An introduction to wood-rotting fungi: ecology, succession and biodiversity. Biological Institute, University of Oslo: Oslo, Norway. 27 p.

Scheffer, T.C., 1957. Decay resistance of western redcedar. J. Forest. 55(6):434-442.

Scheffer, T.C.; Cowling, E.B. 1966. Natural resistance of wood to microbial deterioration. Annu. Rev. Phytopathol. 4:147–170. doi:10.1146/annurev.py.04.090166.001051

Scheffer, T.; Goodell, B.; Lombard, F. 1984. Fungi and decay in western redcedar utility poles. Wood Fiber Sci. 16(4):543–548.

Scheffer, T.C.; Morrell, J.J. 1998. Natural durability of wood: a worldwide checklist of species. Research Contribution 22. Forest Research Laboratory, Oregon State University: Corvallis, Oregon. 58 p.

Schneider, R.; Riopel, M.; Pothier, D.; Côté, L. 2008. Predicting decay and round-wood end use volume in trembling aspen (*Populus tremuloides* Michx.). Ann. For. Sci. 65(6):608. doi:10.1051/forest:2008042

Schultz, T.P.; Nicholas, D.D. 2000. Naturally durable heartwood: evidence for the proposed dual defensive function of the extractives. Phytochemistry 54:47–52. PMID: 10846746

Schultz T.P.; Nicholas, D.D. 2002. Development of environmentally-benign wood preservatives based on the combination of organic biocides with antioxidants and metal chelators. Phytochemistry 61:555–560. PMID:12409022

Sellers, V.O. 1940. A cultural study of the heart rots of western redcedar in northern Idaho. MSc. Thesis. University of Idaho: Moscow, ID. 55 p.

Shigo, A.L. 1967. Successions of organisms in discoloration and decay of wood. Int. Rev. For. Res. 2:237-299.

Shigo, A.L.; Hillis, W.E. 1973. Heartwood, discolored wood, and microorganisms in living trees. Annu. Rev. Phytopathol. 11:197-222. doi:10.1146/annurev.py.11.090173.001213

Singh, T.; Singh, A.P. 2012. A review of natural products as wood protectant. Wood Sci. Technol. 46:851-870.

Singleton, R.; Deell, D.S.; Marshall, D.D.; Gartner, B. 2003. Eccentricity and fluting in young-growth western hemlock in Oregon. West. J. Appl. For. 18(4):221–228.

Smith, H.G. 1964. Root spread can be estimated from crown width of Douglas fir, lodgepole pine, and other British Columbia tree species. For. Chron. 40(4):456-473. doi:10.5558/tfc40456-4

Smith, R.S.; G.W. Swann. 1976. Colonisation of western red cedar shingles and shakes by fungi. Pages 253-262 *in* G. Becker, W. Liese, eds. Organismen und Holz, Internationales Symposium Berlin-Dahlem, Heft 3, Duncker and Humblot: Berlin.

Southam, C.M.; Ehrlich, J. 1943. Decay resistance and physical characteristics of wood. J. For. 41:666-673.

Southam, C.M.; Ehrlich, J. 1950. Etiology of some sap rots of western red cedar poles. Phytopathol. 40(5):439-444.

Sowder, A.M. 1929. Toxicity of water-soluble extractives and relative durability of water-treated wood flour of western red cedar. Ind. Eng. Chem. 21(10):981–984. doi:10.1021/ie50238a022

Stirling, R. 2010. Residual extractives in western red cedar shakes and shingles after long-term field testing. Forest Prod. J. 60(4):353-356.

Stirling, R.; Clark, J.E.; Daniels, C.R.; Morris, P.I. 2007. Methods for determining the role of extractives in the natural durability of western red cedar heartwood. Doc. No. IRG/WP/07-20356. International Research Group on Wood Protection. 12 p.

Stirling, R.; Morris, P.I. 2011. New perspectives on the role of extractives in the durability of western redcedar. Proceedings of Canadian Wood Preservation Association. 32:12 p.

Stirling, R.; Morris, P.I. 2015. Potential contributions of lignans to decay resistance in western red cedar. Wood Sci. Technol. doi 10.1007/s00226-015-0784-y.

