

# Wood Decay Pathology of Fruit and Nut Trees in California

Since 1945, the demand for fruit and nut commodities has increased dramatically in local, national, and worldwide markets. This demand has led to increases in new plantings and extended rotations of established orchards. In California, following development of an extensive aqueduct system in the 1950s and 1960s that provided low-cost water, the Sacramento and San Joaquin valleys have become two of the major agricultural regions in the world. In both valleys, deciduous fruit and nut trees are some of the principal crops and are grown primarily on the irrigated farmland.

Past and current hectares in production, levels of production, and values of selected crops grown in California are shown in Table 1. The high crop values and extensive plantings led to intensive cultural practices. New cultivars, high-density plantings, sprinkler and drip irrigation, high-analysis fertilizers, and chemical control of diseases have all contributed to high productivity of this region. Further, to decrease labor costs, pruning and harvesting also were mechanized on some crops.

Although this new, intensive production system solved many previous problems in production, new diseases and diseases that were previously of little consequence became important. One of the increasing problems in commercial orchards is wood decay, which contributes to premature decline of orchards and shortens the life span of fruit and nut trees. Some of the fungi responsible for wood decay are aggressive pathogens that cause root rots and cankers leading to tree death. These fungi can function as primary colonists of wounds and have the ability to invade and kill functioning xylem and cambial tissue. The best known of these fungi are species in *Armillaria*, *Ganoderma*, and *Cerrena* (2,19,44,46).

In this paper, we describe wood decay pathology of fruit and nut trees, illustrate some of the fungi responsible and report their incidence, and relate wood decay

to changing cultural practices in commercial orchards in California.

## Overview of Wood and Its Decay

Wood is the xylem cylinder of trees. In younger trees, xylem functions in food storage (provided mainly by parenchymal cells), water conduction, and structural support and is referred to as sapwood. In older trees, an outer, lighter region of sapwood surrounds an inner, darker region known as heartwood. This tissue is formed after a number of years, which varies according to the tree species and conditions of growth. In angiosperms, sapwood consists of living parenchyma and dead, lignified vessels and fiber tracheids, whereas heartwood is composed of dead cells that are commonly filled with extractives (organic and inorganic substances). In fruit and nut trees, heartwood is generally formed only after several decades.

Biochemically, wood has three major components: cellulose (a polymer of glucose), hemicellulose (chains of several different monosaccharides), and lignin (a three-dimensional branched polymer of phenylpropanes). The natural resistance of wood to decay results in part from the high crystallinity of cellulose (microfibrils highly ordered with decreased surface area and accessibility to degrading enzymes), lignification (decreases accessibility of polysaccharides), low nitrogen content (high C/N ratios limit growth of many organisms), and toxic substances (phenolic compounds in heartwood).

Decay of xylem is caused primarily by fungi capable of utilizing sound wood as an energy source. Wood-decay fungi degrade polysaccharides by both enzymatic and nonenzymatic chemical reactions, assimilate the resulting monosaccharides, and utilize these simple sugars for growth. Temperature and moisture, two of the more important environmental conditions regulating fungal growth, govern the occurrence and rate of wood decay. Generally, for wood to be decayed by fungi, the moisture content must be above 28–32%, the fiber saturation point of wood. This condition is always met within living trees. Above this

moisture content, the wood cell walls are fully saturated and free water is present in the cell lumen, allowing diffusion of fungal enzymes. Temperature at which fungi can decay wood varies according to the specific fungal species; optimal temperatures range from 20 to 40 C.

Wood decay can be characterized into three major types: brown, white, or soft rots. In brown rots, polysaccharides are degraded into various sugar residues, whereas lignin is left primarily unchanged. The decayed wood is brown, dry, and crumbly with longitudinal and transverse cracks. Brown rots are caused by fungi in the Basidiomycotina. In white rots, all major structural components of the wood—cellulose, hemicellulose, and lignin—are degraded. The decayed wood is moist, soft, or spongy and bleached to a lighter color. White rots have been further characterized microscopically and biochemically on the basis of differential rates of removal of the structural components of wood. Decay may proceed as a simultaneous decay of lignin and polysaccharide components or as a selective delignification where lignin is removed at a faster rate. No decay fungi selectively remove lignin exclusively. White rots are caused predominantly by fungi in the Basidiomycotina; however, some are in the Ascomycotina, especially the Xylariaceae. Under ideal conditions, fungi that cause brown and white rots can decay extensive regions of the wood of living trees in a relatively short period (months to years), significantly reducing the strength of the wood and killing storage and conductive tissue of the sapwood. Further, storage and conductive functions are disrupted when these fungi invade and decay sapwood. These fungi cause serious damage and have become widespread in fruit and nut orchards in California.

Soft rots are caused by bacteria or by fungi in the Ascomycotina and the Deuteromycotina. These organisms also decay cellulose, hemicellulose, and lignin but only in areas directly adjacent to their growth; their rate of decay is slower than that of other organisms that decay wood, and they usually do not cause extensive structural changes in wood of living trees.

**Table 1.** Hectares, production levels, and estimated value of selected fruit and nut crops in California for 1950, 1970, and 1987

Crop	Hectares (×1,000) <sup>x</sup>			Production (×1,000) <sup>y</sup>			Value (× \$10 <sup>6</sup> ) <sup>z</sup>		
	1950	1970	1987	1950	1970	1987	1950	1970	1987
Almond	36.6	68.8	166.3	34.2	112.5	299.4	20.5	80.1	615.6
Apricot	18.8	13.2	8.9	193.2	153.3	99.8	19.4	18.6	33.4
Apple	9.8	8.9	9.1	...	254.0	294.8	7.8	17.9	72.1
Cherry	3.8	4.5	4.2	28.1	23.0	40.8	8.4	12.1	28.4
Nectarine	1.1	3.2	9.3	11.2	60.3	173.3	1.8	10.1	65.6
Peach	31.9	29.5	21.7	636.8	762.9	665.9	42.9	74.0	163.9
Plum	9.7	8.6	15.9	69.9	112.0	222.3	11.0	19.7	75.4
Prune	41.3	39.0	30.5	135.2	181.0	206.8	36.5	40.4	166.4
Walnut	46.7	59.3	73.0	52.6	98.0	224.1	22.7	43.9	234.6

<sup>x</sup> Hectares of bearing trees.

