Ecology of *Armillaria* spp. in Mixed-Hardwood Forests of California

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ABSTRACT

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Incidence of *Armillaria* root disease and the population structure of associated *Armillaria* spp. was studied in California mixed-hardwood forests. Four 3,000-m² plots, consisting of *Quercus kelloggii*, *Q. agrifolia*, *Lithocarpus densiflorus*, *Arbutus menziesii*, *Umbellularia californica*, and *Pseudotsuga menziesii*, were intensively sampled. Root collars were examined for mycelial fans, decayed wood, and rhizomorphs. From 404 trees (333 living, 71 dead), *Armillaria mellea* and *A. gallica* were recovered and identified from 148 isolates. The most abundant tree species in each plot was the tree species most frequently infected by *A. mellea* or *A. gallica*. The majority of *A. mellea* isolates were recovered from mycelial fans on living trees. Recent mortality due to *A. mellea* was found only in one plot. *A. gallica* was mainly identified from epiphytic rhizomorphs. Only one to three somatic incompatibility groups (SIGs) for each species were found in each plot. Estimated sizes of SIGs varied from the extent of a single root system to the entire width of the plot. Based on our results, both *A. mellea* and *A. gallica* are common in mixed-hardwood forests, yet *A. mellea* appears to be a more aggressive pathogen. *A. gallica* is capable of attacking live hosts, but occurs on living roots more frequently as epiphytic rhizomorphs.

Armillaria mellea (Vahl:Fr.) P. Kumm. is common in most regions of California dominated by agricultural and urban development, such as the Central Valley, the San Francisco Bay area, and Los Angeles (5,10). Hardwood forests, especially oak woodlands and riparian habitat, once occupied many of these areas. The common occurrence of *Armillaria* root disease on hosts planted on sites previously inhabited by hardwoods in California has been known since the disease was first described in the 1880s (6). However, most research has focused on epidemiology and control of *Armillaria* root disease on planted hosts (1,2,4,16,17,26,30).

A. mellea occurs in a variety of hardwood forest types in California, including coastal oak woodland, montane hardwood, mixed-hardwood, valley oak woodland, and valley-foothill riparian (5). These hardwood forests are also frequently inhabited by *A. gallica* Marxmüller & Romagn. Both *Armillaria* spp. appear to be common in California hardwood forests listed above, yet their impact on native hosts as root pathogens has not been determined. One of the most widespread hardwood

forest types in California is mixed-hardwood forest. The objectives of this study were to identify *Armillaria* spp. in mixed-hardwood forests and to gain an understanding of the relationship they have with their native hosts (i.e., their ecology). We determined the spatial distribution of somatic incompatibility groups (SIGs), the incidence of root disease, which *Armillaria* spp. were associated with mortality, and whether or not mortality was associated with the presence of certain host species.

MATERIALS AND METHODS

A total of four plots in mixed-hardwood forests were selected for intensive sampling. Plots were located in Napa (38.51° latitude, -122.51° longitude) and Sonoma (38.61° latitude, -122.99° longitude) counties. Plots were selected based on tree species composition, presence of *Armillaria* spp., and accessibility. The plots consisted of a mixture of tree species characteristic of mixed-hardwood forests, including *Quercus kelloggii* Newb., *Q. agrifolia* Née, *Lithocarpus densiflora* (Hook. & Arn.) Rehder, *Arbutus menziesii* Pursh, *Umbellularia californica* (Hook. & Arn.) Nutt., and *Pseudotsuga menziesii* (Mirb.) Franco. Each plot was approximately 3,000 m² in area (Fig. 1). The two Napa plots were 498 m apart. The two Sonoma plots were 560 m apart. The Napa plots were approximately 44 km from the Sonoma plots.

The position of each tree in all four plots was mapped using a global positioning system (Trimble Corp., Sunnyvale, CA). Position coordinates were differentially corrected. Root collars were excavated by hand to 0.5 m from the base of the tree, and the bark was removed to look for my-

celial fans, decay, and rhizomorphs. Mycelial fans, decay, and rhizomorphs collected from the same tree remained separate throughout the identification process. Detailed observations of host colonization types (i.e., pathogenic, epiphytic, or saprobic) and host condition were made. Pathogenic colonization was characterized by the presence of *Armillaria* mycelial fans underneath the bark or *Armillaria* decay in the sapwood or heartwood of living trees. Epiphytic colonization was characterized by the presence of *Armillaria* rhizomorphs on the surface of the bark at the root collars of living trees, in the absence of mycelial fans or decay. Saprobi colonization was characterized by the presence of mycelial fans, decay, or rhizomorphs on dead trees.