Stirling, R.; Morris, P.I.; Grace, J.K. 2015. Prediction of the decay and termite resistance of western red cedar heartwood. Forest Prod. J. 65(3/4):84-92. <u>http://dx.doi.org/10.13073/FPJ-D-14-00056</u>

Sturrock, R.N.; Frankel, S.J.; Brown, A.V.; Hennon, P.E.; Kliejunas, J.T.; Lewis, K.J.; Worrall, J.J.; Woods, A.J. 2011. Climate change and forest diseases. Plant Pathol. 60:133-149. doi:10.1111/j.1365-3059.2010.02406.x

Sturrock, R.N.; Pellow, K.W. 2013. Infection of western redcedar roots by the fungal pathogen *Phellinus weirii* – preliminary results. Can. J. Plant Pathol. 35(1):95.

Sturrock, R.N.; Pellow, K.W.; Hennon, P.E. 2010. *Phellinus weirii* and other fungi causing decay in western redcedar and yellow-cedar. Gen. Tech. Rep. PNW-GTR-828. Pages 47-52 in Harrington, C., ed. Proceedings of A tale of Two Cedars—International Symposium on Western Redcedar and Yellow-cedar. 2010 May 24-28. University of Victoria, Victoria, BC. Gen. Tech. Rep. PNW-GTR-828. USDA, Forest Service, Pacific Northwest Research Station: Portland, OR.

Sudworth, G.B. 1908. Forest trees of the Pacific slope. USDA Forest Service, Gov. Print. Off., Washington, D.C. 441 p.

Swan, E.P.; Jiang, K.C.; Gardner, J.A.F. 1969. The lignans of *Thuja plicata* and the sapwood-heartwood transformation. Phytochemistry 8(2):354-351.

Symmetree Consulting Group. 2008. Western redcedar - issues for managing for desirable characteristics under retention of varying levels. Management to promote desired characteristics. Draft: Version 1.1. Report for the Forest Practices Board.

Tabata, M.; Suyama, Y.; Abe, Y. 2009. Distribution of genets of *Perenniporia subacida* in stands of *Chamaecyparis obtusa* (Japanese cypress) determined by AFLP fingerprints and somatic incompatibility. Plant Dis. 93(8):826–831. <u>http://dx.doi.org/10.1094/PDIS-93-8-0826</u>

Tattar, T.A.; Shortle, W.C.; Rich, A.E. 1971. Sequence of microorganisms and changes in constituents associated with discoloration and decay of sugar maples infected with *Fomes conatus*. Phytopathology 61:556-558. doi:10.1094/Phyto-61-556

Taylor, A.M.; Gartner, B.L.; Morrell, J.J. 2002. Heartwood formation and natural durability—a review. Wood Fiber Sci. 34(4):587-611.

Taylor, A.M.; Gartner, B.L.; Morrell, J.J.; Tsunoda, K. 2006. Effects of heartwood extractive fractions of *Thuja plicata* and *Chamaecy-paris nootkatensis* on wood degradation by termites or fungi. J. Wood Sci. 52:147–153. doi:10.1007/s10086-005-0743

Thies, W.J.; Sturrock, R.S. 1995. Laminated root rot in western North America. Gen. Tech. Rep. PNW-GTR-349. USDA, Forest Service: Portland, OR. 32 p.

Thor, M.; Ståhl, G.; Stenlid, J. 2005. Modelling root rot incidence in Sweden using tree, site and stand variables. Scan. J. For. Res. 20:165–176. doi:10.1080/02827580510008347

(USDA) United States Department of Agriculture. 1990. Western redcedar (*Thuja plicata* Donn ex D. Don). Pages 590-600 *in* R.M Burns and B.H. Honkala, tech. coordinators. Silvics of North America. Volume 1, Conifers. Agriculture Handbook No. 654. USDA, Forest Service: Washington, DC. 675 p.

(USDA) United States Department of Agriculture. 2007. Forest health conditions in Alaska - 2006. R10-PR-11. A forest health protection report. USDA, Forest Service, Alaska Region.

(USDA) United States Department of Agriculture. 2010. Proceedings of A Tale of Two Cedars: International Symposium on Western Redcedar and Yellow-Cedar. 2010 May 24-28. Gen. Tech. Rep. PNW-GTR-828. USDA, Forest Service, Pacific Northwest Research Station: Portland, OR. 177 p.