<sup>y</sup> Metric tons (1,000 kg).

<sup>z</sup> Monetary data are not corrected for inflation.

### Life Cycle of Hymenomyces

Wood-decay fungi enter wood either from spores germinating and hyphae colonizing wounds or from vegetative (somatic) growth through natural tree-to-tree root grafts or contacts. Sexual spores or basidiospores are aerially disseminated from basidiocarps and function as the primary inoculum. These spores are produced by a specialized cell, the basidium, where meiosis occurs. In heterothallic species, after meiosis and spore production, basidiospores germinate

under favorable environmental conditions to produce homokaryotic mycelium capable of independent growth as part of its life cycle. When compatible mating types of homokaryotic mycelium fuse, a dikaryotic mycelium is formed. This stage is found most commonly in nature. In some species of *Armillaria*, however, after somatogamy the nuclei fuse to form a diploid nucleus. In still other species, heterokaryotic hyphae develop directly from basidiospores and the nuclear condition is unknown; pre-

sumably, these fungi are homothallic. In all cases, fungi grow as mycelium within wood and utilize the substrate for energy. After adequate substrate colonization, fruiting body or basidiocarp formation occurs under suitable environmental and physiological conditions. From fruiting bodies, basidiospores are produced and the life cycle is completed. Only a few wood-decay fungi are known to produce asexual spores that can infect woody substrates. *Inonotus rickii* is one species that functions in this manner.



**Fig. 1.** Stars indicate counties surveyed in northern and central California. The Sacramento Valley extends from Sacramento County northward, and the San Joaquin Valley extends from San Joaquin County southward.

### Concepts in Decay Pathology

Tree wounds that expose wood serve as infection courts where spores or somatic propagules germinate and hyphae colonize the wood. Injuries occur from environmental factors (including wind-blown broken limbs, sunburned limbs and trunks, frost cracks, and lightning damage) and from biological factors (such as insects, birds, and mammals). Wounds from pathogens can also function as infection courts for decay fungi. In Montana, Weir (48) associated *Trametes hirsuta* and *Stereum hirsutum* with infections of *Nectria cinnabarina* Fr. on plum, as well as *Phellinus igniarius* with black knot caused by *Apiosporina morbosus* (Schwein.) v. Arx. In cultivated tree crops, however, cultural practices that include cultivation, pruning, and mechanical harvesting are the greatest sources of injury to trees.

In nature, wood-decay fungi are not generally the primary colonizers of wounds. A succession of organisms such as bacteria, yeast, and hyphomycetes may colonize wood after wounding or parasitic infection on forest trees (40,43) and apple (7). These organisms function as primary invaders of wounds and colonize even healthy woody tissues but are not considered to be primary pathogens and do not cause major structural degradation of cell walls. Primary invaders may alter the wound-induced chemical barrier of the host and may further allow other organisms, such as wood-decaying hymenomyces, to colonize the wood. Ecologically, wood-de-

caying hymenomycetes are considered secondary organisms in the succession of wound colonization of trees; however, these fungi are independently capable and pathologically responsible for wood decay. Once established, many of these decay fungi are primary colonists of the sapwood. Some species where pathogenicity on hardwood hosts has been demonstrated include *Armillaria mellea* (46), *Cerrena unicolor* (19), *Ganoderma lucidum* (2), and *Oxyporus latemarginatus* (12).

Wood of living trees is often described as dead tissue; however, it is capable of reacting to injury. Therefore, wood is an integral part of the living tree both structurally in support and functionally in responding to wounds. Shigo and Shortle (41) have developed a model, compartmentalization of decay in trees (CODIT), for describing tree responses to injury and decay. This model is based on anatomical and biochemical barriers already in place that are strengthened or new barriers that are formed in response to injury, thus preventing or hindering invasion of the tree by microorganisms. Immediately after an injury occurs, woody tissues (sapwood or heartwood) react and become discolored from host responses, as well as environmental and biological factors associated with the wound. Discolored wood of hardwood tree species contains phenolic compounds, gums, and other occlusions that occupy cell lumens of the injured areas and provide a chemical barrier against microorganisms. This wood appears similar to heartwood but differs as localized tissue that has responded to injury. Additionally, the structural arrangement of existing cells and new xylem functions to compartmentalize injured tissue. Injured wood of peach trees is consistent with this model and has been described as compartmentalized (42).

The ability of wood-decaying fungi to colonize wood and cause structural damage varies among fungal species. In some, the fungus actively invades cambial tissue, killing it rapidly. This can result in root and trunk rots, e.g., *Armillaria mellea* sensu stricto (44), or in limb and trunk cankers, e.g., *Trametes versicolor* and *Cerrena unicolor* (19,44). Other wood-decay fungi, such as *Chondrostereum purpureum*, release toxins that affect foliage of infected trees (6). Most wood-rotting fungi of fruit and nut trees, however, have been implicated in more subtle diseases that develop over several years. Some of these fungi have been implicated in the decline or gradual loss of vitality and health of fruit trees (4,10,14,15,39). Finally, many decay fungi (e.g., *Schizophyllum commune*) are known primarily as slash fungi or sapwood fungi and commonly occur on wood of nonliving trees as well as on dead tissue of living ones.

Wood-decay fungi that can spread

**Table 2.** Incidence of wood decay in fruit and nut orchards of the Sacramento and San Joaquin valleys in California

Crop <sup>1</sup>	Age <sup>2</sup>	Number surveyed		Percent trees with wood decay
		Orchards	Trees	
Almond	18	15	2,688	25
Apple	16	1	759	18
Apricot	23	4	410	21
Cherry	17	18	739	25
Fig	40	3	150	92
Peach and nectarine	15	4	408	36
Plum and prune	13	4	400	35
Walnut	18	3	133	34
Average or total	20.0	52	5,687	35.8

<sup>1</sup> Orchards surveyed by crop. Cultivars in orchards surveyed were: almond (*Prunus dulcis* (Mill.) W.A. Webb) = Carmel, Drake, Merced, Mission, NePlus Ultra, Nonpareil, and Thompson on peach rootstock (Nemagard); apple (*Malus* spp.) = Granny Smith on White Astrachan interstock on MM.111 rootstock; apricot (*P. armeniaca* L.) = Blenheim and Perfection; cherry (*P. avium* L.) = Bing grafted on mazzard or mahaleb; fig (*Ficus carica* L.) = Calimyrna; nectarine (*P. persica* (L.) Batsch var. *nucipersica* (Suckow) Schneid.) = Flamekist; peach (*P. persica* (L.) Batsch) = Loadel, Starn, and Fay Elberta; plum (*P. americana* L.) = Friar; prune (*P. domestica* L.) = French; walnut (*Juglans* spp.) = English on native Black rootstock.

