# A Chemical Polymorphism in a Multitrophic Setting: Thyme Monoterpene Composition and Food Web Structure

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ABSTRACT: We investigated the effects of chemical variation in thyme (*Thymus vulgaris* L.) on its interactions with competitors, herbivores, and herbivore predators. Four different thyme monoterpene phenotypes (chemotypes) were grown in a 4 × 2 × 2 factorial of chemotype, caging (sham half-cages vs. full cages), and competition (control vs. the grass *Bromus madritensis* L.). Cages reduced numbers of arthropod predators. Thyme-feeding aphids *Aphis serpylli* Koch passed through full cage walls to increase more than fourfold. As a result, freed from their predators, aphids had a large negative effect on thyme size and flowering. Similarly, competition from *Bromus* had a negative effect on thyme size and flowering. Individual effects of aphids and competition were nonadditive, however, and their combined effect was significantly less than that predicted by a multiplicative null model. Differential thyme sizes among chemotypes were not mediated by herbivores or competitors, but differential flowering was due to the effects of chemotype on aphids. We thus document differential selection by aphids among thyme chemotypes and the influence of *Bromus* on the strength of these negative effects of aphids.

*Keywords:* trophic cascade, higher-order effects, chemical polymorphism, plant defense, herbivory, competition.

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The evolutionary dynamics of a species are determined by the interplay between its genetics and its ecological roles in a community. In both genetic and ecological studies, there has been an increasing focus on the complexities of multispecies interactions. For example, the term "community genetics" has been coined to describe the simultaneous influences of multiple ecological variables on the genetics of species interactions (Antonovics 1992; Agrawal 2003). Community ecology has convincingly shown that a network of direct and indirect interactions affects the population dynamics of a species. More recently, it has been recognized that the forms of the direct and indirect interactions between a species and other community members may themselves be contingent on the ecological setting in which they occur. From the study of these complex interactions—so-called higher-order effects (Abrams 1983), emergent properties (Sih et al. 1998), or trait-mediated interactions (Abrams 1995)—it is increasingly appreciated that such complexity plays an important role in community organization and dynamics (Wootton 2002; Hamback and Beckerman 2003; Rand 2003).

Most investigations into higher-order effects can be classified as belonging to one of two types of studies. The first type focuses on ecological effects and tests either whether the interactions between a focal species and two or more community members (e.g., predators, herbivores, mutualists) occur in an additive fashion or whether the pairwise interaction between the focal species and one community member depends on, or is modified by, its interactions with another. Such studies include the investigation of emergent multiple-predator effects (Sih et al. 1998), nonadditivity in the combined influences of herbivory and competition (Hamback and Beckerman 2003), contingency in mutualistic interactions (Bronstein 1994), and the trait-mediated indirect effects of predators on plants (Preisser et al. 2005). When such studies document a context-specific nature for an ecological interaction, there is the implication that natural selection imposed by that interaction on the focal species will likewise be context specific (Thompson 1994), but this assumption is not formally tested.

The second type of study formally tests whether the effect of some biotic factor on a focal species varies as a function of genotype. Such higher-order effects document the presence of selection. With respect to plant evolution, for example, individual herbivores (Denno and McClure 1983; Antonovics 1992) and competitors (Linhart 1988; Kittelson and Maron 2000; Weinig 2000) are known to have differential effects on specific genotypes. While the effects of multiple herbivores and competitors on a focal species may be so documented, such studies measure selection one pairwise interaction at a time. This approach is uninformative about whether multiple selective events are additive.

To explicitly test for additive selection from multiple ecological interactions requires combining the two approaches outlined above. In such studies, the differential performance of multiple genotypes is measured as a function of multiple simultaneous ecological interactions. Here, we add to a small but growing number of studies that do so by asking how the nonadditive nature of multiple community-level effects on a focal species may itself be modified by heritable traits of that species (Agrawal 2004). In this approach, the individual and combined effects of two or more community members on a focal species are measured on individuals of varying genotypes. Such experimental designs, employing three or more factors, are generally difficult to conduct but can provide an important bridge between our understanding of nonadditivity in community ecology and the contextual nature of differential fitness and resulting selection.