(USDA) United States Department of Agriculture. 2011. Western redcedar. Forest Service. <u>http://www.na.fs.fed.us/pubs/silv-ics_manual/Volume_1/thuja/plicata.htm</u>.

(USDA) United States Department of Agriculture. 2012. Forest health conditions in Alaska— 2011. A forest health protection report. R10-PR-25. Forest Service, Alaska Region. 80 p.

(USDA) United States Department of Agriculture. 2015. Forest health conditions in Alaska— 2014. A forest health protection report. R10-PR-32. Forest Service, Alaska Region. 89 p.

van der Kamp, B.J. 1975. The distribution of microorganisms associated with decay of western red cedar. Can. J. Forest Res. 5:61-67. doi:10.1139/x75-008

van der Kamp, B.J. 1986. Effects of heartwood inhabiting fungi on thujaplicin content and decay resistance of western redcedar (*Thuja plicata* Donn). Wood Fiber Sci. 18(3):421–427.

van der Kamp, B.J. 1988. Pests of western redcedar. Pages 145-146 in N.J. Smith, ed. Proceedings of Western Red Cedar—Does it have a Future? 1987 Jul 13-14. University of British Columbia, Faculty of Forestry: Vancouver, BC.

van Mantgem, P.J.; Stephenson, N.L.; Byrne, J.C.; Daniels, L.D.; Franklin, J.F.; Fulé, P.Z.; Harmon, M.E.; Larson, A.J.; Smith, J.M.; Taylor, A.H.; Veblen, T.T. 2009. Widespread increase of tree mortality rates in the western United States. Science 323(5913):521-524. doi:10.1126/science.1165000

Vourch, G.; Russell, J.; Martin, J.-L. 2002. Linking deer browsing and terpene production among genetic identities in *Chamaecyparis nootkatensis* and *Thuja plicata* (Cupressaceae). J. Hered. 93(5):370-376. PMID:12547927

Wagener, W.W.; Davidson, R.W. 1954. Heart rots in living trees. Bot. Rev. 20(2):61-134.

Wallis, G.; Reynolds, G. 1965. The initiation and spread of Poria weirii root rot of Douglas fir. Can. J. Bot. 43:1–9.

Weir, J.R. 1921. Polyporus schweinitzii Fr. on Thuja plicata. Phytopathology 11:176.

White, T.J.; Bruns, T.D.; Lee, S.; Taylor, J.W. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pages 315-322 *in* M.A. Innis, D.H. Gelfand, J.J. Sninsky, and T.J. White, eds. PCR protocols: a guide to methods and applications. Academic Press: San Diego, CA.

Worrall, J.J.; Lee, T.D.; Harrington, T.C. 2005. Forest dynamics and agents that initiate and expand canopy gaps in *Picea-Abies* forests of Crawford Notch, New Hampshire, USA. J. Ecol. 93(1):178–190. doi:10.1111/j.1365-2745.2004.00937.x

Yu, Q.; Yang, D-Q.; Zhang, S.Y.; Beaulieu, J.; Duchesne, I. 2003. Genetic variation in decay resistance and its correlation to wood density and growth in white spruce. Can. J. Forest Res. 33:2177-2183.

Zeglen, S. 1997. Tree wounding and partial-cut harvesting: a literature review for British Columbia. Pest Management Report No. 14. BCMOF, Forest Health, Vancouver Forest Region: Vancouver, BC.