<sup>2</sup> Average tree age based on planting dates or tree rings.

vegetatively through natural root grafts or contacts (i.e., *Armillaria* and *Ganoderma* spp.) often are restricted to the roots and lower portion of the trunk. These fungi are known as root-rot and butt-rot fungi. Other species that grow in the upper trunk and scaffold branches colonize older sapwood and heartwood that function in the structural support of the tree. In apple trees (27) and probably other fruit and nut trees, heartwood generally forms only in older trees that usually are no longer in commercial production. Fungi that attack these tissues traditionally have been described as heart-rot fungi.

### Decay in Commercial Orchards

In fall and winter of 1986–1988, incidence of wood decay in commercial fruit and nut orchards was surveyed in 10 counties throughout the Sacramento and San Joaquin valleys of California (Fig. 1). Fifty-two orchards of 10 crops assessed ranged in age from 10 to 40 years. Excluding fig, tree age ranged from 10 to 23 years (mean 16.3 years). Decay was detected by visual examination of wounds on scaffold branches, trunks, and exposed roots of living trees. Host, age of trees, number of orchards, number of trees, and percentage of trees with either white rots or brown rots for orchards surveyed are shown in Table 2. Incidence of wood decay in the orchards surveyed ranged from 21 to 92%; in orchards less than 20 years old, however, decay incidence did not exceed 36%. Fig orchards, approximately 40 years old, had 92% incidence of decay.

Beginning in the mid-1970s, irrigation practices began to change from furrow to the more water-efficient sprinkler systems. Of 18 cherry orchards that we surveyed (Table 2), nine were sprinkler-

**Table 3.** Incidence of wood decay in cherry orchards with either sprinkler or furrow irrigation systems<sup>1</sup>

Irrigation	Number of orchards surveyed	Percent trees with wood decay
Sprinkler	9	37.8 a <sup>2</sup>
Furrow	9	11.3 b

<sup>1</sup> Cultivar Bing (*Prunus avium*) on mahaleb (*P. mahaleb*) rootstock.

<sup>2</sup> Means followed by different letters are significantly different at  $P = 0.05$  ( $t$  test).

irrigated and nine furrow-irrigated during the past 10–15 years. Incidence of decay was significantly greater in orchards with sprinkler irrigation than in orchards with furrow irrigation (Table 3). In one 15-year-old sprinkler-irrigated almond orchard, approximately 8,000 fallen trees (2% of total orchard) with wood decay in roots and lower trunks were removed per year during the past 3 years. Apparently, wounds on tree trunks kept moist from sprinkler irrigation provided a suitable environment for the establishment of decay fungi.

**Fungi collected.** Basidiocarps of fungi were collected in the counties indicated in Figure 1, as well as Contra Costa, Glenn, El Dorado, Placer, and Kern counties, from living and recently killed hosts listed in Table 2 and from pistachio and olive trees. Thirty-five species of fungi in 25 genera, some of which are illustrated in Figures 2 and 3, were identified. Fungi recorded in our study and previously reported fungi occurring on orchard trees in Pacific Coast states are indicated by host, habit, and type of decay in Table 4. Of the fungi we



Fig. 2. Basidiocarps of wood-decay fungi on fruit and nut trees: (A) *Armillaria mellea* on almond (*Prunus dulcis*). (B) *Pleurotus ostreatus* on walnut (*Juglans regia*). (Inset) Bottom view of basidiocarp showing lamellae, or gills. (C) *Coprinus* sp. on soil above decaying roots of almond. (D) *Schizophyllum commune* on peach (*Prunus persica*). (E) Top and (F) bottom view of *Lenzites betulina*. (G) *Inonotus cuticularis* on fig (*Ficus carica*). (H) *Ganoderma lucidum*, (I) *G. applanatum*, and (J) *G. brownii* on peach. (K) *Phellinus robustus*, (L) *P. pomaceus*, and (M) *P. gilvus* on almond. Scale bars: A, G-J, M = 4.5 cm; B = 7 cm (inset = 1 cm); C-F, K, L = 1 cm.



Fig. 3. Basidiocarps and associated wood decay on fruit and nut trees: *Oxyporus latemarginatus* on (A) trunk of almond (*Prunus dulcis*) and (B) soil surface above diseased roots, respectively. Note pores of the basidiocarp where basidiospores are produced. (C) *Ceriporia spissa* on peach (*Prunus persica*). (D) *Peniophora albobadia* on almond. (E) *Phanerochaete velutina* on almond. (F) *Perennoporia medulla-panis* on almond. (G) *Trametes versicolor* on almond and (H) *T. hirsuta* on peach. (I) *Stereum hirsutum* on almond. (J) *Fomitopsis cajanderi* fruiting at pruning wound on prune (*Prunus domestica*). (K) *Laetiporus sulphureus* and (L) its brown heart rot in an almond trunk; arrow indicates white mycelial mats in cracks in decayed wood. Scale bars: A, H, J, L = 2 cm; B-G, I = 1 cm; K = 10 cm.

