SPATIAL PATTERNS OF *ARMILLARIA* POPULATIONS IN THE WALKER BRANCH WATERSHED THROUGHFALL DISPLACEMENT EXPERIMENT, TENNESSEE, USA.

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Abstract: Species in the white-rot fungal genus *Armillaria* vary in parasitic aggressiveness as root and butt rot pathogens of trees. *Armillaria* genets (individuals) were mapped in the Throughfall Displacement Experiment (TDE) using mushrooms and rhizomorphs collected in 1994 and 1995. Initiated in July 1993, the TDE consists of three 80 x 80 m plots. The "ambient" plot receives natural precipitation; the "wet" plot also receives 33% of throughfall from the "dry" plot (which also had lower pre-treatment mean soil water content). Isolates from 36 rhizomorph and 48 mushroom collections of *A. gallica* Marxmüller & Romagnesi, and from 21 mushroom collections of *A. mellea* (Vahl:Fr.) Kummer, represent 5 *A. gallica* genets and 18 *A. mellea* genets. Only 3 of the 84 *A. gallica* collections, and 1 of the 21 *A. mellea* collections, were obtained from the dry plot. The two largest *A. gallica* genets occupy most of the wet and ambient plots, overlapping very little. Most of the *A. mellea* genets are represented by single collections throughout the wet and ambient plots. At least nine *A. mellea* genets occur within the boundaries of the two largest *A. gallica* genets. *Armillaria* species interactions with each other, with forest community vegetation, and with the TDE treatments are hypothesized.

INTRODUCTION

As atmospheric levels of greenhouse gases increase, climate modelers predict a rise in average global temperature and associated changes in precipitation patterns. Although greater climatic instability, including more frequent summer droughts, has been predicted (Kraüchi 1993, Rind and others 1990), there is some uncertainty whether growing season precipitation within the central hardwood forest region will increase or decrease. To test the responses of a central hardwood forest to both reduced and increased growing season precipitation, the Throughfall Displacement Experiment (TDE) was established on the Walker Branch Watershed, near Oak Ridge, Tennessee (Hanson and others 1995). Pre-treatment soil moisture observations were initiated in April 1992, and treatments were imposed in mid-summer 1993. Treatments consist of transferring one-third of throughfall precipitation from the "dry" plot, across the "ambient" plot, to the "wet" plot. It was anticipated that the dry treatment would reduce soil moisture to approximately the same extent as the driest season of the 1980's drought (Cook and others 1988). Studies of *Armillaria* populations on the TDE plots were initiated in 1994 to evaluate TDE treatment effects on the behavior of this ubiquitous genus of root parasitic wood decay fungi. *Armillaria* spp. (Tricholomataceae, Agaricales) often serve as pivotal contributing factors in stress-mediated forest declines (Manion and Lachance 1992, Wargo 1984). Both excess moisture and drought during the growing season have been implicated as factors inciting Armillaria root disease (e.g., Lonsdale and Gibbs 1996, Wargo and Harrington 1991).

Armillaria (Fr.:Fr.) Staude is a genus of agaric fungi which obtain energy primarily through the white-rot mode of wood decay, metabolizing both cellulose and lignin in the process (Garraway and others 1991). Wood decay is accomplished by the exploitive activity of a highly branched network (mycelium) of microscopic filamentous tubes (hyphae). A portion of the energy derived from wood decay is spent on sexual reproduction. *Armillaria* spp. reproduce by the production of airborne spores on the gills of basidiomata (mushrooms). Each spore which successfully germinates and colonizes a suitable woody substrate (foodbase) generally mates with another sexually compatible germling to form a genetically unique individual (genet), which may establish itself in the landscape as an agent of wood decomposition. *Armillaria* spp. do not produce asexual spores. Instead, genets spread through the forest