Decay Type	Current Name & Pathogen & Disease Common Name(s) (where applicable) ¹	Common Synonyms ¹	Main Sources of Information ²	Notes (& Sources)
Stem	Amylostereum chailletii (Pers.) Boidin	Stereum chailletii	13	Primary invader; causes heart and sap rot in living trees
Root &/ or Butt	Armillaria ostoyae , (Romagn.) Herink, Armillaria root rot	A. mellea s.l., A. solidipes	1, 2, 7, 10, 11	Can attack living trees, although WRC demonstrated to have high frequency of effective resistance mechanism to infection by <i>A. ostoyae</i> (5); capable of causing extensive but limited damage in some areas (2)
Stem	Ganoderma applanatum (Pers.) Pat., white mottled rot	Fomes applanatus, Polyporus ap- planatus	1, 3, 14	Important and significant in localized areas; majority of infections through basal wounds or injured roots (2); secondary invader, causes heart and sap rot in living trees; continues to develop on dead material and can cause damage to wood in service (14)
Root &/ or Butt	Heterobasidion annosum (Fr.) Bref. sensu lato ; annosus root rot, white spongy rot	Fomes annosus, Polyporus annosus	1, 2, 7, 9, 10, 14	Primary invader, causes heart and sap rot in living trees, enters through trunk wounds (14); important in young trees (35-50 yrs) (2); also on wood in service (4)
Unknown	Hymenochaete tenuis (Peck)	Hymenochaete multisetae	8	Secondary importance; typically found in dead/decay- ing WRC material and in association with other white and brown rot fungi (2); often associated with scars or frost cracks (7)
Root &/ or Butt	Obba rivulosa, (Berk. & M.A. Curtis) Miett. & Rajchenb., white butt rot; white laminated rot	Ceriporiopsis rivulosa, Physisporinus rivulosus, Polyporus rivulosus, Poria albipellucida, Poria rivulosa	1, 2, 6, 8, 10, 11, 12, 14	Most Important butt rot of mature WRC in coastal BC (1, 13); important and significant in localized areas; some impor- tance in all WRC stands (2); also on wood in service (2)
Root &/ or Butt	Onnia tomentosa (Fr.) P. Karst., tomentosus root rot	Inonotus tomentosus, Polyporus tomentosus	1, 9, 10	
Root &/ or Butt	Perenniporia subacida , (Peck) Donk, stringy butt rot	Poria subacida	1, 2, 9, 10, 14	WRC is very important host (14); enters through basal wounds and injured roots (2); also on wood in service (4)
Stem	Phellinidium ferrugineofuscum (P. Karst.)	Phellinus fer- rugineofuscus, Polyporus ferrugineofus- cus, Poria fer- rugineofusca	2, 6, 10	Important and significant in localized areas; limited to coastal WRC (2)
Unknown	Phellinus kamahi (G. Cunn.) P.K. Buchanan & Ryvarden	Fuscoporia kamahi	2	Typical in dead WRC material; only two accounts on living WRC (2)
Root &/ or Butt	Phellinus weirii (Murrill) Gilb., cedar laminated butt rot	Phellinidium weirii, Poria weirii	2, 6, 7, 8, 10, 11	Important and significant in localized areas; majority of damage in interior regions (2); very common throughout WRC range in Idaho (13); also on wood in service (2,3)
Stem	Porodaedalea pini (Brot.) Murrill, red ring rot	Fomes pini, Phellinus pini	1, 2, 8, 10, 14	
Root &/ or Butt	Scytinostroma galactinum (Fr.) Donk, yellow stringy butt rot	Corticium galactinum	7, 9, 14	
Root &/ or Butt	Xeromphalina campanella (Batsch) Kühner & Maire	Omphalopsis campanella	2	Secondary importance; typically found in dead WRC material
Unknown	Unknown white rot		5	

Appendix 1: Principal white rot decay fungi occurring on living western redcedar (*Thuja plicata*)

1. Allen et al. 1996, BC, all ages	8. Lewis 1992, interior BC, second-growth
2. Buckland 1946, BC, all ages	9. Minore 1983
3. Chedgy et al. 2009	10. Sturrock et al. 2010, western North America, all ages
4. Clark and Smith 1979 - cited in Scheffer et al. 1984	11. USDA 2007, 2012, Alaska, all ages
5. Cleary et al. 2012b	12. van der Kamp 1975, coastal BC old-growth
6. Kimmey 1956, southeast Alaska, all ages	13. Weir 1921, Idaho, all ages
7. Koenigs 1969, Northern Idaho, ~100 years old	14. Zeglen 1997, BC, all ages

¹ In most cases we have recognized the Latin names and authorities provided at Index Fungorum (<u>http://www.indexfungorum.org/</u>), a global database of fungal names coordinated and supported by the Index Fungorum Partnership (<u>http://www.indexfungorum.org/</u><u>Names/IndexFungorumPartnership.htm</u>). Synonyms are listed in alphabetical order.