**Table 4.** Common wood decay fungi of selected fruit and nut trees in California, Oregon, and Washington

Fungus <sup>w</sup>	Host occurrence by state <sup>x</sup>			HA <sup>y</sup>	Decay <sup>z</sup>
	California	Oregon	Washington		
<i>Abortiporus biennis</i> (Bull.:Fr.) Singer	2,6-8,18	Same	Same	1,2	W
<i>Antrodia malicola</i> (Berk. & W. Curt.) Donk	...	...	7	2	B
<i>Armillaria</i> spp.	1-18	3,6,7,12-14,18	3,6,7,13,14,16,18	1,2	W
<i>A. mellea</i> (Vahl:Fr.) Kummer sensu stricto*	10,14	...	...	1,2	W
<i>Bjerkandera adusta</i> (Willd.:Fr.) Karst.	...	...	6,7	1,2	W
<i>Ceriporia purpurea</i> (Fr.) Donk	...	...	6	2	W
<i>C. spissa</i> (Schw.:Fr.) Rajch.*	14	...	...	2	W
<i>Cerrena unicolor</i> (Bull.:Fr.) Murr.	16	16	...	1	W
<i>Chondrostereum purpureum</i> (Pers.:Fr.) Pouz.	11,13,14,16	7,16,18	7,13,16,19	1,2	W
<i>Coltricia perennis</i> (L.:Fr.) Murr.	...	...	7	3	NS
<i>Coprinus</i> spp.*	16	...	...	1,2	B
<i>Corioloopsis gallica</i> (Fr.) Ryv.	...	16	7	2	W
<i>Cyphellopsis anomala</i> (Pers.:Fr.) Donk	...	...	3	3	NS
<i>Daedalea quercina</i> Fr.	6	...	...	1,2	B
<i>Daedaleopsis confragosa</i> (Bolt.:Fr.) Schroet.	6	...	16	1,2	W
<i>Dendrophora albobadia</i> (Schw.:Fr.) Boidin*	10	...	...	1,2	W
<i>D. erumpens</i> (Burt) Chamuris	...	7,16	16	2	W
<i>Flammulina velutipes</i> (Fr.) Karst.	...	...	7	1,2	W
<i>Fomes fomentarius</i> (L.:Fr.) Kickx.	...	7,13,16,18	Same	1,2	W
<i>Fomitopsis cajanderi</i> (Karst.) Kotl. & Pouz.*	13,16	1,3,13,14,16	1,3,12,13,16	1,2	B
<i>F. pinicola</i> (Swartz:Fr.) Karst.	...	7,13,14,16	7,12	1,2	B
<i>F. rosea</i> (Alb. & Schw.:Fr.) Karst.	...	1,4,14,16	1,4,16	1,2	B
<i>Ganoderma annularis</i> (Fr.) Gilbn.*	10,14	...	...	1,2	W
<i>G. applanatum</i> (Pers.) Pat.*	7,14	2,4,13,16	7,16,18	1,2	W
<i>G. brownii</i> (Murr.) Gilbn.*	10,14	...	...	1,2	W
<i>G. lucidum</i> (W. Curt.:Fr.) Karst.*	7,10,12,14,16	...	...	1,2	W
<i>Gloeophyllum saepiarum</i> (Fr.) Karst.	...	7,13,14,16	12,13,16	2	B
<i>G. trabeum</i> (Fr.) Murr.	...	7,16	16	2	B
<i>Gloeoporus dichrous</i> (Fr.) Bres.*	7,11	...	...	1	W
<i>Hyphoderma puberum</i> (Fr.) Wallr.*	10	...	...	2	W
<i>H. mutatum</i> (Pk.) Donk	...	...	3	2	W
<i>H. setigerum</i> (Fr.:Fr.) Donk	...	...	3	2	W
<i>Hyphodermella corrugata</i> (Fr.) John Erikss. & Ryv.	...	...	16	2	W
<i>Hyphodontia aspera</i> (Fr.) John Erikss.*	10	...	...	2	W
<i>Inonotus cuticularis</i> (Bull.:Fr.) Karst.*	5	...	...	1	W
<i>I. dryophilus</i> (Berk.) Murr.	16	16	...	1	W
<i>I. rickii</i> (Pat.) D.Reid*	5	...	...	1	W
<i>Irpex lacteus</i> (Fr.) Fr.*	12,16	Same	Same	1,2	W
<i>Laetiporus sulphureus</i> (Bull.:Fr.) Murr.*	2,6,10,13,16	6,10,16	6,10,16	1,2	B
<i>Lenzites betulina</i> (Fr.) Fr.*	7,10,12	...	...	1,2	W
<i>Maireina marginata</i> (McAlpine) W.B. Cooke	...	7,10,14	7	1,2	W
<i>Naematoloma fasciculare</i> (Huds.:Fr.) Karst.	...	...	7	2	NS
<i>Oligoporus tephroleucus</i> (Fr.) Gilbn. & Ryv.	...	12	...	2	B
<i>Omphalotus olearius</i> (DC.:Fr.) Singer	8	...	...	1,2	W
<i>Oxyporus corticola</i> (Fr.) Ryv.*	14,16	12,16	16	2	W
<i>O. latemarginatus</i> (Dur. & Mont. ex. Mont.) Donk*	7,10,12,16	...	...	1,2	W
<i>O. populinus</i> (Fr.) Donk	...	16	16	1,2	W
<i>O. similis</i> (Bres.) Ryv.*	7,10,14	...	...	1,2	W
<i>Panellus serotinus</i> (Fr.) Kühn	...	7	7	2	W
<i>Peniophora cinera</i> (Pers.:Fr.) Cke.	...	...	3	2	W
<i>P. nuda</i> (Fr.:Fr.) Bres.	...	...	3	2	W
<i>Perenniporia fraxinophila</i> (Pk.) Ryv.	16	...	...	1	W
<i>P. medulla-panis</i> (Jacq.:Fr.) Donk*	16	...	...	1	W
<i>Phanerochaete velutina</i> (Fr.) Karst.*	14	...	3	2	W
<i>Phellinus ferreus</i> (Pers.) Bourd. & Galz.	3	2,3,16	3	1,2	W
<i>P. ferruginosus</i> (Schard.:Fr.) Bourd. & Galz.	3,16	3,16	7,16	1,2	W
<i>P. gilvus</i> (Schw.) Pat.*	10,14,16	...	...	1,2	W
<i>P. ignarius</i> (L.:Fr.) Quél.	7,16,18	7,16,18	7,16	1	W
<i>P. pomaceus</i> (Pers.: S.F. Gray) Maire*	10	13,16	3,16	1,2	W
<i>P. robustus</i> (Karst.) Bourd. & Galz.*	7,10,13	...	...	1	W

(continued on next page)

<sup>w</sup>Fungi collected on hosts in California by the authors are indicated by an asterisk. Host records of other fungi listed by state were obtained from references 13, 20, and 50.

