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# Allelopathic effects of *Ceratiola ericoides* (Empetraceae) on germination and survival of six Florida scrub species

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**Abstract** Allelopathic inhibition of germination by Florida scrub plants has been demonstrated in the greenhouse and lab, but not in the field. We studied the allelopathic effects of Florida rosemary (*Ceratiola ericoides*) roots, leaves, and litter leachates on field germination and three-month survival of six Florida scrub species, three habitat generalists (*Lechea deckertii, Palafoxia feayi, and Polygonella robusta*), and three rosemary scrub specialists (*Hypericum cumulicola, Lechea cernua*, and *Polygonella basiramia*). We used AIC and model averaging to evaluate support for a series of non-exclusive hypotheses. Species varied in germination (2.7–24.6%) and survival (39.2–71%) percentages, and in their sensitivity to leachates. Germination of scrub species was most negatively affected by leaf > root > litter leachates, although not all species followed the overall trend. Additional germination suppression by leachate combinations (relative to single leachates) was minimal. Sites did not vary in germination, but seedling survival did differ among sites. This study further documents the negative impact of Florida rosemary leachates on the germination of co-occurring plant species. Allelopathy may be partly responsible for bare sand gaps in Florida rosemary scrub, and therefore be one of the forces structuring Florida rosemary scrub ecosystems.

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## Introduction

In 300 B.C., Theophrastus made the first known observation of allelopathy (Rice 1984). Since then allelopathy, the direct or indirect harmful or stimulatory effect of one plant on another through the production and release of chemical compounds, has been noted as an important form of plant-to-plant interference in natural and agricultural settings (Rice 1984). Allelochemicals, secondary compounds produced by plants, occur in leaves and stems, though roots also have some allelopathic toxins (Harborne 1988). These chemicals are released into the environment by plants through volatilization, root exudation, leaching, and decomposition of plant materials (Rice 1984; Putnam 1985; Putnam and Tang 1986). Allelochemicals can negatively influence neighboring plants by inhibition of the microbial symbionts (Putnam 1985; Einhellig 1995), fungal-root colonization, and free-living nitrogen-fixing bacteria (Einhellig 1995).

There have been several studies in Florida scrub and sandhill documenting the release of allelochemicals and their significant inhibition of germination and radicle growth (Fischer et al. 1989; Williamson 1992b; Fischer et al. 1994), and root and shoot biomass of sandhill grasses (Richard and Williamson

1988; Williamson 1992a). Most of these have been lab experiments, including analysis of ceratiolin, proposed as the primary allelopathic compound released from Florida rosemary, *Ceratiola ericoides* Michx., and its derivative hydrocinnamic acid (Tanrisever et al. 1987; Williamson et al. 1992a). These studies evaluated whether allelochemicals can inhibit the invasion of rosemary scrub by grasses from adjacent sandhill habitat (Richardson and Williamson 1988; Fischer et al. 1989; Williamson et al. 1992b; Fischer 1994). Germination percentage was the primary dependent variable in these studies (Richardson and Williamson 1988; Weidenhamer and Romeo 1989; Williamson et al. 1992a, b; Fischer et al. 1994).

Washes of *Ceratiola ericoides* leaves have been shown to release ceratiolin, a phenolic compound. Phenolic compounds interfere with critical plant processes such as cell division (Einhellig 1995), mineral and nutrient uptake (Einhellig 1995; Chaves and Escudero 1997), stomatal function, water balance, respiration, photosynthesis, protein and chlorophyll synthesis, and phytohormone activity (Einhellig 1995). In aqueous solution, ceratiolin degrades into hydrocinnamic acid when exposed to heat and light (Tanrisever et al. 1987; Obara et al. 1989; Williamson et al. 1992a;). Hydrocinnamic acid degrades further into acetophenone, another allelopathic compound (Williamson et al. 1992a), when exposed to microbial degradation (Fischer et al. 1994).

More recent studies have looked at the effects of leachates on germination of rosemary scrub species (Hunter and Menges 2002; Calabrese and Menges 2007). Germination is especially important for scrub species which do not resprout after fire (Hawkes and Menges 1995; Menges and Kohfeldt 1995; Hawkes 2004). Rosemary scrub supports many endemic species in gaps within the shrub matrix (Menges and Hawkes 1998). These gaps stay open long after fire, and allelochemicals from Florida rosemary may keep these gaps open (Hunter and Menges 2002).

Field studies are necessary to evaluate the relevance of laboratory results on species interactions in nature. When greenhouse and laboratory studies indicate allelopathic interactions, field experiments are necessary to show that the significant effect of allelochemicals indoors under simplified conditions is still important in the field where there are many factors influencing plant success. This article uses a field experiment to follow up a greenhouse study by Hunter and Menges (2002), who examined allelopathy and competition by Florida rosemary. They looked at the effect of leaf and litter leachates from FL rosemary on germination of seven scrub species and the field distribution of litter and roots. They found that litter leachates limited germination more than leaf leachates, and that Florida rosemary roots extended into gaps while litter was found directly beneath shrub canopies. To extend the study of allelopathy into in situ rosemary scrub sites and to add the potential chemical effects of roots, we looked at the leachates of Florida rosemary roots, litter, and leaves on the germination and survival of six scrub species in the field.

We examined the effect of leaf, litter, and root leachates on the germination and early seedling survival of six Florida scrub species. Most studies focus on the negative effect of allelochemicals on germination and growth (Tanrisever et al. 1987; Richardson and Williamson 1988; Fischer et al.