² Main sources of information are numbered and listed in alphabetical order at bottom of Appendix 1. Full citations for the sources are provided in the Literature Cited section. Some sources include an indication of the geographic area the studies focussed on and the general age/type of trees studied.

Appendix 2:	Principal brown rot decay fungi occurring on living western redcedar
	(Thuja plicata)

Decay Type	Current Name & Pathogen & Disease Common Name(s) (where applicable) ¹	Common Synonyms ¹	Main Sources of Information ²	Notes (& Sources)
Heart	Antrodia serialis (Fr.) Donk, brown pocket rot		14	
Trunk	Coniophora puteana (Schumach.) P. Karst., brown cubical trunk rot	Coniopohora cerebella	14	Minor brown cubical rot (2); identified as a saprobe on dead, fallen, decayed material; also on wood in service (3, 4, 5, 11)
Heart	Echinodontium tinctorium (Ellis & Everh.), brown stringy trunk rot (Indian paint fungus)	Fomes tinctorius	14	True heart rot
Heart	Fomitopsis pinicola (Sw.) P. Karst., red belt fungus, brown crumbly rot	Fomes pinicola	1, 2, 12, 14	Minor brown cubical rot (2); primary and secondary invader, causes heart- and sap rot in living trees, continues to develop on dead material and can cause damage to wood in service
Heart	Laetiporus sulphureus (Bull.) Murrill, brown cubical rot	Polyporus sulphureus	1, 12, 14	Occasionally attacks living trees; not of economic impor- tance
Butt	Merulius (Fr.) brown crumbly butt rot		2	Sufficient frequency to warrant attention as a butt rot of cedar (2)
Heart	Neolentinus lepideus (Fr.) Red- head & Ginns, scaly cap fungus, brown cubical rot	Lentinus Iepideus	14	Causes heart rot in living trees
Root &/ or Butt	Phaeolus schweinitzii (Fr.) Pat., velvet top fungus, brown cubical butt rot	Polyporus schweinitzii	1, 2, 9, 12, 14	Rare, first record (13); minor brown cubical rot - past identifications as brown cubical butt rot later identified as <i>P. asiatica</i> (2)
Butt	Postia balsamea (Peck) Jülich, brown cubical butt rot	Oligoporus balsameus, Polyporus balsameus,	2, 5, 14	Minor - found only in a few trees from North Thompson and Revelstoke regions (2)
Heart	Postia sericeomollis (Romell) Jülich, brown cubical butt and pocket rot	Oligoporus sericeomollis, Polyporus seri- ceomollis, Poria asiatica, Poria sericeomollis	1, 2, 7, 12, 14	WRC very important host (14); primary invader, causes heart and sap rot in living trees (14); major heart rot fungus on coast and in interior; 'black rot' responsible for greatest loss in living WRC in the interior (2)
Trunk	Rhodonia placenta (Fr.) Niemelä, K.H. Larss. & Schigel, brown cubical rot	Ceriporiopsis placenta, Polyporus placenta, Poria monticola, Pos- tia placenta	14	Also on wood in service (11)
Heart	Stereum sanguinolentum (Alb. & Schwein.) Fr., red heart rot	Haematostere- um sanguinol- entum, Stereum balsameum	14	Also on WRC fence posts (8)
Unknown	Unknown A. B		7	
Unknown	Unknown		6	
Unknown	Unknown; possibly Tyromyces amarus (Hedgc.) J. Lowe	Oligoporus amarus, Polyporus amarus, Postia amara	13	Common, destructive, of economic importance; dark brown, crumbly, carbonizing pocket and ring rot

1. Allen et al. 1996, BC, all ages	8. Lim et al. 2005a
2. Buckland 1946, BC, all ages	9. Minore 1983
3. Chedgy et al. 2009	10. Morris and Stirling 2012
4. Clark and Smith 1979 - cited in Scheffer et al. 1984	11. Southam and Ehrlich 1950
5. Eslyn 1970	12. Sturrock et al. 2010, western North America, all ages
6. Kimmey 1956, southeast Alaska, all ages	13. Weir 1921, Idaho, all ages
7. Lewis 1992, interior BC, second-growth	14. Zeglen 1997, BC, all ages

¹ In most cases we have recognized the Latin names and authorities provided at Index Fungorum (<u>http://www.indexfungorum.org/</u>), a global database of fungal names coordinated and supported by the Index Fungorum Partnership (<u>http://www.indexfungorum.org/</u><u>Names/IndexFungorumPartnership.htm</u>). Synonyms are listed in alphabetical order.