<sup>x</sup>Numbers correspond to the following hosts: 1 = pecan (*Carya illinoensis* (Wang.) K. Koch); 2 = chestnut (*Castanea* spp.); 3 = filbert (*Corylus* spp.); 4 = persimmon (*Diospyros* spp.); 5 = fig (*Ficus carica* L.); 6 = walnut (*Juglans* spp.); 7 = apple (*Malus* spp.); 8 = olive (*Olea europea* L.); 9 = pistachio (*Pistacia vera* L.); 10 = almond (*Prunus dulcis* (Mill.) W.A. Webb); 11 = apricot (*P. armeniaca* L.); 12 = cherry (*P. avium* L. and *P. mahaleb* L.); 13 = prune (*P. domestica* L.) and plum (*P. americana* L.); 14 = peach (*P. persica* (L.) Batsch); 15 = Japanese plum (*P. salicina* Lindl.); 16 = *Prunus* spp.; 17 = pomegranate (*Punica granatum* L.); 18 = pear (*Pyrus* spp.); 19 = quince (*Cydonia oblonga* Mill.).

<sup>y</sup>Host association: 1 = living trees, 2 = dead trees, 3 = not specified.

<sup>z</sup>W = white rot, B = brown rot, NS = not specified.

Table 4. (continued from preceding page)

Fungus*	Host occurrence by state <sup>†</sup>				
	California	Oregon	Washington	HA <sup>‡</sup>	Decay <sup>§</sup>
<i>P. texanus</i> (Murr.) A. Ames*	13	...	...	1	W
<i>Phlebia concentrica</i> (Cke. & Ell.) Kropp & Nakasone	...	...	3	2	W
<i>P. merismoides</i> (Fr.:Fr.) Fr.	3	...	...	2	W
<i>P. radiata</i> Fr.*	7	...	...	1,2	W
<i>P. rufa</i> (Fr.) M.P. Christ.*	10	...	...	2	W
<i>Pholiota</i> sp.*	16	...	...	1	NS
<i>P. adiposa</i> (Fr.:Fr.) Kummer	...	...	7	1,2	W
<i>P. squarrosa</i> (Mull.:Fr.) Kummer	...	...	7	1,2	W
<i>Pleurotus</i> sp.*	7	...	7	1,2	W
<i>P. ostreatus</i> (Fr.) Kummer*	5,6,8	...	...	1,2	W
<i>Plicaturopsis crispa</i> (Pers.:Fr.) D. Reid	...	13	...	2	W
<i>Polyporus elegans</i> Bull.:Fr.	...	...	16	2	W
<i>P. varius</i> Fr.	16	...	16	2	W
<i>Pycnoporus cinnabarinus</i> (Jacq.:Fr.) Karst.	16	...	...	2	W
<i>Schizophyllum commune</i> Fr.*	2,5-7,9-12,14	2,7,16	7,11-14,16	1,2	W
<i>Schizopora flavipora</i> (Cke.) Ryv.*	10	...	...	2	W
<i>Sistotrema brinkmannii</i> (Bres.) J. Erikss.*	14	...	...	2	W
<i>Stereum</i> spp.	...	3,6,16	7	3	W
<i>S. hirsutum</i> (Willd.:Fr.) S.F. Gray*	9,10	2,10,13,14,18	3	1,2	W
<i>Trametes hirsuta</i> (Wulf.:Fr.) Pilát*	7,11,14,16	3,6,7,12-14,16,18	6,7,12,14,16,18	1,2	W
<i>T. ochracea</i> (Pers.) Gilbn. & Ryv.*	7	...	7	1,2	W
<i>T. pubescens</i> (Schum.:Fr.) Pilát*	7	12	7	1,2	W
<i>T. versicolor</i> (L.:Fr.) Pilát*	7,8,10-14,18	2,3,7,10,12-14,16,18	6,7,12,14,16	1,2	W
<i>Tremella mesenterica</i> Retz.:Fr.	...	...	3	2	W
<i>Trichaptum bifforme</i> (Fr. in Klotzsch) Ryv.	...	18	...	2	W
<i>Tyromyces chioneus</i> (Fr.) Karst.	...	7,13,16	7,13,16	2	W
<i>T. galactinus</i> (Berk.) Lowe	...	13,16	...	2	W

collected, species in four genera (*Daedalea*, *Coprinus*, *Fomitopsis*, and *Laetiporus*) caused brown wood rots, whereas species of the remaining genera caused white rots.

**Incidence.** Frequency of common genera of decay fungi was compiled on the basis of field identifications, collections of basidiocarps, or cultures from decayed wood for eight crops (Fig. 4). Species of *Trametes*, *Ganoderma*, *Oxyporus*, and *Phellinus* were the most common, although predominant genera of fungi varied among crops. For example, species of *Pleurotus*, *Armillaria*, and *Laetiporus* were the most common on walnut, whereas species of *Oxyporus*, *Ganoderma*, and *Trametes* were the most common on cherry. Incidence of fungi also varied within geographic locations. Almond, which is planted extensively throughout the Sacramento and San Joaquin valleys, was affected by different species over this range. For example, *Phellinus pomaceus* on almond was found only in the mid to southern San Joaquin Valley, whereas *P. robustus* and *Perenniporia medulla-panis* were collected from the mid to northern Sacramento Valley. Similarly, *Lenzites betulina* was collected from almond only in the northern Sacramento Valley and from cherry in the higher elevations of Placer County.

Basidiocarps and decayed wood were commonly associated with sunburn injuries and wounds created by cultivation equipment, mechanical harvesters, canopy supports, and pruning (Fig. 5). In some cases, species of specific genera

were associated with wounds in certain portions of the tree. For example, species of *Perenniporia*, *Schizophyllum*, *Stereum*, *Trametes*, and *Fomitopsis* were commonly found on scaffold branches associated with pruning, sunburn, and canopy support wounds, whereas *Armillaria mellea* and species of *Ganoderma* and *Oxyporus* were primarily collected from root and lower trunk wounds caused by harvesters and cultivation equipment. Basidiocarps of *Laetiporus sulphureus* and *Oxyporus latemarginatus* also commonly occurred on the soil surface growing from decaying roots. Further, fungi like *L. sulphureus* and some species of *Phellinus* can cause decay in all portions of the tree.