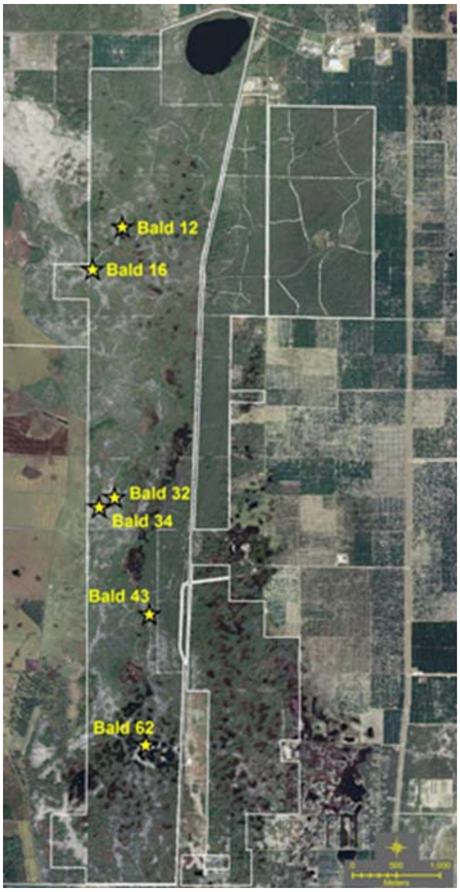



**Fig. 1** Map of Archbold Biological Station, Lake Placid, FL showing the location of six study sites

**Table 1** Characteristics of six target species used in germination experiment

| Species | *Hypericum cumulicola* | *Lechea cernua* | *Lechea deckertii* | *Palafoxia feayi* | *Polygonella basiramia* | *Polygonella robusta* |
|---|---|---|---|---|---|---|
| Family | Hypericaceae | Cistaceae | Cistaceae | Asteraceae | Polygonaceae | Polygonaceae |
| Common name | Scrub Hypericum | Nodding Pinweed | Woody Pineweed | Palafoxia | Hairy Wireweed | Sandhill Wireweed |
| Guild | habitat specialists[a] | habitat specialists[b] | habitat generalists[a,b] | habitat generalists[a,b,c] | habitat specialists[b] | habitat generalists[b] |
| Range | endemic to the Lake Wales Ridge in Polk and Highlands Counties[d] | endemic to Lake Wales Ridge and the east coast of peninsular FL[d] | coastal plain of Georgia south to peninsular FL[d] | endemic to FL[d] | endemic to Lake Wales and Bombing Range Ridges[d] | endemic to peninsular FL[d] |
| Local distribution | found in rosemary scrub and oak scrub[d] | locally common in rosemary scrub[d] | common in rosemary scrub and scrubby flatwoods[d] | common in scrubby flatwoods and gaps in oak scrub[d] | common in scrubby flatwoods and rosemary scrub especially in open sand[d] | locally common in rosemary scrub[d] |

[a] Hunter and Menges (2002)

[b] Maliakal-Witt et al. (2005)

[c] Petru and Menges (2003)

[d] Weekley et al. (2006)

1989, 1994) with little attention given to whether survival is affected. In this study, we posited the following hypotheses:

- Roots, leaves, and litter leachates will decrease germination.
- Litter will have the greatest effect on germination and survival.
- Roots will have the least effect on germination and survival.
- Combinations will have different effects on germination and survival.
- Species will vary in germination and survival.
- Species' germination percentages will vary in sensitivity to leachates.
- Germination of gap specialists will be most sensitive to leachates.
- Selected sites will not differ in germination, but will differ in survival of germinants.

## Methods

### Study sites

We conducted this study at Archbold Biological Station (ABS), 13 km south of Lake Placid in Highlands County, Florida at the southern end of the Lake Wales Ridge. Predominant vegetation types at ABS include scrub, flatwoods, and seasonal ponds (Abrahamson et al. 1984). The rosemary phase of sand pine scrub is dominated by Florida rosemary (*Ceratiola ericoides*) and sand pine (*Pinus clausa*), and is characterized by areas of open sand (>20%) and herbs living in the gaps of the rosemary shrub matrix (Menges and Hawkes 1998). We selected six sites for this study (Fig. 1); all designated as rosemary scrub (Abrahamson et al. 1984). We chose sites based on vegetation, the absence of mature rosemary shrubs, and a recorded fire within the last 8 years.

### Study species

Florida rosemary, *Ceratiola ericoides* (Empetraceae), is a locally dominant endemic species of Florida scrub (Fischer et al. 1989). Allelopathic properties of *Ceratiola ericoides* roots, leaves, and litter were assessed on six target species, *Lechea deckertii,*

**Table 2** Links between hypotheses and logistic regression models predicting either germination or seedling survival

| Hypothesis | Model | Hypothesis |
|---|---|---|
| 1. Roots, leaves, and litter leachates will decrease germination | Roots | 1–3 |
| | Leaves | 1–3 |
| | Litter | 1–3 |
| 2. Litter will have the greatest effect on germination and survival | Roots + leaves | 1–3 |
| | Roots + litter | 1–3 |
| 3. Roots will have the least effect on germination and survival | Litter + leaves | 1–3 |
| | Roots + leaves + litter | 1–3 |
| | Roots + leaves + roots × leaves | 4 |
| 4. Combinations will have different effects on germination and survival | Roots + litter + roots × litter | 4 |
| | Leaves + litter + leaves × litter | 4 |
| 5. Species will vary in germination and survival | Roots + leaves + litter + all 2-ways | 4 |
| | Species | 5 |
| 6. Species' germination percentages will vary in sensitivity to leachates | Roots + species | 6 |
| | Leaves + species | 6 |
| | Litter + species | 6 |
| 7. Germination of gap specialists will be most sensitive to leachates (evaluated graphically rather than in logistic regression models, because of strong relationship with "species") | Roots + leaves + species | 6 |
| | Roots + litter + species | 6 |
| | Litter + leaves + species | 6 |
| | Roots + leaves + litter + species | 6 |
| | Roots + leaves + species + roots × leaves | 6 |
| | Roots + litter + species + roots × litter | 6 |
| | Leaves + litter + species + leaves × litter | 6 |
| 8. Selected sites will not differ in germination, but will differ in survival of germinants | Roots + leaves + litter + species + all 2-ways | 6 |
| | Roots + species + roots × species | 6 |
| | Leaves + species + leaves × species | 6 |
| | Litter + species + litter × species | 6 |
| | Site | 8 |