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floor by the foraging growth of exploratory organs called rhizomorphs, which are branching networks of cord-like hyphal aggregates. Because most of the resources required to fuel rhizomorph growth are provided by decay of the source foodbase, the aggressiveness of *Armillaria* activity is directly related to the distribution and abundance of woody foodbases fueling rhizomorph growth (Garrett 1956). When a rhizomorph encounters an appropriate foodbase, it penetrates the bark and differentiates back into a mycelium. Thus, a single genet has the potential to occupy numerous foodbases simultaneously, and to maintain physical continuity indefinitely within the area of forest floor it occupies. Dead or severely stressed roots of living trees may be colonized in this manner, and live roots may have their resistance tested repeatedly by rhizomorphs. Established genets appear to have a preemptive advantage over invading conspecific genets in acquiring foodbase resources which become available within their boundaries. As a result, it appears that survival of new genets is very poor within the bounds of established genets of the same species (Smith and others 1992, 1994). Therefore, genet maps of a single *Armillaria* sp. often form a mosaic of non-overlapping pieces of various sizes. Perhaps due to differences in host specialization and virulence, genet mosaics of different *Armillaria* spp. often occupy the same area (e.g., Anderson and Kohn 1995, Kile and others 1991, Rizzo and Harrington 1993). *Armillaria* spp. vary in their relative aggressiveness toward different kinds of trees, and different genets of the same *Armillaria* sp. often differ in aggressiveness toward their preferred host species (Omdal and others 1995). A loose relationship has been noted between the rhizomorph growth characteristics of different *Armillaria* spp. and their relative ability to cause root disease (Morrison 1989). Thus, *A. gallica*, a prolific producer of rhizomorphs capable of establishing very large genets, is only very weakly pathogenic, whereas *A. mellea*, producing smaller rhizomorph systems and genets, is much more pathogenic (e.g., Gregory and others 1991, Rishbeth 1991).

Our immediate study objectives were to identify to species all *Armillaria* genets occupying the TDE plots, and to determine their spatial distributions with respect to each other and the TDE design. Long-term objectives are: to (1) determine the influences of TDE treatments on wood decay, rhizomorph initiation and growth, and fruiting by *A. gallica* and *A. mellea*, (2) determine the ecology of competition between genets of *A. gallica* and *A. mellea* as affected by the TDE treatments, and (3) evaluate the epidemiology of Armillaria root disease on the TDE plots.

METHODS

Site Description

The Throughfall Displacement Experiment (TDE) is located just below the top of a south-facing slope (approximately 30%) of the Walker Branch Watershed (35°58' N latitude, 84°17' W longitude) near Oak Ridge, Tennessee. Mean annual precipitation and temperature are 140 cm and 13.3° C, respectively (Hanson and others 1995). Soils at the TDE site are primarily typic Paleudults: acidic (pH 3.5-4.6), cherty, infertile, permeable, approximately 30 m deep overlying dolomitic bedrock (Hanson and others 1995). Tree cover is dominated by *Quercus prinus* L., *Q. alba* L., *Nyssa sylvatica* Marsh. and *Acer rubrum* L. (Table 1, raw data provided by P. J. Hanson, Oak Ridge National Laboratory, Environmental Sciences Division, Oak Ridge, TN).

Study Design

The TDE. The TDE site is divided into three contiguous 80 x 80 m treatment plots (designated dry, ambient, and wet, from east to west) along the upper slope of the watershed. Each plot is subdivided into 100 subplots for sampling purposes. Precipitation throughfall reaching the forest floor is manipulated by a system of suspended subcanopy troughs in the dry plot which intercept approximately 33% of canopy throughfall, coupled to a system of pipes which transfer the intercepted throughfall by gravity flow across the ambient plot and distribute it uniformly onto the wet plot (Hanson and others 1995). Soil moisture in the upper 35 cm is monitored by time domain reflectometry (TDR) at 310 sample locations across the TDE site. Soil matric potentials are estimated from the TDR data using moisture retention curves generated for the TDE site soils. Pre-treatment evaluations of seasonal soil water content indicated significant spatial patterns: soil water content decreased with increasing elevation and was lower in the eastern one-third of the site than in the remaining two-thirds. Because these spatial patterns were seasonally consistent, they have been captured in a covariance matrix which permits analysis of the effectiveness with which the TDE influences soil water contents of the wet and dry treatment plots with respect to the ambient plot (Hanson and others 1995).

Table 1. Characteristics of the tree cover (stems >10 cm dbh) on the Walker Branch Watershed Throughfall Displacement Experiment site as of May 1991[1].

