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## Allelopathic Dominance by a Tree-Associated Herb in a California Annual Grassland

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**Summary.** In some parts of southern California, *Pholistoma auritum* dominates understory vegetation beneath isolated *Quercus agrifolia* trees occurring in annual grasslands. Pure stands of *P. auritum* are maintained in successive years although adjacent to grasses with easily dispersed propagules. Lack of establishment by the grasses in areas covered with previous season's *P. auritum* litter suggested a germination inhibition mechanism. Laboratory and field tests indicated allelopathic inhibition of grass seedlings by the herb litter. Dominance by an understory species is evaluated in reference to community organization and stability.

### Introduction

Associations of plants which can tolerate the climatic and geological conditions of an area become structurally organized as a result of interactions. In some cases, associations are the result of strong dominance reactions by the most abundant plants and the tolerances of the other associated species. Any plant reaction which can significantly influence environmental conditions may control the distribution and abundance of other species. These reaction may take many forms such as the shade cast by dominant broad-leaved trees in eastern forests (Spurr and Barnes, 1973) or salt deposited by coastal succulents (Vivrette and Muller, 1977). Allelopathy is another reaction which has been shown to underlie dominance in some plant interaction situations (Muller, 1966, 1974; Rice, 1974). This paper describes the allelopathic impact of one species, *Pholistoma auritum* (Lindl.) Lilja (Hydrophyllaceae)<sup>1</sup>, as it relates to the functional dominance by that species of herbaceous vegetation associated with trees in an annual grassland.

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<sup>1</sup> Nomenclature follows Munz (1974)

Isolated live oak trees, *Quercus agrifolia* Neé, often occur in the annual grasslands of southern California, USA. The understory vegetation of these live oaks is structurally and compositionally different from that which characterizes the open annual grasslands. *Pholistoma auritum*, a broad-leaved dicotyledonous plant characteristic of semi-shaded habitats and the annual grass, *Bromus diandrus* Roth, dominate beneath the canopies with similar coverage. The surrounding grasslands are primarily composed of the annual, *Avena fatua* L., with *B. diandrus* of lesser importance. These three species, in different combination, make up over 80% of the annual plant cover in both habitats.

The extensiveness of *P. auritum* beneath some of the *Q. agrifolia* canopies suggested that this herb has a dominance mechanism of great effectiveness. Frequently the stands of this annual forb are distinctly pure or nearly so. This purity reoccurs in consecutive years even though the stands are surrounded by grassland species with easily dispersed propagules. Germination in these areas can be observed in the field after the first winter rains characteristic of southern California's Mediterranean climate. Studies revealed that few seedlings of other species were found in areas covered by *Pholistoma* litter from the previous growing season. The failure of grasses to become established in these areas either naturally from adjacent stands or in test plots with added seeds suggested a germination inhibition mechanism. Such a field pattern apparently resulted from differential germination and not from seedling competition for light, nutrients, or some other resource factor. This implies an allelopathic mechanism; that is, the seeds of the grasses were biochemically inhibited from germinating by the litter of *Pholistoma auritum*.

## Materials and Methods

Seeds of *A. fatua* and *B. diandrus* were field-collected in June, 1974 and stored dry at room temperature. These seeds were used to bioassay the toxicity to germination and growth of either *Pholistoma* litter or a leachate of that litter.

Litter of *Pholistoma* was collected in October, 1973, and September, 1974, before any leaching by rainfall occurred, and was stored dry until used. A leachate of the litter was made by shaking 5 g of litter for 2 h in 100 ml distilled water. Fresh leachate was made from stored litter for each experiment. The germination beds were petri dishes in which filter paper covering cellulose sponges had been soaked in leachate (test) or deionized water (control). Five petri dishes containing 20 seeds each per treatment per trial were sealed with Parafilm® to reduce evaporation. The leachate was further assayed in acid-washed sand and in field soil from beneath *Q. agrifolia* canopies. Into 5 petri dishes containing 20 seeds each per treatment per trial, either 15 ml of leachate (test) or water (control) was added to 75 g of sand in one experiment and to 50 g of field soil in a second.