Isolations were made on water agar amended with benomyl 50WP (4 mg/ml) and streptomycin sulfate (100 mg/ml) after autoclaving. Samples were asexually removed in the laboratory from portions of mycelial fans and decayed wood that were previously not exposed. Rhizomorphs were scrubbed with cheesecloth, surface sterilized with 95% ethanol for 10 min, and rinsed in sterile distilled water prior to plating on water agar. Isolation plates were incubated at room temperature in the dark and examined after 5 to 10 days. Isolates were then transferred to 1% malt extract agar with an overlay of sterile cellophane.

Armillaria spp. were identified using a polymerase chain reaction (PCR)-based technique developed by Harrington and Wingfield (9). For most isolates, the first intergenic spacer region (IGS-I) of the rDNA was amplified directly from the mycelium by gently scraping a pipette tip over the surface of the mycelium and dipping it into the PCR vial immediately before starting the reaction. For isolates that would not amplify directly from mycelia, DNA was extracted from the mycelium, collected from on top of the cellophane, using the extraction technique of Cenis (6). Restriction digests of PCR products were then done by adding *AluI* directly to the PCR vial and incubating it in a 37°C water bath for 2 h. Restriction patterns were obtained by running restriction fragments on 3% agarose gels, followed by staining with ethidium-bromide.

Somatic incompatibility tests were done to distinguish genetically distinct individuals within a species at each plot (27). Mycelial plugs of isolates were placed 4 mm apart on Shaw-Roth agar and plates were incubated at room temperature in the dark for 4 weeks. Isolates from the same plot were paired in all possible combinations,

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including self-pairings as controls. Paired isolates that grew together to form a homogenous colony with no dark lines or other barrage zones were considered to be of the same SIG. Once SIGs were identified within plots, pairings were done between plots with isolates representative of each SIG.

RESULTS

From a total of 404 examined trees (333 living, 71 dead), 148 *Armillaria* isolates were successfully cultured from 146 trees (120 living, 26 dead). All isolates were identified as *A. mellea* or *A. gallica*. The *AluI* restriction patterns of the IGS-I rDNA for *A. mellea* (fragment sizes 320 and 155

bp) and *A. gallica* (fragment sizes 399, 240, and 183 bp) corresponded with published patterns (9).

All four plots had similar tree species composition, but tree species varied in relative abundance. The most abundant tree species in each plot was the tree species most frequently infected (Table 1). For example, in Napa plot 1, 38 of the 54 *A. gallica* isolates were recovered from *U. californica*, the most common tree species in Napa plot 1. Incidence of infection generally corresponded with host species abundance, regardless of which *Armillaria* sp. was identified in the plot.

Both Napa plots and Sonoma plot 1 had a similar ratio of living to dead trees (ap-

proximately 4:1). Sonoma plot 2 had a higher ratio of living trees (approximately 9:1). Both *A. mellea* and *A. gallica* were collected from living or dead trees at an equal frequency; living trees did not have a disproportionate number of *A. mellea* or *A. gallica* isolates recovered from them when compared to dead trees. In cases in which either *Armillaria* sp. was identified on more than two trees per plot, pathogenic infections (infections on living trees) were always more common than saprobic decay (a dead tree colonized by either *Armillaria* spp.) and epiphytic infection (rhizomorphs present on the root surface of a living tree).