	Basal Area ($m^2 \cdot ha^{-1}$)			Stems ($n \cdot ha^{-1}$)		
Species[2]	Wet	Ambient	Dry	Wet	Ambient	Dry
Quercus prinus L.	5.3	3.3	8.3	56.2	25.0	68.8
Quercus alba L.	6.4	4.7	2.0	53.1	64.0	21.9
Nyssa sylvatica Marsh.	1.9	3.8	2.9	51.6	118.8	95.3
Acer rubrum L.	2.4	2.6	2.5	68.8	53.1	65.6
other *Quercus* spp.	2.2	1.5	1.7	20.3	14.1	12.5
Liriodendron tulipifera L.	1.3	1.4	2.3	14.1	17.2	31.2
Oxydendrum arboreum (L.) D.C.	0.5	1.0	1.0	20.3	50.0	29.6
Acer saccharum Marsh.	0.4	1.0	0.3	7.8	9.3	6.3
Carya spp.	0.6	0.3	0.4	7.8	3.1	3.1
Cornus florida L.	0.0	0.3	0.3	0.0	18.8	20.3
Prunus serotina Ehrh.	0.1	0.1	0.1	3.1	6.3	6.3
conifers (*Pinus, Juniperus*)	0.0	0.3	0.1	0.0	3.1	7.8

[1]Raw data provided by P.J. Hanson, Oak Ridge National Laboratory, Environmental Sciences Division, Oak Ridge, TN.
[2]Trees >10 cm dbh on the experimental site represent 18 species; nine of these species were grouped into three categories for representation in this table.

Armillaria Population Studies. The forest floor surface in each TDE subplot was repeatedly searched during the *Armillaria* fruiting seasons (mid-September through early-November) of both 1994 and 1995 for *Armillaria* basidiomata and for rhizomorphs colonizing woody debris. All collections were mapped. *Armillaria* isolates were identified to genet based on vegetative compatibility tests among the collected field isolates (Adams 1974, Guillaumin and others 1996, Smith and others 1994). Vegetative compatibility was determined through confrontational pairings of isolates on agar-solidified (2% w/v) malt extract (3% w/v) growth medium. Pairings were duplicated for confirmation of results. Isolates belonging to the same genet are vegetatively compatible and grow together freely, whereas isolates representing different genets (regardless of species) are vegetatively incompatible and form a visible reaction at close proximity. A diploid field isolate representing each *Armillaria* genet was then used to identify that genet to species in mating tests with voucher single-basidiospore (haploid) isolates of *Armillaria* spp. (Korhonen 1978, Rizzo and Harrington 1992). The voucher isolates used in these matings were verified and supplied to the senior author by J. B. Anderson (Department of Botany, Erindale College, University of Toronto).

A map showing approximate locations of *Armillaria* genets for the TDE site was produced, in which each genet is represented as a polygon containing all collection points for that genet and bounded by straight line segments which connect collection points. We have represented each genet as a spatially continuous individual, recognizing that individual genets may repeatedly fragment and rejoin depending on conditions of forest health perceived by the fungi as periods of famine or feast (Anderson and Kohn 1995; Garrett 1956; Rayner 1991; Smith and others 1992, 1994).

Statistical Analysis

For each *Armillaria* species, we tested the null hypothesis that the numbers of field isolates collected in the three TDE treatment plots were not significantly different from expected values ($\alpha = .05$). A chi-square test of a 3 X 1 contingency table (Sokal and Rohlf 1995) was used to test this hypothesis for each species. For each species, the expected number of isolates collected from each plot was one-third of the total number of isolates collected from all three plots.

RESULTS

Covariate analyses of soil moisture data indicate that the TDE accomplishes both significant drying of the "dry" plot and significant wetting of the "wet" plot during both relatively dry and wet growing seasons (Hanson and others 1995). All *Armillaria* isolate collections were made from basidiomata and rhizomorphs associated with woody debris on the forest floor. Isolates from 36 rhizomorph and 48 basidioma collections of *A. gallica*, and from 21 basidioma collections of *A. mellea*, represent 5 *A. gallica* genets and 18 *A. mellea* genets. Basidiomata of *A. gallica* were collected between 13 October and 2 November 1994; basidiomata of both species were collected on 11 October 1995. While rhizomorph collection is not seasonally limited, most rhizomorph collections were also made in the late autumn.

Three points stand out from inspection of the *Armillaria* field isolate map (Figure 1). First, genets of *A. gallica* achieve much greater size than do genets of *A. mellea*, probably due to *A. gallica*'s greater production of rhizomorphs (see Redfern and Filip 1991). In this regard, we note that all rhizomorph collections from the TDE plots belonged to *A. gallica* genets. The two largest *A. gallica* genets were represented by isolates collected from 9 and 46 subplots, respectively, and appear to occupy approximately 0.33 ha and 0.54 ha, respectively. Fifteen of the 18 *A. mellea* genets were recovered from only one subplot (0.0064 ha) each; only three *A. mellea* genets were recovered from two adjacent TDE subplots (Figures 1 and 2).