*Palafoxia feayi, Polygonella robusta*, *Hypericum cumulicola, Lechea cernua*, and *Polygonella basiramia*, with varying degrees of habitat specialization (Table 1). We also chose target species because of their overlap with the species used in Hunter and Menges (2002).

## Field methods

In December 2006, we installed 48 PVC tubes (10 cm in diameter and 10-cm height), with 2 cm extending above the soil surface, in each of the six sites at ABS. Minimum distance between neighboring PVC tubes was 75 cm (we determined that this was an ample distance to ensure independence of treatments through a preliminary test of lateral spread of water poured through PVC tubes) and minimum distance to neighboring shrubs was 1 m. Florida rosemary plants were avoided when installing the PVC. We also placed PVC tubes at least 1 m away from *Calamintha ashei*, another woody plant known to have allelopathic properties (Richardson and Williamson 1988).

Seeds from all six species were collected in October and November 2006, examined under a microscope to assess damage, sorted, and stored at ambient temperature. We planted 25 seeds of a single species in each tube and sprinkled sand over them. Tubes were randomly assigned species and treatments. Species received one replicate of each of eight treatments per site following a complete randomized block design. The six sites served as replicates for each species.

The eight treatments included application of exudates derived from: (1) leaves, (2) litter, (3) roots,

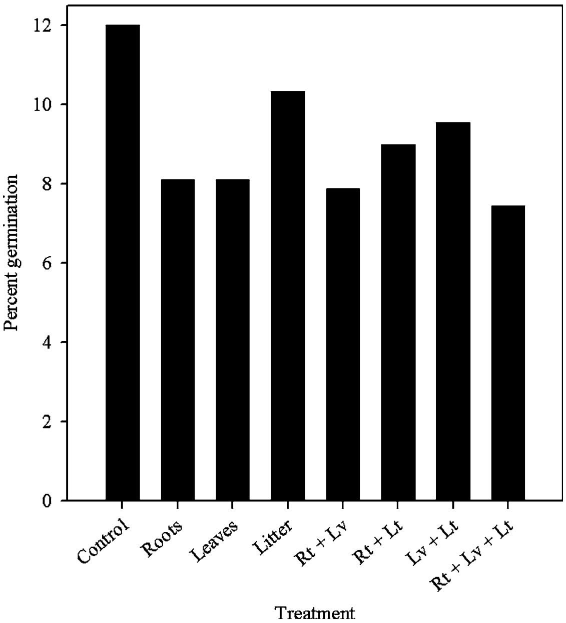



**Fig. 2** Percent germination of six Florida scrub species (pooled) per leachate treatment Figure abbreviations: Rt, roots; Lv, leaves; Lt, litter

(4) leaves and litter, (5) litter and roots, (6) leaves and roots, (7) leaves, litter, and roots, and (8) an untreated control ($H_2O$). We designed the treatments to mimic rainfall on rosemary leaves and litter, and the release of allelochemicals into the soil by roots. We sifted litter and roots through a number 18 1-mm mesh sieve, easily separating rosemary roots due to their red color and flaky texture.

To apply the leachates, we placed a standard amount of rosemary leaves, litter, and roots in a "watering can" made of a PVC tube with mesh over the bottom. Treatments included (1) control with water, (2) 50 g leaves, (3) 50 g litter, (4) 50 g roots, (5) 25 g leaves + 25 g litter, (6) 25 g leaves + 25 g roots, (7) 25 g litter + 25 g roots, and (8) 16.7 g leaves + 16.7 g litter +16.7 g roots. We then poured 125 ml of water through the rosemary material. The control treatment involved adding 125 ml of water through the mesh watering can with no rosemary material. Leaves, litter and roots were collected weekly from different *Ceratiola* plants of varying ages in different parts of the ABS. We used the rosemary material within the week it was collected. The leaves, litter, and roots were used for two consecutive treatments. We applied treatments every third day starting 15 December 2006 through 14 March 2007, with the exception of two occasions when we watered after 7 days because of high rainfall. The timeframe of this experiment coincided with the time of maximum germination in Florida rosemary scrub (November through March) (Hawkes 2004).

We checked germination and seedling survival weekly for 14 weeks starting December 18, 2006, ending March 19, 2007, including a final visit 1 week after we applied the last treatments. Final analyses were performed on the total number of germinants for each of the target species. We also recorded germination of non-sown study species enabling us to calculate background germination rates.

### Analysis

We organized the analyses by considering a set of non-exclusive hypotheses (Table 2). Each hypothesis, represented as a model that could be tested using binary logistic regression, was performed with germination or survival as the dependent variable and species, roots, litter, leaves, and site as categorical covariates. We used bias-corrected Akaike information criteria ($AIC_c$) to evaluate the support for each model and to evaluate the relative weights of models (Burnham and Anderson 1998). We used model averaging to evaluate the overall importance of species, roots, litter, and leaves, and interactions between these parameters. We also graphically explored germination differences between two guilds: habitat generalists and habitat specialists. Since some species' germination percentages were low, we analyzed seedling survival on species with at least 40 germinants.