In this study, we compare the performance of genetically controlled chemical phenotypes ("chemotypes") in common thyme *Thymus vulgaris* L. (Lamiaceae) exposed to the individual and combined influences of herbivores, herbivore predators, and competition. Before this study, chemical variation in thyme was already known to influence interactions between individual thyme plants and their associated species, which included microorganisms (de Buochberg 1976; Vokou et al. 1984), herbivores (Gouyon et al. 1983; Linhart and Thompson 1995, 1999), and other competing plants (Tarayre et al. 1995; Y. B. Linhart, P. Gauthier, and J. D. Thompson, unpublished data). The results of these pairwise interactions provided convincing evidence that thyme chemistry can indeed play a crucial role in these contexts.

Our goal was to expand on these findings and determine the extent to which variability in performance among thyme chemotypes may be influenced by higher-order effects. We exposed thyme plants of varying chemotypes to variation in herbivory—achieved via predator exclusion and control treatments—crossed with the presence and absence of competition, under experimentally manipulated field conditions, and asked two questions: How does thyme chemotype affect its direct interactions with herbivores and competitors and its indirect interactions with predators? Is the differential fitness of thyme chemotypes with respect to these ecological factors additive? That is to say, does selection on thyme chemotype from one factor vary as the function of the presence or absence of thyme interactions with other factors?

## Methods

### *The Species and Its Defenses*

Thyme is a short-lived (3–10 years) aromatic perennial of the western Mediterranean. Its aroma is produced by monoterpenes whose synthesis is controlled by a well-defined, genetically controlled polymorphism and that are sequestered in trichomes on leaf and stem surfaces. An individual plant produces predominantly a single monoterpene that gives the plant its characteristic taste and smell. The biosynthetic pathway and the genetic control of this synthesis are well understood (Passet 1971; Gouyon et al. 1986; Vernet et al. 1986). In the south of France, individual thyme plants produce as their dominant monoterpene one of six molecules: geraniol (G), $\alpha$-terpineol (A), thuyanol (U), linalol (L), carvacrol (C), or thymol (T). Each plant thus has a specific chemical phenotype, or chemotype. The genetic control of this pathway involves an epistatic series of at least five loci. At each locus, there are two alleles, one dominant to the other. The epistatic effects are such that G > A > U > L > C > T (Vernet et al. 1986). The four chemotypes used in this study include the nonphenolic, acyclic alcohols (G and L) and the phenolics (C and T). The two phenolic terpenes (C and T) are most toxic (Budavari et al. 2000) and most deterrent to multiple herbivores (Linhart and Thompson 1999), and they have more negative effects on germination and growth of potential competitors than do nonphenolic terpenes (Tarayre et al. 1995; Stahl-Biskup and Saez 2002). Three of the chemotypes we tested (G, C, and T) produce the same terpene from germination onward, so they are constitutive, and they remain stable despite herbivory, cloning, or growth in diverse habitats (Lamy 1985; Vernet et al. 1986; Thompson 2002). Plants of the L chemotype apparently assume this chemotype at about 2–4 months of age; before that age, they exhibit either a C or a T chemotype (Passet 1971; Vernet et al. 1986). This delay may be relevant to protection of young seedlings against certain herbivores (Linhart and Thompson 1995). Natural populations are highly polymorphic (about 90% of more than 400 populations analyzed to date contain two or more chemotypes), and the frequencies of the six chemotypes vary markedly over these complex landscapes (Mazzoni and Gouyon 1984; Gouyon et al. 1986; Thompson 2002, 2005).

Thyme occurs from northern Italy to southeastern Spain in open garrigues and similar shrub-dominated habitats. The climate is Mediterranean, with a summer drought and irregular but often intense precipitation the rest of the year. It often grows on highly weathered soils that are deficient in many nutrients (Foth and Schafer 1980; Specht and Moll 1983). Under these conditions, competition can have important influences on population dynamics and community structure (Fowler 1986), and its role as a selective agent in plant populations has been documented in multiple settings (Linhart 1988; Goldringer et al. 2001; Kittelson and Maron 2001). Thyme seldom grows taller than 40 cm, so that competitors, including grasses such as *Bromus* spp. that reach such heights, quickly overtop thyme and shade it. Competition in these habitats can be influenced by the production of secondary compounds by certain species (Weidenhamer et al. 1989; Ross and Sombrero 1991; Vila and Sardans 1999), including *Thymus* spp. (Vokou and Margaris 1982; Katz et al. 1987; Fisher 1991; Tarayre et al. 1995).