Second, genets of *A. gallica* appear to represent continuous and territorial individuals, with little tendency to overlap one another. The large size of *A. gallica* genets "a" and "b" may explain the smaller number of *A. gallica* genets detected compared with *A. mellea*. While genets of *A. mellea* in the TDE plots are apparently too small to evaluate their territoriality, 11 of the 18 *A. mellea* genets appear to occur within the bounds of the two largest *A. gallica* genets.

Third, surprisingly few collections of either *Armillaria* species were made in the dry plot, compared with either the wet or ambient plots. The two largest *A. gallica* genets occupy most of the wet and ambient plots. Only one genet of each species, represented by 3 of the 84 *A. gallica* collections and 1 of the 21 *A. mellea* collections, was detected in the dry plot. For both *A. mellea* and *A. gallica*, the distributions of isolates among the three TDE plots differed significantly from expectation (Table 2). For both species, more collections than expected were made in the ambient plot, and fewer collections than expected were made in the dry plot.

DISCUSSION

It is most appropriate to think of *Armillaria* populations as consisting of typically territorial, long-lived, stable genets of various sizes. This requires a conceptual adjustment for many forest scientists, since (superficially) genets are only apparent as scattered, seasonal, ephemeral, sporadically produced clusters of mid-size basidiomata (Watling 1995).

The spatial distributions and ecological attributes of *Armillaria* spp. genets in a forest community have important implications for forest community responses to perturbations ranging from silvicultural operations to climate change. Each *Armillaria* genet exercises ecological influence through its unique genetic potential for woody resource foraging, wood decomposition and nutrient recycling, and root parasitism, as mediated by environmental constraints on the expression of these potentials. Without supplemental controlled experimentation, it is difficult to establish (e.g., Bruhn and others 1994, 1996) whether the differences observed in behavior of neighboring