**Symptoms.** Of the fungi collected or reported on fruit and nut trees in California, the majority caused white rots (Figs. 3 and 5). Macroscopically, these rots varied from laminated decays caused by some species of *Phellinus* to uniform decays caused by species of *Trametes* and *Oxyporus*. Wood decayed by some species of *Perenniporia* and *Ganoderma* had specific regions that were delignified, causing a mottled rot. These regions have been described as fibrous and strongly bleached, with middle lamellae removed between various wood cells and a loss of lignin that exceeds that of glucose or cellulose (1,8). Wood decayed by other fungi, such as species of *Oxyporus* and *Trametes*, is generally uniform in color (tan to white, lighter in color than healthy wood), middle lamellae and secondary walls are partially or completely removed from

various wood cells, and percent loss of lignin is similar to that of glucose or cellulose. Wood rot of this nature is considered simultaneously decayed (1,8).

Brown wood rots were either brown cubical pocket rots, with decay restricted to localized zones scattered within apparently nondecayed wood (e.g., decay caused by *Fomitopsis cajanderi*), or generalized brown cubical rots, with decay occurring uniformly throughout colonized wood (e.g., decay caused by *Laetiporus sulphureus*). In both of these rots, decayed wood was dark brown, dry, and crumbly. Further, mycelial mats were present in the transverse and longitudinal shrinkage cracks; these mats varied in color from pinkish, as in *F. cajanderi*, to white or slightly yellow, as in *L. sulphureus*.

Direct effects of wood decay for both white and brown rots were observed as breakage of scaffold branches during fruit production, resulting from loss of wood strength, and uprooting of trees, weakened from root decay, during windstorms or mechanical harvesting (Fig. 5). Limb decay was associated with pruning wounds or, ironically, with wounds from mechanical supports that are commonly used in fruit production to prevent breakage of scaffold branches. Root decay was most common in trees planted in poorly drained clay soils or in old riverbeds or flood plains.

### Some Specific Diseases in California

Decayed wood is the primary symptom for detecting wood-rotting fungi.

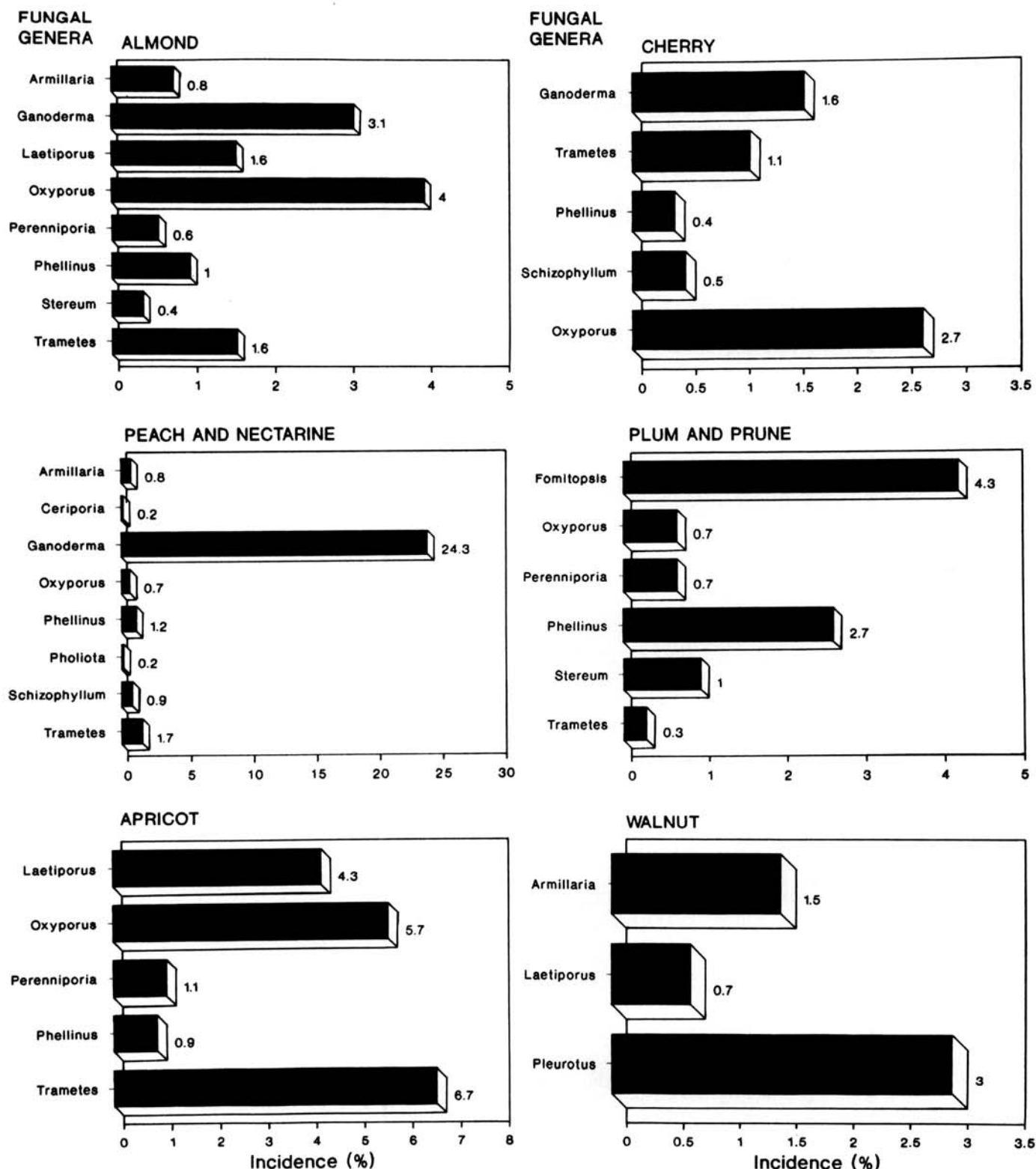


Fig. 4. Incidence of selected genera of wood-decay fungi by crop, based on field identifications, basidiocarps and cultures collected from trees with decay, and the total number of trees surveyed (Table 2).