### *Experimental Design*

The experiment was carried out on the grounds of the Centre d'Ecologie Fonctionnelle et Evolutive (CEFE)–Centre National de la Recherche Scientifique (CNRS) in Montpellier, France. Before being an experimental field (about 40 years ago), the site was a vineyard and before that, garrigue. The overall environment of this field is typical of thyme habitats in terms of precipitation, temperatures, soils, and presence of some of the common plants and animals associated with thyme. In the surrounding garrigue, the most frequent chemotype is C. The experimental plot had been plowed immediately before our planting of thyme; this reduced small-scale heterogeneity, but in the process, all vegetation and associated fauna were disturbed, so that the plot represents an example of an early-successional setting. However, it is near populations of mature *Thymus vulgaris* from which thyme competitors and herbivores recolonized the plot (Harant and Jarry 1987; Prieur-Richard et al. 2002).

We used a fully crossed three-factor design. The factors were four thyme chemotypes, the presence or absence of competition by the grass *Bromus madritensis* L., and whether thyme plants were within open half-cages and accessible to all arthropods and mollusks or protected within closed cages against all large mollusks and arthropods, including herbivores and predators, but accessible to microorganisms and very small arthropods, such as aphids. The only herbivore of any significance during the course of this experiment was the aphid *Aphis serpylli* Koch, and it passed freely through the cage mesh, while predators, principally coccinellid beetles and spiders, were significantly reduced in cages (see "Results" for details). The caging of thyme plants functioned as a predator exclusion treatment and is referred to as such below. Individual plants of each of the four chemotypes were thus exposed to one of four conditions: thyme in cages with no competition; thyme in cages with competition; thyme in half-cages with no competition; and thyme in half cages with competition. The layout was a single randomized block with a grid of 20 × 24 locations (480 plants), with plants set 1 m apart. Thyme seedlings were 8–10 cm tall and 4 months old in November 2001 at the time of planting. We replaced dead individuals (<1%) with plants of comparable size in February 2002. The design was balanced with respect to cage and competition treatments but unbalanced with respect to available chemotypes: there were 226 T, 83 C, 57 L, and 114 G.

Cages were 60 cm in diameter by 70 cm tall, constructed of wire frame cylinders around which plastic screen mesh (0.9-mm opening) was wrapped and then gathered and tied at the top with wire. To control for the physical effects of cages (e.g., partial shade) but allow all access to all arthropods and mollusks, open half-cages of the same dimensions and construction were used. We refer to plants within full cages as "caged" plants and those in half-cages as "control" or "uncaged" plants.

Competition was provided by the annual grass *B. madritensis*. Seeds were sown adjacent to thyme plants at the same time as thyme were planted in November 2001. Seedlings were thinned to four *Bromus* in February 2002. Some additional *B. madritensis* subsequently germinated after thinning, so that some thyme were exposed to five or six *Bromus* between March and the conclusion of the experiment (November 2002). Such densities of *Bromus* and other competitors are commonly encountered by thyme in garrigue.

### *Invertebrates*

In mid-May 2002, we recorded aphid abundance in all 480 cages. We did not count aphid individuals but instead recorded the total length of thyme stem on which they were feeding. In a different system, we found aphid number to be highly correlated with the length of plant stem occupied ($r = 0.89$, $P < .0001$; K. A. Mooney, unpublished data). We also recorded other arthropods and mollusks on a representative subset of the thyme plants, including 49 caged plants and 125 plants in half-cages. The weather was warm and relatively humid at this time, which was therefore a time of peak activity for mollusks and arthropods. Before this period, the weather in this area is typically cooler, and frosts are common into March, so invertebrate activity is lower. In June, faced with the increasing heat and dry conditions typical of the Mediterranean, many

annual plants begin to senesce, and once again invertebrate abundance declines.

### *Measurements of Performance*

We first measured thyme plants in mid-May 2002. We calculated plant volume as the volume described from plant height and two orthogonal measures of crown width. The correlation between volume and biomass as estimated from 140 plants at the conclusion of the experiment was high ($r = 0.89$; $P < .001$). Although final biomass was obtained in November, it is a reasonable predictor of the volume-to-biomass relationship in May, which is near the end of thyme's growing season. We quantified thyme flowering by counting all branches that had at least one cluster of flowers. Most branches had several such clusters. In November 2002, thyme were mature, and we collected the aboveground biomass from all thyme and *Bromus* and oven-dried and weighed it.