Armillaria spp. were more common in the two Napa plots than in the two Sonoma

Fig. 1. Distribution of somatic incompatibility groups (SIGs) of *Armillaria mellea* and *A. gallica* in four mixed-hardwood plots: **A**, Napa plot 1; **B**, Napa plot 2; **C**, Sonoma plot 1; and **D**, Sonoma plot 2. SIGs are represented by patterned areas. Trees from which *Armillaria* spp. were identified are represented by the following symbols: ■ = *A. mellea*; ▲ = *A. gallica*; ⊙ = both species. Trees from which no *Armillaria* sp. was identified are represented by solid circles (●).

plots (Table 1). In Napa plot 1, *A. mellea* was recovered from 2 of 89 examined trees and *A. gallica* was recovered from 54 of 89 examined trees. Both *A. mellea* and *A. gallica* were abundant in Napa plot 2; *A. mellea* was recovered from 22 of 76 examined trees, while *A. gallica* was recovered from 30 of 76 examined trees. Both Sonoma plots had fewer infected trees than the Napa plots, even though they had more trees per plot. *A. mellea* was recovered from only 16 of 119 examined trees in Sonoma plot 1. In Sonoma plot 2, *A. gallica* was recovered from 23 trees, while *A. mellea* was recovered from only 1 tree.

A. mellea was identified in all four plots. Recovery of *A. mellea* from mycelial fans or decay collected from the root collars of living trees, indicating pathogenic colonization, accounted for 32 of 41 *A. mellea* isolates (Table 2). The remaining *A. mellea* isolates were recovered from decay collected from dead trees. In Napa plot 1 and Sonoma plot 2, *A. mellea* was identified from a small percentage of trees (Table 2). In Sonoma plot 1, where *A. mellea* was the only species collected, there were only three infected trees showing foliar symptoms of root disease (thin crown with many dead tips). Substantial mortality associated with *A. mellea* was found only in Napa plot 2, where *A. mellea* was recovered from 22 of 76 examined trees. The majority of trees from which *A. mellea* was recovered in Napa plot 2 had pathogenic infections (Table 2). The most concentrated area of dead and symptomatic trees was adjacent to several large stumps that were extensively decayed by *A. mellea*. Root-collar excavation of *P. menziesii* within this disease center revealed mycelial fans and resin-soaked xylem above the lesions.

A. gallica was identified in three of four plots. Most *A. gallica* isolates (58 out of 107) were recovered from epiphytic rhizomorphs collected from living trees (Table 2). The remaining collections were found on living or dead trees. Decayed wood and mycelial fans were collected from the root collars of some dead trunks on multi-trunked tree species such as *U. californica*. These were categorized as pathogenic colonization because they were found on living trees. It is not known whether the dead trunks were killed by *A. gallica* or were colonized by the fungus saprobially after they died from something other than root disease.

We recovered both *A. mellea* and *A. gallica* from three *P. menziesii* stumps in Napa plot 2. In all three cases, *A. mellea* was recovered from decayed wood and mycelial fans found underneath the bark, while *A. gallica* was recovered from epiphytic rhizomorphs collected on the surface of the root bark.

Of the 41 isolates of *A. mellea* and 107 isolates of *A. gallica*, we identified six and four SIGs, respectively. The SIGs, with respect to the trees they were collected

from in each plot, are shown in Figure 1A–D. Few SIGs were found in each plot (Fig. 1). In most cases, both *Armillaria* spp. were represented by a single SIG per plot. The extent of each SIG was estimated based on the locations of trees from which each was collected. Sizes varied from a single root system to the entire width of the plot. The largest *A. mellea* SIG was 33 m wide, based on the distance between the two most distant collections in Sonoma plot 1 (Fig. 1C). The other five *A. mellea* SIGs had widths between 3 and 16 m. The largest *A. gallica* SIG was 47 m wide (in Napa plot 1), while the remaining three were approximately 30 m wide. None of the plots shared SIGs of either *Armillaria* spp.

Napa plot 2 was the only site with symptomatic trees that had pathogenic infections

of *A. mellea*. Three SIGs of *A. mellea* were identified in this center (Fig. 1B). Their sizes varied from that of a single root system (approximately 3 m wide) to 16 m wide. Napa plot 2 was almost completely covered by a single SIG of *A. gallica* (Fig. 1B). In Sonoma plot 2, all *A. gallica* isolates represented one SIG (Fig. 1D). In Napa plot 1, there were two SIGs that, together, covered the extent of the plot (Fig. 1A).

DISCUSSION

The presence of *A. mellea* and *A. gallica* on all common tree species in the mixed-hardwood forest plots we surveyed corresponds with results from a broader survey of *Armillaria* spp. in California forest types (5). *A. mellea* is the most common

Table 1. Tree species composition of mixed-hardwood forest plots and number of trees colonized by *Armillaria* spp.