*Pholistoma* litter was assayed directly by placing 3 g of either untreated litter (test) or litter leached with running deionized water for 48 hr and redried (control) on top of 75 g of soil from the oak canopy areas in 8 cm high storage dishes with Parafilm® and lids. Four replicates of 80 seeds per treatment were used per trial. Seeds were added to the top of the litter in one experiment and beneath in a second. The dishes were sprayed with water sufficient to wet the litter and bring the soil to field capacity. All laboratory tests were performed at 25° C in a dark incubator.

Field toxicity of the litter was bioassayed in two ways. The effect on *B. diandrus* was determined in areas covered by *Pholistoma* litter. One hundred seeds of *B. diandrus* were added to each of 5 pairs of plots, 20 × 50 cm, one of which was untreated (test) and one with the *Pholistoma* litter removed (control). A second type of field bioassay was designed so that all the experimental seeds could be recovered. In this experiment, 25 seeds of both *A. fatua* and *B. diandrus* were

wedged in the mesh of 20.5 × 30 cm strips of fiberglass screen (500 seeds total) and placed in areas with (test) or without (control) *Pholistoma* litter. In both cases the control was oak leaf litter alone. Germination was determined 10–14 days following the first significant winter rain which initiated the growing season.

To test litter penetrability by the grass seeds, five 50 × 80 cm blocks of *Pholistoma* litter were cut out, lifted into hardware cloth baskets (1.27 cm mesh), and replaced in the spaces from which they were removed. Two hundred seeds of each grass species per basket were marked by paint, dropped on the litter in the baskets, and left in the field from late June until either mid-September (1976) or late October (1975) when the baskets were lifted. The number of seeds either in or on the soil or at the bottom of the baskets were counted as penetrating the litter.

## Results and Discussion

The preliminary bioassay which was performed to gauge the affect of the *Pholistoma* litter on germination and growth of the two grasses, *Avena fatua* and *Bromus diandrus*, showed that the leachate provided considerable inhibition of growth of *Avena* (32% of control,  $p < 0.01$ ) and of *Bromus* (36% of control,  $P < 0.01$ ). Thus *Pholistoma* litter contained water-soluble phytotoxic compounds of significant potency. The toxicity was comparable to or more toxic than other demonstrations of inhibition of these species using the same technique (Chou and Muller, 1972; Tinnin and Muller, 1972; Bell and Muller, 1973). Germination was not inhibited in this experiment, however, while in the field germination is rarely observed in areas covered with litter.

In contrast to the leachate, the litter of *Pholistoma auritum* demonstrated a considerable impact on the germination of both *Avena fatua* and *Bromus diandrus* (Table 1). The fresh litter completely inhibited all germination by the grass seeds. In the control, using leached litter as the germination bed, over 92% of the seeds of both species germinated in every experiment. These data supported the allelopathic hypothesis that the lack of grass invasion into areas previously occupied by *Pholistoma* was due to biochemical inhibition of seed germination.

Field plots established to assay the litter toxicity on *B. diandrus* seeds demonstrated significant inhibition of germination by *Pholistoma* litter (Fig. 1). The disadvantage of not knowing the whereabouts of the seeds in the plots before the first winter rains began germination was resolved in a second field bioassay. By entrapping the test seeds in fiberglass screen they could readily be recovered, eliminating uncertainty about their fate. After the first winter rains, these seeds were retrieved and the results indicated that, again, the *Pholistoma* litter significantly inhibited the germination of both grasses (4% and 27% of control) and, therefore, support the hypothesis that the observed field distributional pattern results from an inhibition mechanism (Fig. 2).