Depending on the fungal species, other symptoms associated with wood decay are: cankers; papery, discolored bark; gumming of old wounds; black or brown zones within the wood; silvery leaves; dieback and general decline of trees; and death. Examples of wood-decay fungi that cause some of these symptoms are: *Armillaria mellea* (dieback and death), *Trametes versicolor* (cankers with papery

bark), *Chondrostereum purpureum* (silver leaf), *Fomitopsis cajanderi* (decline), and *Oxyporus latemarginatus* (decline and death).

**Shoestring root rot.** In California, shoestring root rot is caused by *Armillaria mellea* sensu stricto, which is a virulent pathogen of almost all fruit and nut trees. Diseased trees usually grow slowly, show dieback and premature

yellowing of leaves, and can die in 2-3 years after onset of symptoms. The fungus causes a white rot in the roots and lower trunk. Severely decayed wood is tan to yellowish and spongy. Signs of the fungus include rhizomorphs that extend along the surface of the roots; mycelial fans that develop between the bark and wood, killing cambial cells; and basidiocarps that develop from de-





Fig. 5. Symptoms caused by wood-decay fungi in stone fruit trees: (A) Heart rot of trunk of almond (*Prunus dulcis*) caused by the white-rot fungus *Oxyporus latemarginatus*. (B) Bird nesting cavity in a broken branch of prune (*Prunus domestica*) with heart rot caused by the brown-rot fungus *Fomitopsis cajanderi*. (C) Wind-twisting crack of an almond scaffold branch with a brown heart rot caused by *Laetiporus sulphureus*. (D) Wind-thrown, uprooted trees with root and butt rot caused by *Oxyporus latemarginatus*. (E) Dieback (arrow) of prune with wood decay in scaffold branches; decay was associated with scaffold support band (double arrows). (F) Broken scaffold branch of prune with white wood rot caused by *Perennoporia medulla-panis* associated with a wound caused by a scaffold support band (arrow). (G) Close-up of tree in foreground of D, showing white rot in decayed trunk (arrow).

caying wood. The fungus spreads to healthy trees aerially by basidiospores (38) or in the soil by rhizomorphs developing across root contacts (51). Unlike other wood-decay fungi, *A. mellea* requires no wounds for penetration and infection (46) and can survive in wood in the soil for many years.

Several biological species have been segregated from the complex once known as *Armillaria mellea* sensu lato (3). Using basidiocarp and cultural characteristics of the biological species identified by Bérubé and Dessureault (5), we have identified the fungus collected from almond and peach as *Armillaria mellea* sensu stricto (formerly identified as biological species VI). Different isolates of the fungus have been found to exhibit various degrees of virulence on peaches (49) and potted plants (35). Further, the fungus appears to have an extensive host range (36). In Michigan, however, Proffer et al (33) used mating-type studies with haploid and diploid isolates to identify three biological species occurring in cherry orchards: *A. mellea* (group VI), *A. ostoyae* (group I), and *A. calvescens* (group III).

**Papery bark of apple.** This disease is caused by *T. versicolor* and is characterized by a white rot of wood, gummosis at lesions, papery bark (or phellem) that peels away from the trunk, dieback (14,27,28), and in some cases death of young trees (10). In California, we have noticed similar symptoms seemingly caused by this fungus on other fruit trees, including peach and apricot. On apple trees that we surveyed, the disease was found on the rootstock after "top-working" with scionwood. The fungus invades living sapwood throughout the year, aggressively invading tissue in the summer and causing extensive decay (26). Papery bark has been considered a low-sugar disease, since wood is more susceptible to decay when free sugars are not available (11). Other symptoms that occur with papery bark and other, but not all, wood decay diseases are black zones or dark lines within affected wood (14,27,28). These structures are not clearly understood for all types of decay but have been described as host reactions containing oxidized polyphenols and gums (28), mycelial interactions between genetically distinct isolates of the same species, or interactions between different xylophilic fungal species (37). In California, these symptoms have also been observed within wood of fruit trees decayed by species of *Ganoderma* and *Trametes hirsuta*.

**Silver leaf.** *Chondrostereum purpureum* is a wood decay fungus that causes silver leaf of fruit and nut trees. The disease has been reported on apple in Washington (45) and in Minnesota (39). Although the fungus is rarely found in California, Chaney et al (9) isolated it and identified the disease in an 8-year-

old orchard of cling peach in northern California. Infected wood becomes dark brown from accumulated material in the vessels. The fungus releases toxins that are translocated to leaves, causing separation of the upper epidermis from the palisade layer (6,31). The translucent epidermis appears silvery, thus giving the disease its common name. Severely affected leaves become necrotic and fall.

**Root, crown, and heart rots.** General symptoms, such as dieback, early decline, or short-life, have been associated with both management practices and wood-decay fungi. In the Pacific Coast states, Zeller (50) considered wood decay, caused primarily by *F. cajanderi*, to be one of the major contributing factors in early senescence of peach and prune. The fungus was commonly associated with pruning wounds  $\geq 5$  cm in diameter and was isolated from 73% of the 1,212 trees with heart rot. Wilting of leaves on affected branches (a prominent symptom) was attributed to tyloses, stimulated by decay, blocking water movement in xylem.

In California, *Oxyporus latemarginatus* causes a root and crown rot of fruit and nut trees. This fungus, shown to be pathogenic on cherry trees, invaded healthy sapwood and killed mature, 16-year-old trees within 2 years after inoculation (12). The disease had been associated with both overirrigated or water-stressed trees. We have also made this observation with cherry and other fruit and nut trees, as well as with trees lacking any apparent stress (Fig. 3 and Table 4).