### *Statistical Analyses*

This experiment was a three-factor design of chemotype (G, L, C, T), predator exclusion (exclusion, control), and competition (presence, absence). Flower production and arthropod abundance (May only) and *Bromus* biomass (November only) were measured at only one time. Thyme plant size was measured as plant volume in May 2002 and plant biomass in November 2002, and we treated these two estimates of plant size as separate variables. In all instances we tested for two- and three-way interactions. With tests showing significant effects of chemistry, we conducted Duncan's a posteriori tests to determine the patterns of differences among the four chemotypes (Zar 1999). After these factorial analyses, we performed further analyses to provide specific details of the possible mechanisms behind some of the treatment effects we observed. Because our design was unbalanced with respect to plant chemotypes, we used Type III sums of squares in all cases (Zar 1999). A multiplicative null model provided the appropriate tests for interaction in this experiment (Sih et al. 1998; Hamback and Beckerman 2003), and testing against this null model with ANOVA required the use of log-transformed ($\ln[\text{variable} + 1]$) data (Zar 1999). All analyses were performed using PROC GLM of SAS, version 8.02 (SAS Institute 2001).

## Results

### *Invertebrate Surveys*

Cages reduced predator abundance by three-fourths. Seven of 49 thyme plants (14%) surveyed within cages were occupied by one or more predators (coccinellids or spiders), while 75 of 125 (60%) surveyed control plants had one of those predators ($\chi^2_{(1)} = 67.9$; $P < .0001$). Predators (i.e., half-cage vs. cage) reduced overall aphid abundance by 77% (fig. 1; table 1), as determined by aphid accumulation, that is, the length of stem occupied by aphids. Plants in cages had a mean ($\pm 1$ SE) $295 \pm 27$ mm of stem occupied by aphids, while aphids occupied only $72 \pm 11$ mm of stem in plants in half-cages. Aphid abundance also differed among thyme chemotypes, with ~70% fewer aphids on fully caged L plants (the chemotype with the lowest abundance) than on fully caged T plants (the chemotype with the highest abundance; fig. 1; table 1). There was a significant cage × chemotype interaction on aphids (fig. 1; table 1). A posteriori tests showed that aphids increased with caging on G, C, and T plants but not on L plants. Competition from *Bromus* reduced aphid abundance by 40% (fig. 1; table 1), but results of a test for the effects of competition on aphid density (aphids per unit thyme volume [$mm/cm^3$]) were not significant ($F = 1.55$, $df = 1, 467$, $P = .21$), indicating that the negative effect of competition on aphid abundance was due to *Bromus* reducing host plant size.

Except for aphids, herbivores (snails, other larger arthropods) were relatively rare. Only 19 of 125 thyme plants in half-cages (15%) were occupied by nonaphid herbivores, while 77 of 125 (62%) plants in half-cages hosted aphids. We found very minor evidence of leaf chewing, stem clipping, or other damage typical of mollusks and larger insects (Linhart and Thompson 1999; Y. B. Linhart, K. Keefover-Ring, B. Breland, and K. A. Mooney, unpublished data).

### *Thyme Reproduction*

Predators increased thyme flower production by 32% (fig. 2*A*; table 1). Competition from *Bromus* reduced flower production by 66% (fig. 2*A*; table 1). Chemotype also affected reproduction, with C (the most fecund chemotype) producing 89% more flowers than G (the least fecund chemotype; fig. 2*A*; table 1). There were no interactions between caging, competition, and chemotype on thyme flower production (table 1).