² Main sources of information are numbered and listed in alphabetical order at bottom of Appendix 2. Full citations for the sources are provided in the Literature Cited section. Some sources include an indication of the geographic area the studies focussed on and the general age/type of trees studied.

Appendix 3: Principal sap rots, canker diseases, and needle diseases occurring on western redcedar (*Thuja plicata*)

Decay Type	Current Name & Pathogen & Disease Common Name(s) (where applicable) ¹	Common Synonyms ¹	Notes (& Sources)
Sap rot - white	Chondrostereum purpureum (Pers.) Pouzar, silver leaf disease	Stereum purpureum	(1, 4)
Sap rot -brown cubical	Coniophora arida (Fr.) P. Karst.		WRC poles in northern Idaho (3)
Sap rot - brown cubical	Coniophora olivacea (Fr.) P. Karst.		In association with 'golden glow' (caused by <i>Ptychogaster rubescens</i>); WRC poles in northern Idaho (3)
Sap rot - brown cubical	Fibroporia vaillantii (DC.) Parmasto	Poria vaillantii	WRC poles in northern Idaho (3)
Sap rot - brown	Gloeophyllum sepiarium (Wulfen) P. Karst.	Lenzites sepiarium	(1)
Sap rot - brown cubical	Leucogyrophana olivascens (Berk. & M.A. Curtis) Ginns & Weresub	Coniophora olivascens	In association with 'golden glow' (caused by <i>Ptychogaster rubescens</i>); WRC poles in northern Idaho (3)
Sap rot - brown cubical	Ptychogaster rubescens Boud.		(2,3)
Sap rot - brown cubical	Tapinella panuoides (Fr.) EJ. Gilbert	Paxillus panuoides	WRC poles in northern Idaho (3)
Sap rot - white spongy	<i>Trametes versicolor</i> (L.) Lloyd, cedar pocket rot	Polyporus versicolor	(1, 4)
Sap rot – white pitted	Trichaptum abietinum (Dicks.) Ryvarden, purple conk fungus	Hirschioporus abietinus, Polyporus abietinus	(1, 4)
Canker	Diaporthe lokoyae A. Funk		(1)
Needle disease	Didymascella thujina (E.J. Durand) Maire	Keithia thujina	(1)
Needle disease	Herpotrichia pinetorum (Fuckel) G. Winter	Herpotrichia juniper, Herpotrichia nigra	(1)

1. Allen et al. 1996

2. Eslyn 1970

3. Southam & Ehrlich 1950

4. Zeglen 1997

¹ In most cases we have recognized the Latin names and authorities provided at Index Fungorum (<u>http://www.indexfungorum.org/</u>), a global database of fungal names coordinated and supported by the Index Fungorum Partnership (<u>http://www.indexfungorum.org/</u><u>Names/IndexFungorumPartnership.htm</u>). Synonyms are listed in alphabetical order.

² Main sources of information are numbered and listed in alphabetical order at bottom of Appendix 3. Full citations for the sources are provided in the Literature Cited section.

Glossary

Advance regeneration (also called advance growth) — seedlings or saplings that develop or are present in the understory and that take advantage of the increased light, water and nutrients caused by fire, harvest, storm and disease.

AM (arbuscular mycorrhizae) — type of mycorrhiza in which the fungus penetrates the cortical cells of the roots of a vascular plant, producing structures that are dichotomously branching invaginations (arbuscules).

Ascomycota — a phylum of the kingdom Fungi characterized by bearing sexual spores (ascospores) in a sac (ascus).

Basidiomycota — a phylum of the kingdom Fungi characterized by bearing sexual spores (basidiospores) on specialized structures (basidia) of fruiting bodies (e.g., conks and mushrooms, also known as sporophores).

Brown rot — decay that is characterized by break down of cellulose and hemicellulose but almost no degradation of lignin; decayed wood becomes brown in colour and breaks into roughly cubical pieces.