## Results

### Overall Germination

Leachates inhibited germination percentages, which ranged between 7.4 and 10.3% among treatments compared to 12% in the control (Fig. 2). Models incorporating species, leaf leachates, and root leachates received the greatest support (Table 3). AIC analysis indicated that there was 2/3 probability

**Table 3** Akaike Information Criterion (AIC) analysis for all considered models for germination of six FL scrub species, ranked in order of support (minimum $AIC_c$)

| Model | $K$ | log likelihood | $AIC_c$ | delta | $w_i$ |
|---|---|---|---|---|---|
| Leaves + species + leaves × species | 8 | 3869.587 | 3885.607 | 0.000 | 0.667 |
| Roots + leave + species + roots × leaves | 9 | 3871.030 | 3889.055 | 3.448 | 0.119 |
| Roots + leaves + litter + species | 9 | 3871.652 | 3889.677 | 4.070 | 0.087 |
| Roots + species + roots × species | 8 | 3875.004 | 3891.024 | 5.417 | 0.044 |
| Litter + species + litter × species | 8 | 3875.377 | 3891.397 | 5.790 | 0.037 |
| Roots + species | 7 | 3878.280 | 3892.296 | 6.689 | 0.024 |
| Roots + leaves + litter + species + all 2-ways | 12 | 3870.275 | 3894.318 | 8.711 | 0.009 |
| Leaves + species | 7 | 3880.668 | 3894.684 | 9.077 | 0.007 |
| Roots + litter + species + roots × litter | 9 | 3878.118 | 3896.143 | 10.536 | 0.003 |
| Leaves + litter + species + leaves × litter | 9 | 3880.014 | 3898.039 | 12.432 | 0.001 |
| Species | 6 | 3887.309 | 3899.321 | 13.714 | 0.001 |
| Litter + species | 7 | 3887.275 | 3901.291 | 15.684 | 0.000 |
| Site | 6 | 4295.090 | 4307.102 | 421.495 | 0.000 |
| Roots + leaves | 3 | 4361.529 | 4367.532 | 481.925 | 0.000 |
| Roots + leaves + roots × leaves | 4 | 4360.805 | 4368.811 | 483.204 | 0.000 |
| Roots + leaves + litter | 4 | 4361.523 | 4369.529 | 483.922 | 0.000 |
| Roots | 2 | 4367.216 | 4371.218 | 485.611 | 0.000 |
| Roots + litter | 3 | 4367.209 | 4373.212 | 487.605 | 0.000 |
| Leaves | 2 | 4369.347 | 4373.349 | 487.742 | 0.000 |
| Roots + leaves + litter + all 2-ways | 7 | 4360.298 | 4374.314 | 488.707 | 0.000 |
| Roots + litter + roots × litter | 4 | 4367.144 | 4375.150 | 489.543 | 0.000 |
| Litter + leaves | 3 | 4369.340 | 4375.343 | 489.736 | 0.000 |
| Roots + leaves + species | 8 | 4360.298 | 4376.318 | 490.711 | 0.000 |
| Roots + litter + species | 8 | 4360.298 | 4376.318 | 490.711 | 0.000 |
| Litter + leaves + species | 8 | 4360.298 | 4376.318 | 490.711 | 0.000 |
| Leaves + litter + leaves × litter | 4 | 4368.896 | 4376.902 | 491.295 | 0.000 |
| Litter | 2 | 4375.020 | 4379.022 | 493.415 | 0.000 |

**Table 4** Sum of Akaike weights (model averaging) by parameter for germination models

| Parameter | Relative weight |
|---|---|
| Species | 1.0000 |
| Leaves | 0.8907 |
| Leaves × species | 0.6674 |
| Roots | 0.2863 |
| Litter | 0.1377 |
| Roots × leaves | 0.1190 |
| Roots × species | 0.0445 |
| Litter × species | 0.0369 |
| Roots × litter | 0.0034 |
| Leaves × litter | 0.0013 |
| Site | 0.0000 |

($w_i = 0.667$) that the model containing leaves, species, and the interaction between leaves and species was the best model for germination percentages of those considered (Table 3). Model averaging showed that species was the most important model parameter (Table 4), followed by individual leachates (leaves, roots, litter). Site was in none of the important models for germination. Leachates in combination did not additionally suppress germination. Some of the seeds given combination leachate treatments had higher germination than single leachates (roots + litter 9.0% germination and leaves + litter 9.6% germination), while some had lower germination (roots + leaves 7.9% germination and roots + leaves + litter 7.4% germination) (Fig. 2).