### *Thyme Size*

Thyme volume in May 2002 (fig. 2*B*; table 1) and biomass in November 2002 (fig. 2*C*; table 1) differed significantly as a function of predator exclusion, competition, and plant chemotype in very similar patterns of treatment effects. Predators increased thyme plant size by 15% and 10% in May and November, respectively (fig. 2*B*, 2*C*; table 1). Competition reduced thyme size by 45% and 43% in May

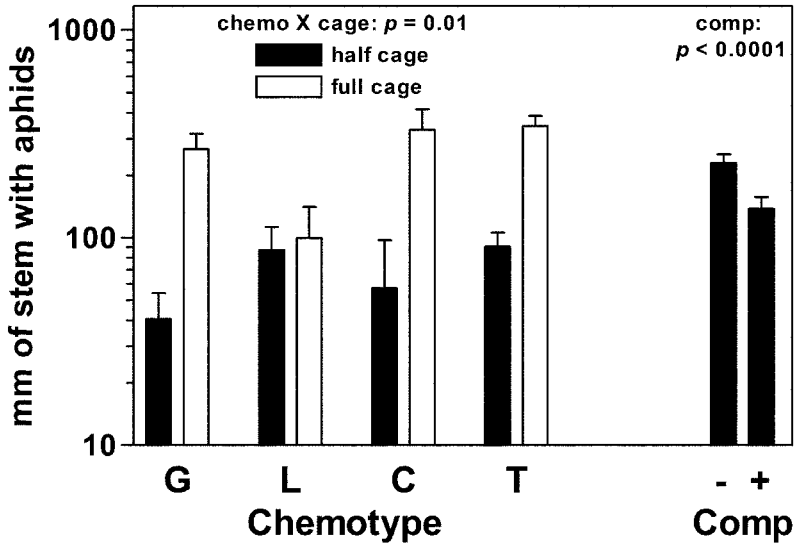


**Figure 1:** Aphid (*Aphis serpylli*) abundance on thyme in chemotype, predator exclusion (*cage*), and competition treatments. Aphid abundances within cage and chemotype treatments are shown together because these two factors interacted significantly. Competition did not interact with other treatments.

and November, respectively (fig. 2*B*, 2*C*; table 1). Chemotype was significant, with C (the largest chemotype) being 75% and 45% larger than G (the smallest chemotype) in May and November, respectively (fig. 2; table 1). There were no significant interactions between chemotype, cage, and competition for thyme size in either May or November (table 1).

### Bromus *Biomass*

Total *Bromus* biomass was not significantly influenced by the chemotype of its neighbor (table 1), but grasses were 38% larger in full cages than in half-cages.

### *Detailed Analyses of Interactions*

We performed several analyses to elucidate the mechanisms by which our manipulations influenced thyme plant size and flower number and grass biomass. Because aphid abundance was markedly higher within cages, we hypothesized that increased aphid herbivory in cages was directly responsible for the cage effects on thyme size and reproduction. To test this hypothesis, we repeated our original factorial analysis but with the addition of aphid abundance as a covariate (table 2). Aphid abundance was significant for all three thyme response variables, but what was significant was not the number of aphids alone but rather the aphid × competition interaction (table 2). This result in-

**Table 1:** Statistical results of three-factor ANOVA of chemotype, competition, and predator effects on thyme, aphids, and *Bromus*

| | May | | | | | | November | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Flowering branches | | Thyme volume ($cm^3$) | | Length of stem with aphids (mm) | | Thyme mass (g) | | *Bromus* mass (g) | |
| Sources | *F* (df) | *P* | *F* (df) | *P* | *F* (df) | *P* | *F* (df) | *P* | *F* (df) | *P* |
| Chemotype | **2.7** (3, 451) | **.04** | **5.6** (3, 451) | **.0009** | **5.2** (3, 449) | **.002** | **7.8** (3, 452) | **.0001** | .8 (1, 224) | .5 |
| Cage | **10.6** (1, 451) | **.001** | **13.7** (1, 451) | **.0002** | **31.6** (1, 449) | **<.0001** | **10.5** (1, 452) | **.001** | **7.2** (1, 224) | **.008** |
| Competition | **51.6** (1, 451) | **<.0001** | **33.6** (1, 451) | **<.0001** | **19.7** (1, 449) | **<.0001** | **66.7** (1, 452) | **<.0001** | NA | NA |
| Chemo × cage | .08 (3, 451) | 1.0 | 1.6 (3, 451) | .2 | **3.5** (3, 449) | **.01** | 1.1 (3, 452) | .3 | .2 (3, 224) | .9 |
| Chemo × comp | .2 (3, 451) | .9 | .2 (3, 451) | .9 | .5 (3, 449) | .7 | .1 (3, 452) | 1.0 | NA | NA |
| Cage × comp | 1.3 (1, 451) | .3 | 1.1 (1, 451) | .3 | .01 (1, 449) | .9 | 1.8 (1, 452) | .2 | NA | NA |
| Chemo × comp × cage | .4 (3, 451) | .8 | .07 (3, 451) | 1.0 | 2.4 (3, 449) | .06 | .2 (3, 452) | .9 | NA | NA |

Note: Significant results in boldface. Chemo = chemotype; Comp = competition. NA = not applicable. Degrees of freedom are in parentheses.