Plot, species	No. of trees ^a	No. of trees from which each species was recovered	
		<i>A. mellea</i>	<i>A. gallica</i>
Napa plot 1			
<i>Acer macrophyllum</i> (big-leaf maple)	2	0	1
<i>Arbutus menziesii</i> (madrone)	6	0	5
<i>Lithocarpus densiflorus</i> (tanoak)	1	0	0
<i>Pseudotsuga menziesii</i> (Douglas-fir)	1	0	1
<i>Quercus agrifolia</i> (coast live oak)	15	1	7
<i>Quercus kelloggii</i> (California black oak)	6	1	2
<i>Umbellularia californica</i> (California laurel)	58	0	38
Napa plot 2			
<i>Arbutus menziesii</i>	10	0	7
<i>Lithocarpus densiflorus</i>	11	1	6
<i>Pseudotsuga menziesii</i>	35	17	9
<i>Quercus agrifolia</i>	3	0	2
<i>Quercus kelloggii</i>	8	3	2
<i>Umbellularia californica</i>	9	1	4
Sonoma plot 1			
<i>Arbutus menziesii</i>	37	4	0
<i>Lithocarpus densiflorus</i>	8	1	0
<i>Pseudotsuga menziesii</i>	8	1	0
<i>Quercus agrifolia</i>	64	10	0
<i>Umbellularia californica</i>	2	0	0
Sonoma plot 2			
<i>Arbutus menziesii</i>	56	0	9
<i>Lithocarpus densiflorus</i>	2	0	1
<i>Pseudotsuga menziesii</i>	1	0	0
<i>Quercus agrifolia</i>	48	1	11
<i>Umbellularia californica</i>	13	0	2

^a Includes living and dead trees examined.

Table 2. Host colonization types of two *Armillaria* spp. on four mixed-hardwood forest plots

Species, type ^b	Plot (no. of trees) ^a			
	Napa 1 (n = 56)	Napa 2 (n = 52)	Sonoma 1 (n = 16)	Sonoma 2 (n = 24)
<i>A. mellea</i>				
Pathogenic	2	14	15	1
Epiphytic	0	0	0	0
Saprobic	0	8	1	0
<i>A. gallica</i>				
Pathogenic	23	7	0	0
Epiphytic	19	18	0	21
Saprobic	12	5	0	2
Total trees examined	89	76	119	120

^a Number in parenthesis = total number of trees from which *Armillaria* spp. were identified.

^b Colonization types were identified as follows: pathogenic from mycelial fans or decayed wood from living hosts; epiphytic from rhizomorphs on living hosts (no mycelial fans or decayed wood were present); and saprobic from mycelial fans or decayed wood from dead hosts.

Armillaria spp. in California. Its range extends across the entire state, excluding deserts in southeastern California, and occupies a variety of native forest types, including those dominated by both hardwoods and conifers. The range of *A. gallica* overlaps almost completely with that of *A. mellea*, excluding the Central Valley, but including higher-elevation forest types such as Sierran mixed conifer (elevation 770 to 3,076 m). Although it has been reported elsewhere in western North America (14,31), we have not identified *A. ostoyae* in California.

Many observations documented in past research on *A. mellea* and *A. gallica* in hardwood forests of England (8,20–23) correspond with ours made in California. *A. mellea* appears to be a more aggressive pathogen, based on its frequency of attacking apparently vigorous trees (20). In contrast, *A. gallica* infections occur more often on suppressed trees, suggesting that this species is a weaker pathogen. Rishbeth (20) found that *A. gallica* was consistently associated with butt-rot of living hardwoods.

A. mellea is one of the most aggressive *Armillaria* spp. in the Northern Hemisphere (20). Although *A. mellea* infection is often associated with obvious foliar symptoms of root disease and mortality in planted hosts in California (5), this is not the case for native hosts in mixed-hardwood forests. Decreased severity of root disease is likely due to small lesion size on the infected root collars we observed. Possible reasons for restricted lesion size on native hosts include low inoculum potential and unfavorable soil conditions for *Armillaria* spp. growth.