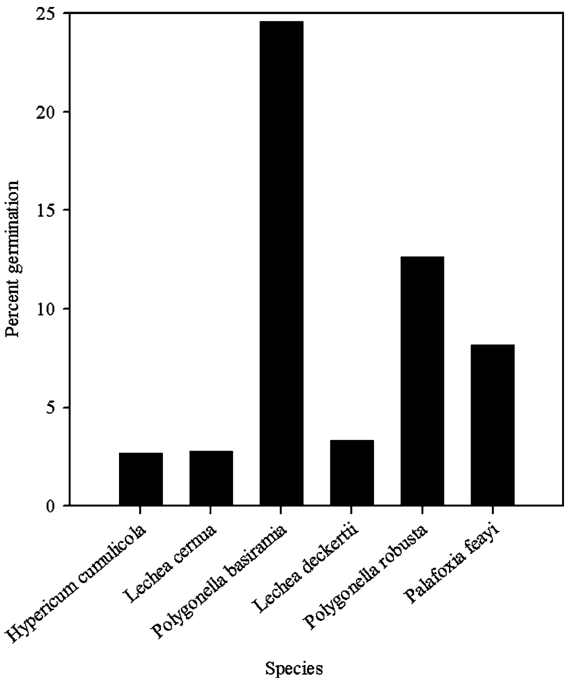



**Fig. 3** Percent germination of six Florida scrub species, pooled across all treatments

Germination by species

Percent germination varied among species from 2.7 to 24.6% (Fig. 3). *P. basiramia* ($n = 295$ of 1,200), *Polygonella robusta* ($n = 155$ of 1,200), and *Palafoxia feayi* ($n = 98$ of 1,200) had the highest germination percentages. The six species also varied in their sensitivity to the different leachates, with the interaction between species and leaves particularly important (Table 4). Some species followed the same trends seen for overall germination. *P. basiramia* and *P. feayi* had higher germination in the control, while individual leachates reduced germination (Fig. 4a, b). *P. robusta* also had reduced germination with roots, leaves, and root × leaves leachates, but germination in the control was slightly lower than germination with leaves × litter leachates (Fig. 4c). *H. cumulicola*, *L. cernua*, and *L. deckertii* germination did not follow the overall general trend (Fig. 4d–f). The germination success for all these species was lower than 3.3%. More specialists (*Hypericum cumulicola, Lechea cernua, Polygonella basiramia*) germinated than generalists (*Lechea deckertii, Palafoxia feayi, Polygonella robusta*). However, there were no clear patterns as to how the two guilds responded to different leachates (Fig. 5).

Survival

Leachates did not have consistent negative effects on early (14 weeks) survival of germinants (Fig. 6). In contrast to the germination data, which suggested that leaves had the most negative effect on germination rates, litter had the most positive effect on survival, as suggested by AIC (Tables 5, 6). Site was a more important parameter for survival than germination. Out of the total number of 652 seeds germinated, 402 survived. Many of the species had such low germination that it was difficult to evaluate leachate effects on survival. The three species with over 40 germinants, included in analyses had high survival: *P. basiramia* (67.5%), *P. robusta* (71.0%), and *P. feayi* (39.2%) (Fig. 7). Out of the species with the highest germination, only *P. feayi* had higher survival in the control than in leachate treatments (Fig. 8a–c). For species with low germination, overall survival was not strongly affected by leachate application.

## Discussion

Field germination of six Florida scrub species was inhibited by Florida rosemary leachates. This is consistent with several lab and greenhouse studies which have shown that allelochemicals from Florida rosemary reduced germination of pyrogenic sandhill grasses (Tanrisever et al. 1987; Richardson and Williamson 1988; Fischer et al. 1989; Williamson et al. 1992b) and some rosemary scrub species (Hunter and Menges 2002). Survival was not strongly affected by leachate application in our experiment. However, demography studies have shown that survival of *Hypericum cumulicola* (Quintana-Ascencio and Menges 2000) and *Eryngium cuneifolium* (Menges and Kimmich 1996, Quintana-Ascencio and Menges 2000) is highly correlated with distance from rosemary shrubs. We addressed germination and survival in this study; however leachates from Florida rosemary have also been shown to reduce growth in lab studies (Richardson and Williamson 1988; Weidenhamer and Romeo 1989).