In many cases, decline of orchard trees associated with wood decay has not been attributed to any one species but rather to a complex of decay fungi that are usually found. In Minnesota, Eide and Christensen (18) found a number of wood-decay fungi on apple trees, while Bergdahl and French (4) indicated that *Irpex lacteus*, *Trametes versicolor*, and *Schizophyllum commune* could cause decline in 3-year-old apple trees located on less than optimal sites for growth. Decline of peach trees in South Australia has been associated with pruning of large scaffold branches that led to unhealed cankers and wood decay caused by *T. ochracea* and *Stereum strigosozonatum* (Schw.) G.H. Cunn. (15).

### Control Practices

Control of wood decay in living trees traditionally involves cultural practices that prevent stress and promote adequate tree vigor for rapid wound healing. Control practices include appropriate site and cultivar selection, proper irrigation and fertilization programs, and orchard management practices that minimize tree wounding. Chemical and mechanical methods of weed control can injure roots and lower trunks, and mechanical harvesters may cause substantial trunk damage when misused. Large pruning

wounds are also common points of infection for wood-decay fungi. Therefore, when possible, pruning should be done when branches are small, and large living branches should be removed with cuts close to the supporting branch or trunk. Cuts that leave stubs or horizontal surfaces that allow water accumulation should be avoided (14,47). *Trametes versicolor* may infect old wounds (47), but aging of wounds before inoculation reduced the growth of this fungus regardless of the season (26). In vitro wood-decay studies indicated that discolored wood formed in response to wounding was more resistant to decay by *T. versicolor* than normal sapwood (28).

Pruning should be done when inoculum is low or absent. Unfortunately, wood-decay fungi produce basidiocarps at different times of the year depending on the species, temperature, and moisture conditions. In California, where moisture is not limiting in irrigated orchards, some species can produce basidiocarps and basidiospores in all seasons of the year, although not continuously. Wood-decay fungi observed periodically sporulating year-round include species of *Ganoderma* (e.g., *G. brownii*) and *Trametes* (e.g., *T. versicolor*). Other species, such as *Armillaria mellea*, fruit only during the cooler, winter months, providing moisture is present. After basidiocarps have formed, relative humidity and temperature also are limiting factors for sporulation (30).

In California, some growers have used copper-based tree paints and linseed oil mixtures to protect wounds. In laboratory studies, asphalt paints were not fungitoxic and did not protect wood against several wood-decay fungi unless they were amended with copper naphthenate (16) or other fungitoxicants (29). In the field, bituminous compounds did not protect wounds (14,48). Dilley and Covey (14) observed decay in apple trees in Washington affecting both painted and nonpainted wounds. Wound protection depends on complete coverage and maintenance of an intact layer. Although paints may promote callus formation, cracking of the sealant may expose unprotected wood and allow invasion by wood-decay fungi. Polyvinyl acetate, however, was found to provide a flexible, protective layer on apple tree wounds (47). Fungicides have also been used as protectants for control of wood-decay fungi. Several systemic fungicides, particularly triadimenol and captafol, were active in protecting wounds from *T. versicolor* and *C. purpureum* (17, 22,23). Triadimenol has limited registration in some western states for treatment of pruning wounds against decay fungi.

Upon tree death, fumigants such as chloropicrin and methyl bromide have been used to disinfest soil after trees and major roots have been removed and have controlled root rots such as those caused

by species of *Armillaria*. Because complete eradication is rarely achieved, continued localized fumigation may be required. Success of fumigants has been related, in part, to weakening of the pathogen and favoring the fungus *Trichoderma viride*, which is antagonistic to *Armillaria* (32). Filip and Roth (21), using another approach to control *Armillaria*, eradicated the fungus by directly injecting stumps with fumigants.

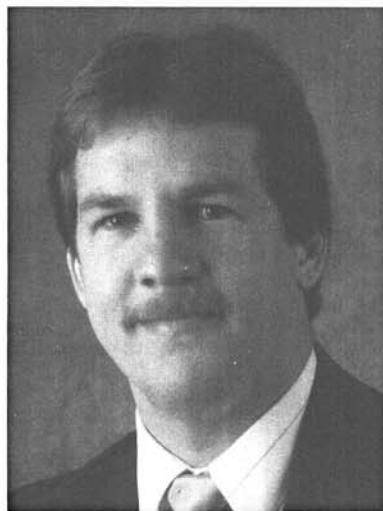
Biological control and breeding for host resistance to wood-decay fungi have also been attempted. Spore suspensions of *Trichoderma viride* have been applied to fresh pruning wounds to control infections by *C. purpureum* (25). Resistant rootstocks of fruit and nut trees selected to control *Armillaria* root rot include: cherry (34); apple; pear; quince; and plum rootstocks for almonds. Cultivars of plum resistant to silver leaf disease have also been identified (24). Another practice, sanitation, has been used for control of wood-decay fungi and includes the removal of dead trees, branches, and other hosts, to reduce the supply of inoculum.

### Conclusion

In California, fruit and nut trees are major, long-term, perennial crops, and their commodities continue to be in high demand. With expanding efforts to increase production, effective management

practices are essential to develop and maintain high-yielding trees over one or two, and sometimes several, decades, depending on the crop. Some wood-decay fungi, e.g., species of *Armillaria*, can cause decline and death of trees within a short time. Many other wood-decay fungi, however, cause chronic diseases that reduce yields, progress steadily as decline of trees over a number of years, and may be difficult to recognize and assess. Although wood decay is influenced by environmental and host factors, tree decline is often attributed solely to environmental stresses, nutritional deficiencies, or obvious pest problems rather than to the pathological consequences of the fungi that induced the problems.

In our study, diverse species of wood-decay fungi were found in orchards surveyed, and these fungi sometimes contributed to extensive wood decay in more than one-third of the trees examined. The pathological outcome of this decay ranged from apparently no effect to decline or death of trees. Perhaps wood-decay fungi interact with stress factors, such as excessive irrigation or extensive pruning, that together contribute to overall tree decline. Although direct effects such as broken branches or tree death can be assessed in yield loss, the effects of wood-decay fungi on yield, life span of trees, and cost-effectiveness



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of short-term crop rotation of trees in commercial production remain to be evaluated. Future research should include recognition of the diseases and their etiology, including pathogenicity tests, epidemiological investigations encompassing yield assessments, and development of management and control practices compatible with orchard culture.

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