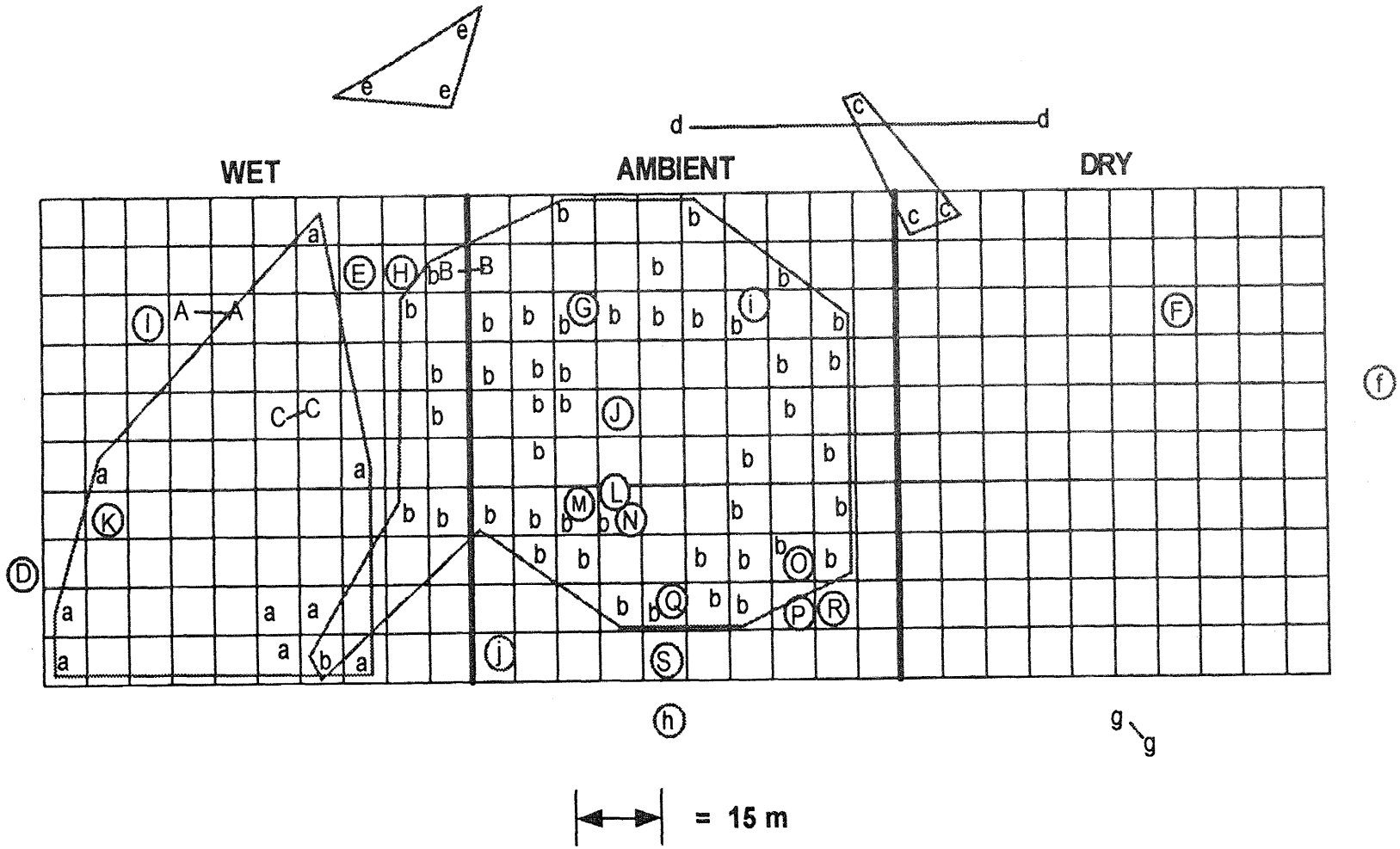

Figure. 1. Spatial distribution of *Armillaria* genets in the TDE plots. Each collection point is marked with a letter; lower-case letters indicate *A. gallica* isolates, upper-case letters indicate *A. mellea* isolates. Isolates belonging to the same genet share the same upper- or lower-case letter. Approximate boundaries of each genet are indicated.

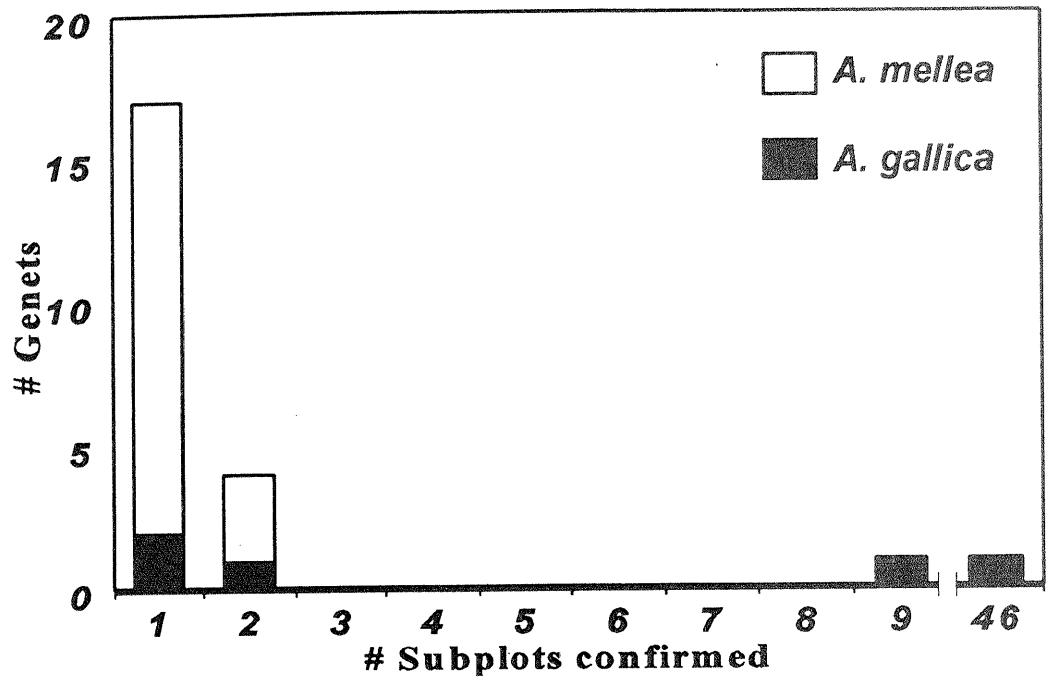

Figure 2. Relative sizes of *A. gallica* and *A. mellea* genets occupying the TDE plots, expressed as the number of genets of each species recovered from different numbers of subplots.