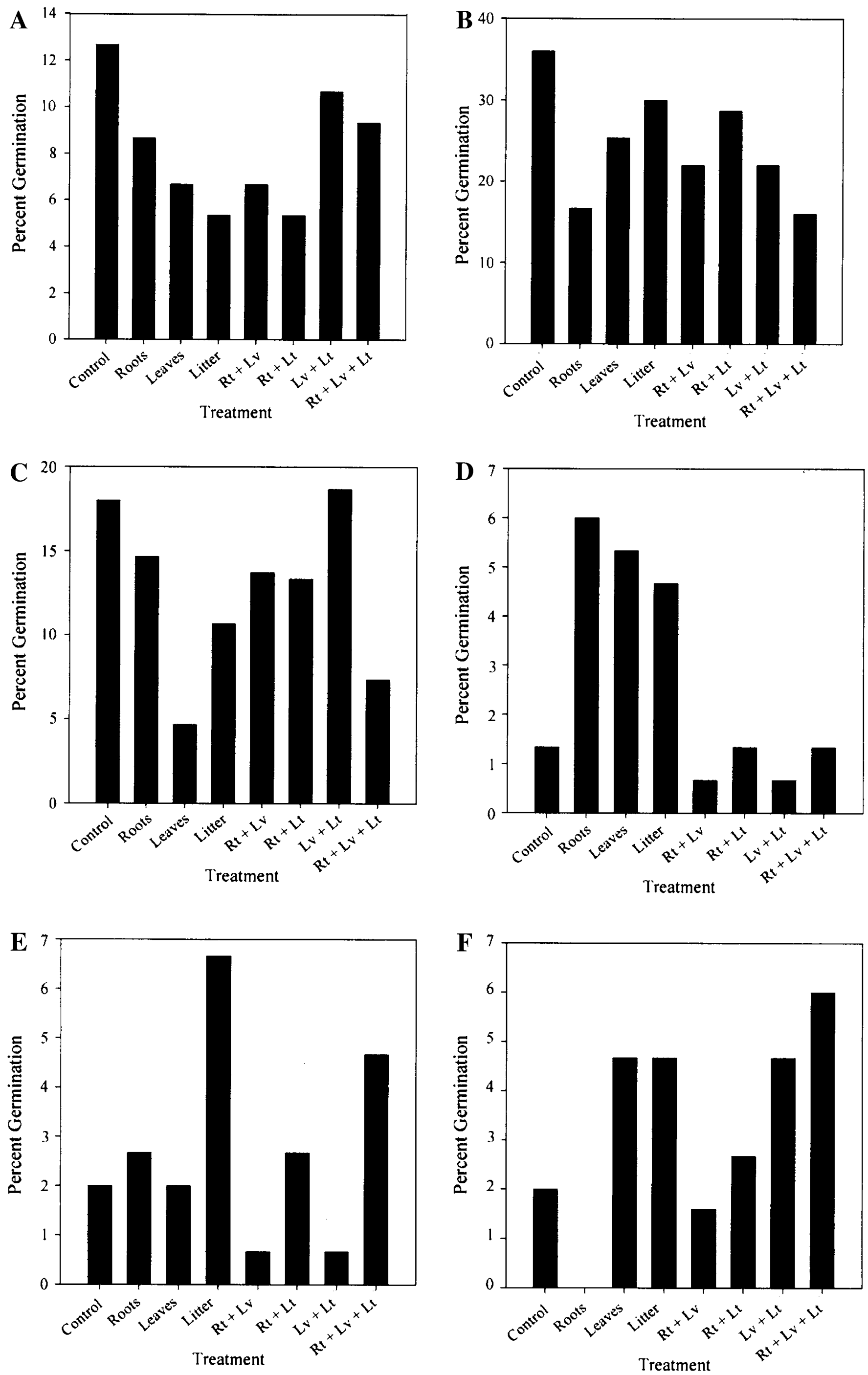



**Fig. 4** Percent germination of individual species by treatment (abbreviations as in Fig. 3). (**A**) Percent germination of *Polygonella basiramia* by treatment. (**B**) Percent germination of *Palafoxia feayi* by treatment. (**C**) Percent germination of *Polygonella robusta* by treatment. (**D**) Percent germination of *Hypericum cumulicola* by treatment. (**E**) Percent germination of *Lechea cernua* by treatment. (**F**) Percent germination of *Lechea deckertii* per treatment

In our study, leaf leachates reduced germination more effectively than root and litter leachates. Ceratiolin, a mild allelochemical, is released from fresh rosemary leaves via water washes or rain (Tanrisever et al. 1987; Fischer et al. 1994). Hydrocinnamic acid (HCA), a stronger allelochemical, is produced when ceratiolin is exposed to light and heat (Williamson et al. 1992a). HCA is found in litter of Florida rosemary (Williamson et al. 1992a). However, if litter is old, then the release of

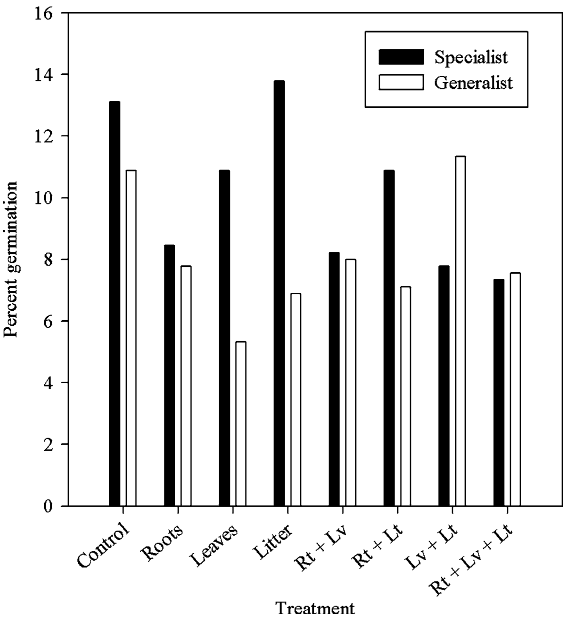



**Fig. 5** Percent germination of rosemary scrub specialists and habitat generalists by treatment. Rosemary scrub specialists are *Hypericum cumulicola*, *Lechea cernua*, and *Polygonella basiramia*. Habitat generalists are *Lechea deckertii*, *Palafoxia feayi*, and *Polygonella robusta*

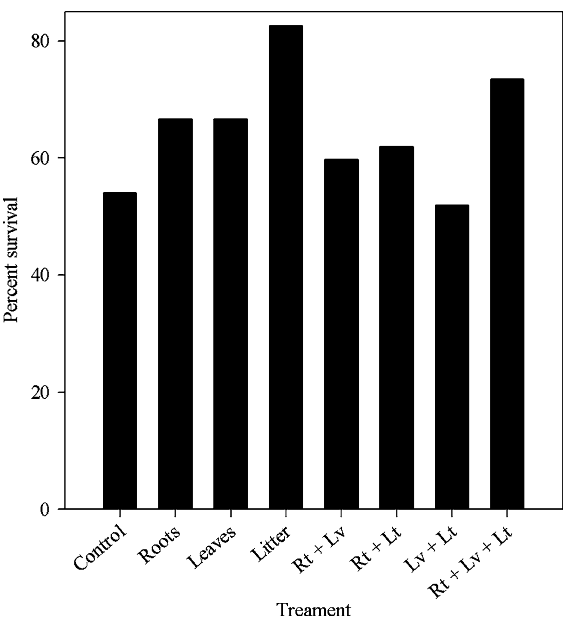



**Fig. 6** Percent survival of three Florida scrub species *Polygonella basiramia*, *Palafoxia feayi*, and *Polygonella robusta* by treatment

ceratiolin and subsequent production of HCA may have stopped. Bioassays of acetophenone, produced by degraded HCA, did not inhibit germination of *Rudbeckia hirta* or *Leptochloa dubia* (G.B. Williamson, Louisiana State University, unpublished data).