Burl — an abnormal swelling of a tree trunk characterized by swirling wood grain and meristematic tissue (undifferentiated plant tissue from which new cells are formed).

Cork (also known as phellem) — cells that develop outwards from the phellogen (cork cambium) (see also phellogen).

Cull — trees or logs or portions thereof that are unmerchantable because of defects, which may be caused by biotic (e.g., fungi, insects) or abiotic agents (e.g., machines).

Dry-side (also known as 'dry-face') — condition occurring in a tree with significant decay that results in a conspicuous flattening of the bole; condition may extend from the butt to as much as 13 m or more up stems and is normally covered with bark so decayed wood underneath is not visible.

Extractives — in plants, non-cell wall compounds composed of relatively small molecules that can be extracted by organic solvents; these extractives usually comprise only 1-5% of wood tissues and can vary considerably between and within genera, families and individuals.

Fork(ed) top — trees with forked tops have a main bole that subdivided at some point above the base and subsequently supported two or more live crowns; such trees have 'candelabra-like' tops.

Fungistatic — inhibitory to the growth of fungi.

Fungitoxic — toxic to (kills) fungi.

Heartwood — the nonliving, inner and often dark-coloured wood in the center of a tree bole or root in which no water transport occurs. Heartwood is surrounded by sapwood and has preformed defenses but no active defenses.

Incipient decay — an early stage in decay in which the affected wood may show discoloration but is not otherwise visibly altered. Wood with incipient decay is generally firm and sound.

Lignans — a group of polyphenolic chemical compounds found in plants. Lignans serve an antioxidant role in plant defenses against biotic and abiotic factors.

Mycelia — the vegetative part of a fungus, consisting of a network of fine white filaments (hyphae).

Necrophylactic periderm(s) — certain sequent periderms and other periderms that are always found adjacent to dead tissue (non-suberized impervious tissue or NIT), which are thought to protect living tissues from the adverse effects of cell death.

Pathological rotation — age at which volume added by growth equals the volume lost to decay. In practice, it is the age beyond which carrying a forested stand is not economically feasible because net volume growth is decreased by decay.

Periderm — the outer tissue layers of woody roots and stems, consisting of the cork cambium and the tissues produced by it such as cork.

Phellogen — the meristematic cell layer responsible for the development of the periderm of a stem or root. Cells that grow inwards from the phellogen are termed phelloderm and cells that develop outwards are termed phellem or cork.

Plicatic acid — a lignan and major component of heartwood extractives in western redcedar.

Pyrosequencing — A technique used to sequence DNA using chemiluminescent enzymatic reactions.

Saprophyte — an organism using dead organic as food; such organisms live saprophytically.

Sapwood — the outer part of the wood (xylem) in a tree bole or root; sapwood tissues are alive and actively conduct water. Sapwood is usually lighter in colour than heartwood.

Slash — coarse and fine woody debris generated during harvesting operations or through wind, snow or other forest disturbances.

Snag — any standing dead tree (no living foliage).

Soil block test — test whereby cubes of test wood are exposed to a pure culture of a test fungus growing on a wood feeder strip on sterile soil; durability/decay resistance of test wood of interest is assessed by determining weight loss of test blocks after an incubation period.

Spike top — any tree in which the crown (top portion) is more than 50% dead.

Sporophores (also called fruiting bodies) — see Basidiomycota.

Terpenes — any of a large group of volatile unsaturated hydrocarbons found in the essential oils of plants, especially conifers and citrus trees.

Thujaplicins — chemical substances isolated from western redcedar (*Thuja plicata*) and known for their potent anti-fungal properties.

Thujin — a substance extracted from trees of the genus *Thuja* believed to be formed by microbial degradation of thujaplicins.

Traumatic phloem resin ducts — resin ducts (tubes or ducts in a woody stem or a leaf, especially in conifers, lined with cells that secrete resins) formed in phloem tissue in response to abiotic wounding, fungal invasion, or insect attack; relatively common in members of the Cupressaceae.

Tropolones — organic compounds present in a variety of plants; includes thujaplicins.

Typical decay — advanced decay in wood; deterioration is visible and wood is not sound.

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