Table 2. Numbers of *Armillaria gallica* and *A. mellea* field isolates collected from the three TDE plots (for 1994 and 1995 combined), and the associated Pearson statistic (X^2 for goodness of fit) values. The tabular value of $\chi^2_{.05[2]}$ is 5.991.

		TDE plot				
		Wet	Ambient	Dry	Total	χ^2
A. gallica	Observed	16	65	3	84	76.4
A. mellea	Observed	9	11	1	21	8.0

Armillaria genets are due to differences among those genets' genetic potentials (e.g., Omdal and others 1995) or to limitations of the local environment in which each genet functions (such as soil structure, distribution of suitable foodbase resources, interactions with competitors, etc.). Because *Armillaria* genets are fundamentally territorial, continuously distributed in the forest floor, and long-lived, they exercise their ecological influences in discrete portions of the forest landscape over time frames of centuries or even millennia (e.g., Anderson and others 1979, Shaw and Roth 1976, Smith and others 1992). In this way, the spatial pattern of *Armillaria* genets represents one component of a forest landscape's genetic "memory" of how to respond to change, thus helping to determine long-term forest community structure. As a result, the spatial pattern of *Armillaria* genets even influences wildlife populations through effects on vegetation structure.

Until more work is done, we can only speculate on the interactions occurring in the forest floor between *Armillaria* genets of the same or different species. Territorial behavior of con-specific *Armillaria* genets coupled with the apparent overlap of genets of different species has been noted previously (e.g., Kile and others 1991; Rizzo and Harrington 1993; Smith and others 1992, 1994). We assume that the unique genetic potential of each *Armillaria* genet is expressed exclusively within that genet's boundary, as appeared to be the case for *A. ostoyae* (Romagnesi) Herink genets in red pine plantations (Bruhn and others 1994, 1996). When genets of certain *Armillaria* spp. occupy the same landscape, it may be possible as a result of niche overlap (see Leibold 1995) for genets of the different species to influence each other's behavior in areas of genet contact or overlap. For example, since both *A. gallica* and *A. mellea* are hardwood-specializing fungi, and *A. gallica* is a much more aggressive producer of rhizomorphs, *A. mellea* may often have less access to the portion of foodbase resources suitable for both species within the boundaries of *A. gallica* genets, resulting in a smaller "realized niche" than elsewhere in the absence of competition from *A. gallica*. Thus, as a result of niche overlap, *A. gallica* might be expected to mitigate the expression of plant root parasitic virulence by a co-occurring *A. mellea* genet. On the other hand, because of their greater virulence as root parasites, it may be possible for *A. mellea* genets to become established within the bounds of *A. gallica* genets by colonizing stressed root systems before they become vulnerable to *A. gallica*. Mohammed and Guillaumin (1989) found that when *A. gallica* and *A. mellea* occupied the same substrate, *A. mellea* inhibited *A. gallica*, without being inhibited in return by *A. gallica*.

Collection of additional isolates (e.g., autumn 1996) will undoubtedly refine genet map precision, and may reveal the existence of previously undetected genets or even species (Watling 1995). We do not expect that *Armillaria* genet boundaries shift rapidly, especially along borders shared with other genets of the same species. Neither do we expect to witness a sudden abundance of *Armillaria* activity in the dry plot. The lower activity of *Armillaria* spp. in the dry plot may be due to: (1) the random failure of any *Armillaria* genets to establish over time in that portion of the landscape, (2) a less suitable distribution or lower volume of foodbase material to support rhizomorph growth and/or fruiting, or (3) long-term effects of the dryer nature of the dry plot. Wood decay and/or rhizomorph growth rate(s) may be reduced in scale and occur deeper in the soil profile on the dry plot than on the ambient and wet plots, thus perhaps also influencing fruiting at the soil surface of the dry plot. *Armillaria* spp. rhizomorph biomass, and rates of *Armillaria* spp. wood decay and rhizomorph production and growth at various depths in the TDE soils would be worth studying.

Regardless of the reasons for the current distributions of *A. gallica* and *A. mellea* genets in the TDE plots, these distributions have the potential to influence the expression of TDE treatment effects in ways that confound the experimental design. Knowledge of *Armillaria* genet distributions and their levels of activity will be important for the interpretation of TDE results. Though impractical for the TDE, substantial treatment replication along with due consideration for plot size would be helpful to statistically absorb the influences of *Armillaria* genets in field experiment designs.

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