Different conditions in Florida rosemary allelopathy experiments have probably affected results. For example, Hunter and Menges (2002) reported litter leachates had a more inhibitory effect on greenhouse germination of Florida scrub species than leaf leachates, a result opposite to our study. However, it is important to keep in mind the different conditions present in greenhouse versus field. Relative to greenhouse conditions, field sites have higher light levels, greater fluctuations in soil moisture and temperature, and possibly different concentrations of soil nutrients. It is possible that in this field study, when leaf leachates were exposed to the sun and heat, ceratiolin was converted to the more active HCA, therefore producing stronger leaf leachate inhibition. In comparison, field litter leachates may have had relatively low concentrations of HCA. The higher activity of allelochemicals in litter vs. leaves, reported in other studies, is dependent on litter age and the preparation of leachates (G.B. Williamson, Louisiana State University, personal communication). It is also possible that misting water through the litter versus pouring water through the litter would release more active HCA. Our experiment poured water through plant material, while other studies used misting (Hunter and Menges 2002) or soaking (Williamson 1992b) to acquire bioassays.

Combination leachates did not additionally suppress germination compared to the influence of single leachates. The lack of an interaction among leachates could reflect that allelochemicals produced by Florida rosemary are all derived from ceratiolin, and that the various chemicals are somewhat redundant in inhibiting germination. In fact, ceratiolin and its derivatives have different abilities to inhibit germination (Williamson et al. 1992a; Fischer et al. 1994). Since a standard weight of rosemary material was used to produce all leachates, combination leachates of ceratiolin and its derivatives had similar concentrations of allelochemicals.

This field study gives context to the Hunter and Menges (2002) greenhouse study, and helps to show how allelochemicals can influence the structure of

**Table 5** AIC analysis for all considered models for seedling survival of three FL scrub species ranked in order of support (minimum $AIC_c$). The three species, *Polygonella basiramia*, *Polygonella robusta*, and *Palafoxia feayi*, with over 40 germinants, were analyzed

| Model | K | log likelihood | AICc | delta | $w_i$ |
|---|---|---|---|---|---|
| Litter + species + litter × species | 5 | 675.791 | 685.799 | 0.000 | 0.609 |
| Site | 6 | 676.060 | 688.072 | 2.272 | 0.196 |
| Leaves + species + leaves × species | 5 | 678.586 | 688.594 | 2.795 | 0.151 |
| Roots + species + roots × species | 5 | 684.012 | 694.020 | 8.221 | 0.010 |
| Litter + species | 4 | 686.760 | 694.766 | 8.966 | 0.007 |
| Species | 3 | 688.870 | 694.873 | 9.074 | 0.007 |
| Leaves + litter + species + leaves × litter | 6 | 684.120 | 696.132 | 10.332 | 0.003 |
| Litter + leaves + species | 5 | 686.324 | 696.332 | 10.533 | 0.003 |
| Roots + litter + species | 5 | 686.371 | 696.379 | 10.580 | 0.003 |
| Roots + species | 4 | 688.477 | 696.483 | 10.683 | 0.003 |
| Leaves + species | 4 | 688.520 | 696.526 | 10.726 | 0.003 |
| Roots + leaves + litter + species | 6 | 685.901 | 697.913 | 12.113 | 0.001 |
| Roots + leaves + species | 5 | 688.102 | 698.110 | 12.311 | 0.001 |
| Roots + litter + species + roots × litter | 6 | 686.233 | 698.245 | 12.445 | 0.001 |
| Roots + leave + species + roots × leaves | 6 | 686.712 | 698.724 | 12.924 | 0.001 |
| Roots + leaves + litter + species + all 2-ways | 9 | 681.785 | 699.810 | 14.011 | 0.001 |
| Leaves + litter + leaves × litter | 4 | 711.509 | 719.515 | 33.715 | 0.000 |
| Litter | 2 | 716.154 | 720.156 | 34.356 | 0.000 |
| Litter + leaves | 3 | 715.340 | 721.343 | 35.544 | 0.000 |
| Leaves | 2 | 717.610 | 721.612 | 35.812 | 0.000 |
| Roots + litter | 3 | 715.802 | 721.805 | 36.006 | 0.000 |
| Roots | 2 | 717.959 | 721.961 | 36.161 | 0.000 |
| Roots + leaves + litter | 4 | 714.944 | 722.950 | 37.150 | 0.000 |
| Roots + leaves | 3 | 717.226 | 723.229 | 37.430 | 0.000 |
| Roots + leaves + litter + all 2-ways | 7 | 709.301 | 723.317 | 37.517 | 0.000 |
| Roots + litter + roots × litter | 4 | 715.548 | 723.554 | 37.754 | 0.000 |
| Roots + leave + roots × leaves | 4 | 716.064 | 724.070 | 38.270 | 0.000 |

**Table 6** Sum of Akaike weights by parameter for seedling survival models

| Parameter | Relative weight |
|---|---|
| Species | 0.804 |
| Litter | 0.629 |
| Litter × species | 0.609 |
| Site | 0.196 |
| Leaves | 0.164 |
| Leaves × species | 0.151 |
| Roots | 0.021 |
| Roots × species | 0.010 |
| Leaves × litter | 0.003 |
| Roots × litter | 0.001 |
| Roots × leaves | 0.001 |

rosemary scrub. With leaf, root, and litter leachates all showing inhibitory effects on germination, the influence of allelochemicals from Florida rosemary may influence community structure far beyond the canopy of the shrub matrix. Previously, allelochemicals from roots were not studied. Florida rosemary root abundance increases with time since fire and decreases with distance from the shrub, with the highest root abundance at 0-15 cm in depth (Hunter and Menges 2002). Our study indicated that root leachates were more inhibitory than litter leachates, meaning rosemary is capable of influencing other plants meters from aboveground parts.