**Table 1** Results of laboratory litter bioassay of *Pholistoma auritum* litter. The data are the average % germination with standard error of three experiments

	% Germination	
	Test	Control
<i>Bromus diandrus</i>	0 ± 0*	95.75 ± 1.50
<i>Avena fatua</i>	0 ± 0*	93.25 ± 1.90

\* Results differ significantly from control  
 $P < 0.001$

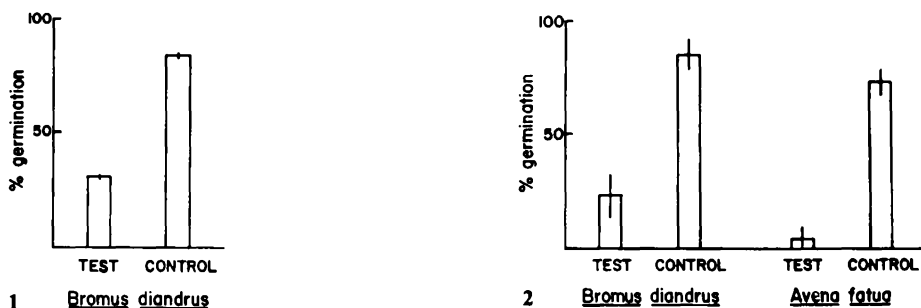


Fig. 1. Results of the field bioassay of *Pholistoma* litter in the plot experiment showing average of 5 plots with standard errors

Fig. 2. Results of the field bioassay of *Pholistoma* litter in the screen litter experiment showing mean % germination with standard errors

Two factors were further investigated to evaluate their potential influence on the extent of inhibition by the litter in the field. Since some germination occurred in *Pholistoma* litter in the field experiments, but none in the laboratory, and leached litter allowed nearly complete germination, one critical factor may be the amount of rain received in the first storms and the degree of leaching experienced by the litter. The amount of rain reaching the ground at any particular point beneath the trees depends upon the geometry of the canopy, the direction of the winds, and the intensity of the storm. Under the canopy, the amount of leaching occurring in particular areas will be highly variable. The field data were obtained following an unusually heavy (140 mm) rain over a 5 day period. Thus the observed germination in the *Pholistoma* litter could have resulted from the seeds being located in heavily rain-leached litter. These field germination data are probably much higher than normal considering that the first rains usually range between 25–75 mm. So while leaching could increase germination of grasses, it would seem unwarranted to assume that usual amounts of rainfall would reduce the impact of *Pholistoma* litter so much as observed here.

A second factor which might compensate for the litter toxicity is the ability of the seeds to penetrate the litter and come into contact with the soil. This was suggested by preliminary bioassays which indicated that seeds in contact with soil had improved germination. Laboratory bioassays were then performed with the seeds positioned between the soil and the litter. Results of these experiments (Fig. 3) indicated that while there was still significant inhibition of germination the degree of inhibition was lessened compared to bioassays with the seeds in the litter (Table 1). These data suggest that the soil by some property can buffer against or compensate for the toxic compounds in the litter. Seeds of *B. diandrus* germinated in sand or field soil wetted with the leachate indicated that the soil compensated for the toxic effects of the leachate (Table 2). For *B. diandrus* growth in sand was only 17.87% of control while in the field soil it was 39.85% of control.

Because the soil negates the effects of the litter to some degree, it was important to know if the seeds of these grasses can penetrate the litter in

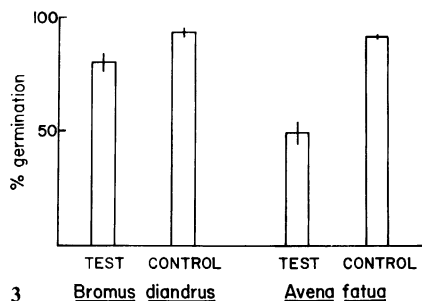


Fig. 3. Results of the laboratory bioassay with the seeds placed between the soil and litter showing mean of 3 experiments with standard errors