Even though *A. mellea* was identified in all four plots, only one plot (Napa plot 2) contained an active disease center, likely due to the high amount of inoculum created by logging. It was the only plot with stumps and the only plot with substantial mortality. Although there were only three stumps, they were each approximately 0.6 m in diameter. It is likely that these stumps became prime substrate for *A. mellea* colonization after the trees were cut and now serve as substantial inoculum sources. Not surprisingly, trees showing the most severe symptoms of root disease in Napa plot 2 were directly adjacent to stumps. The relationship between logging operations, specifically thinning, and *Armillaria* root disease is well documented (12). Healthy trees restrict *A. mellea* infections to small root lesions when living, but the fungus can colonize entire woody root systems after trees are cut. It is likely that root infection in Napa plot 2 existed prior to logging, but was restricted to small lesions, and after the trees were cut, *A. mellea* fully colonized their dying root systems and built up enough inoculum to attack healthy, neighboring trees, creating a disease center.

Armillaria disease centers are usually

occupied by one to several SIGs (27). We identified three SIGs of *A. mellea* in a single disease center in Napa plot 2. *Armillaria* infections resulting from basidiospore colonization of stumps have been implicated by Rishbeth (23) and Worrall (32) as an explanation for the presence of small, scattered SIGs. Size of SIGs, assuming they represent actual genets, is not indicative of age (11). Small genets may represent pieces of large genets fragmented by disturbances such as fire, logging, or competition. Since we have no available data on stand history, it is impossible to determine whether or not existing SIGs were present prior to logging.

Unlike our *A. gallica* collections, none of the *A. mellea* collections from living hosts were cultured from rhizomorphs. All *A. mellea* infections were associated with mycelial fans with underlying root collar lesions or decay. Rhizomorphs are frequently found on orchard trees and ornamentals with *A. mellea* infections (26). The apparent lack of *A. mellea* rhizomorphs from our plots is consistent with past results of a statewide survey of California forest types for *Armillaria* spp. (3). Possible reasons for their absence include limited capacity for rhizomorph production and lack of a suitable soil environment. *A. mellea* is known to produce short rhizomorphs, in comparison to more saprobic species such as *A. gallica* (23). Limited rhizomorph growth of *A. luteobubalina* Watling & Kile in Western Australia was attributed to unsuitable soil conditions (15). Despite the absence of *A. mellea* rhizomorphs, it seems that vegetative growth is responsible for the observed distributions of *A. mellea* SIGs in Sonoma plot 2 and Napa plot 1, assuming that each SIG represents a single genet.

In all four plots, *A. gallica* was collected from living hosts more frequently than from dead hosts. On living hosts, *A. gallica* was mainly in the form of epiphytic rhizomorphs. *A. gallica* is known to produce abundant rhizomorph networks on the roots of living trees that, presumably, provide competitive advantage in pathogenically colonizing the host if it becomes stressed and saprobially colonizing the host once it dies (20). Most authors consider *A. gallica* a weak pathogen that preferentially attacks stressed trees (13,19). *A. gallica* was identified from butt rot in the trunks of living *U. californica* and *L. densiflorus* that did not show signs or symptoms of other pathogens or insect pests. These results suggest that *A. gallica* may be a primary pathogen in mixed-hardwood forests of California, although it may only infrequently cause mortality.

Past research on spatial distribution of SIGs suggests that genets of *A. mellea* are usually small, in comparison to most *Armillaria* spp. (18). Our results and other recent research found that they can reach a width of at least 100 m (7,26). It is likely

that the SIGs we identified, especially those of *A. gallica*, extend past the plot boundaries. *A. gallica* is the best known of all *Armillaria* spp. for its large genets in forest habitats (28). Considering the large distance between the plots, it is not surprising that SIGs of both *A. mellea* and *A. gallica* were unique to each plot.

Genetically distinct genets may exist within the SIGs we identified. Somatic incompatibility tests do not always distinguish closely related individuals (11,13). However, more recent research on *Armillaria* spp. population structure shows that somatic incompatibility tests and molecular markers often give the same results; isolates within a SIG are rarely representative of different genets (24,25,29). We did not use molecular markers to compare isolates within and among SIGs; therefore, it is impossible to know their relatedness. Based on their spatial distributions and presence on neighboring trees, it is likely that the SIGs in the four plots represent distinct genets.

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