Two factors may influence the ability of allelochemicals from Florida rosemary to affect co-occurring species: gap size and fire. Gaps influence

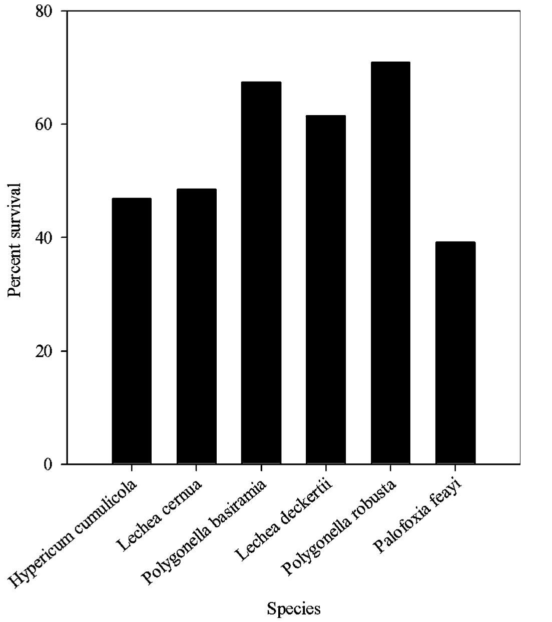
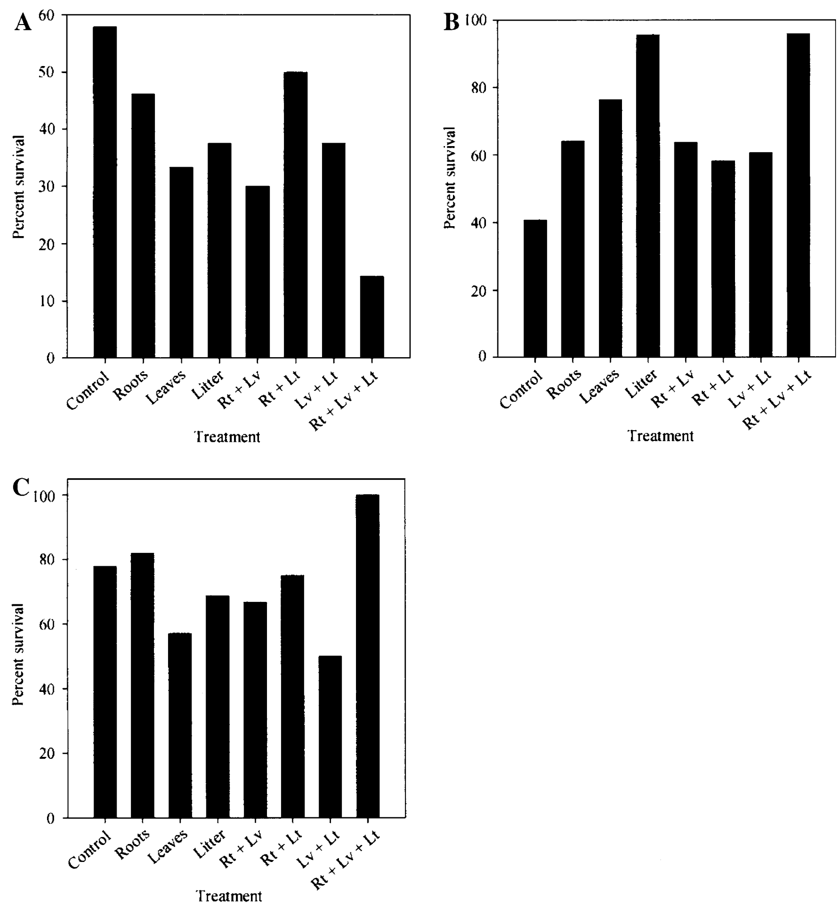



**Fig. 7** Percent survival of six Florida scrub species, pooled across treatments

life history of many scrub herbs (Hawkes and Menges 1995; Quintana-Ascencio and Menges 2000) and several species increase in occupancy or density with more open space or larger gaps (Hawkes and Menges 1995, 1996; Menges and Kimmich 1996; Menges et al. in press). In large gaps, Florida scrub herbs can flourish in the absence of Florida rosemary allelochemicals. Smaller aboveground gaps are colonized by Florida rosemary roots, which may chemically suppress germination and plant growth. Many species that are found in rosemary scrub also respond well to fire (Menges and Hawkes 1998). After fire, there is time for species to germinate and grow uninhibited by Florida rosemary allelochemicals since Florida rosemary is killed by fire and recovers via seedbank recruitment and slow growth of seedlings (Johnson 1982). With increased time since fire, obligate seeders decrease in frequency (Menges and Kohfeldt 1995) perhaps due to the presence of Florida rosemary allelochemicals. Frequent fire, by maintaining

**Fig. 8** Percent survival of individual species by treatment (abbreviations as in Fig. 3). (**A**) Percent survival of *Palafoxia feayi* per treatment. (**B**) Percent survival of *Polygonella basiramia* per treatment. (**C**) Percent survival of *Polygonella robusta* per treatment



conditions with fewer rosemary roots, can reduce the importance of allelopathy in Florida rosemary scrub.

This study further documents the negative impact of Florida rosemary leachates on the germination of co-occurring plant species. Not only do Florida rosemary leachates influence germination in a greenhouse, the negative effects are also apparent in the field. Allelochemicals from Florida rosemary can affect species not only under the canopy of the shrubs but far into the gaps in the shrub matrix. The influence of root leachates has not been previously documented for Florida rosemary, and the inhibitory effect of root leachates on germination may influence community dynamics and structure of rosemary scrub communities, depending on time since fire and the size of the gaps.

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