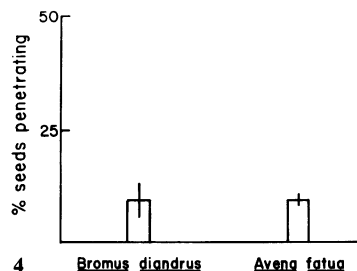


Fig. 4. Results of the field experiment on seed penetration through *Pholistoma* litter showing the mean plus standard errors of experiments of different years with 5 replicates per experiment

Table 2. Results of the laboratory bioassay determining the ability of field soil to compensate for leachate toxicity compared to sand. Data shown are mean root elongation of *Bromus diandrus*

mm mean radicle elongation (48 h)			
Sand		Field soil	
Test	Control	Test	Control
3.68 <sup>a</sup>	20.59	11.93 <sup>a</sup>	29.93
(17.87%)		(39.85%)	

<sup>a</sup> Results are significantly different from the control at  $P < 0.001$

the field and come into contact with the soil. The litter thickness is variable in the field, but in the areas exhibiting relatively pure stands the litter is quite thick, ranging from 4–8 cm. *Pholistoma* litter is in general quite tangled and contains large numbers of retrorse prickles which hold the litter masses together in a single structure. The seeds of both *A. fatua* and *B. diandrus*, however, are well adapted to litter penetration. *Avena* seeds have bent, stout awns which twist and curl in changing humidities driving the seeds through litter. *Bromus diandrus* seeds have long scabrous awns with retrorse barbs which move the seeds through with any movement of the litter. The data from the field experiment indicate, however, that only about 10% of grass seeds are able to penetrate *Pholistoma* litter (Fig. 4). The continuity of the *Pholistoma* litter apparently prevents the many grass seeds from penetrating and consequently entraps them.

In evaluating the overall influence of *Pholistoma auritum*, it seems evident that the plant has an effective allelopathic mechanism in the field. Large areas are dominated by this species in pure or relatively pure stands and, with the summer drought, the plants die back leaving a thick litter layer. The litter has been shown to contain toxic compounds which are water soluble and leachable. Studies are presently under way to identify these compounds. Under both field and laboratory conditions the litter has proved effective in inhibiting the germination and growth of adjacent co-dominating species. Under the appropriate conditions the litter's toxicity can be compensated for either by leaching or by seeds penetrating the litter. However, the data indicate that these factors do not substantially increase germination in the field. Thus although *Pholistoma* is dependent upon the oak tree for its own establishment, *Pholistoma* itself

demonstrates a dominance mechanism which can severely limit the presence and growth of other understory species.

The existence of dominance mechanisms in understory vegetation has not been well studied. Muller (1969) and Whittaker (1971) stated the hypothesis that allelopathy may be important in the formation of intracommunity patterns in forests and, while they referred primarily to the action of dominant canopy members, they proposed that chemical interactions are a widespread phenomenon. *Pteridium aquilinum* (L.) Kuhn (bracken fern) is one species with a strong allelopathic mechanism of dominance (Gliessman and Muller, 1972, 1978) which occurs in a large number of communities sometimes holding forest areas in early stages of recovery following destruction (Gliessman, 1976). In such communities, bracken can be effectively dominant even with relatively very low levels of biomass (Muller, 1974). Considering that such mechanisms may be important in the overall organization and stability of structurally complex vegetation, this implies that functional relationships of communities are even more complex than is presently appreciated in the literature. These kinds of reactions must certainly operate to some degree at every level in a community and consequently participate in the ultimate organization and stability of the vegetation. Such relative stability is self-reinforcing in vegetation exhibiting strong dominance reactions at different structural levels, for invading plant species must not only tolerate the reactions of the dominants but also those of the other species which make up the associated vegetation. The case of *Pholistoma auritum* demonstrates functional dominance at the understory level in natural vegetation.

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