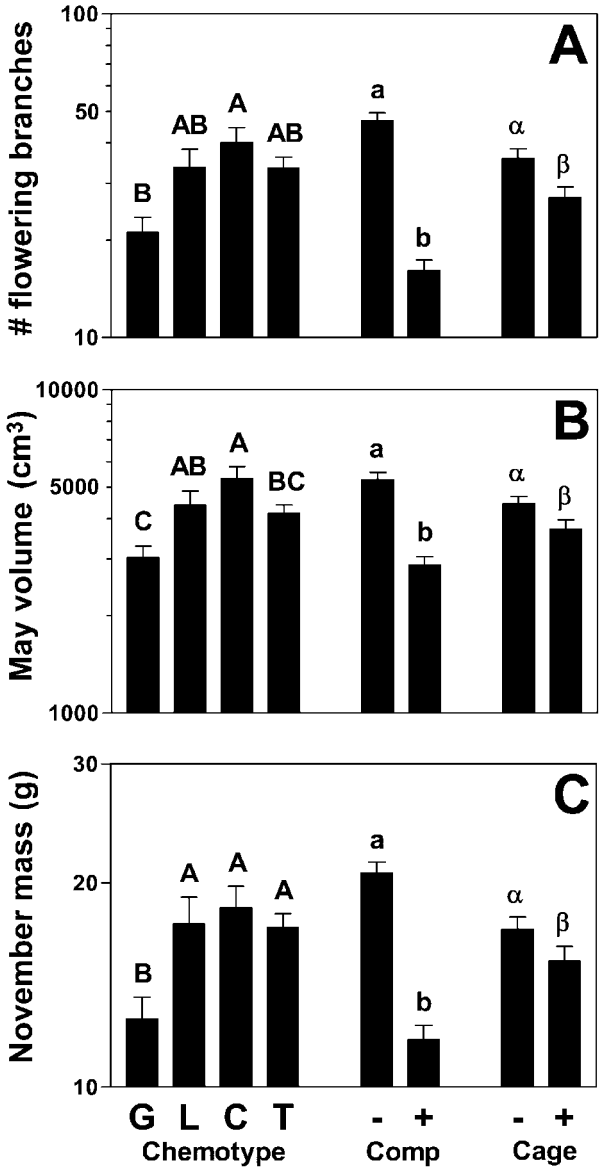


**Figure 2:** Mean (+1 SE) thyme performance under chemotype, competition, and predator exclusion (*cage*) treatments. Thyme performance measured as (*A*) branches with flowers in May, (*B*) volume in May, and (*C*) dry aboveground biomass in November. Competition was either absent (*minus sign*) or provided by *Bromus madritensis* (*plus sign*). Cages either were open and allowed all herbivores and predators access to thyme (*minus sign*) or prevented predator entry and concomitantly allowed buildup of aphids and associated heavy herbivory (*plus sign*). Significant differences ($P < .05$) are indicated by differing letters (for chemotype: *A* and *B*; for competition: *a* and *b*; for cage: $\alpha$ and $\beta$). Detailed statistics are provided in table 1.

dicates that aphids affect thyme but that the effect depends on or is altered by the presence of competing *Bromus*.

For all three thyme response variables, the effect of caging was no longer significant with this aphid × competition interaction in the model. We thus conclude that the effect of caging on thyme was due largely to aphid buildup within predator-excluding cages but that the negative effects of these aphids differed between thyme plants growing with and without competing *Bromus*. To illustrate the magnitude of this interaction between the effects of herbivory and competition, we wished to compare the effects of herbivory and competition acting alone, the effects we observed of the two acting together, and the expected effects of the two acting together with additivity under a multiplicative null model (Sih et al. 1998; Hamback and Beckerman 2003). While effects of competition can be quantified as the percentage change in thyme response variables between presence and absence of *Bromus*, the comparable descriptor for the aphid effect is more complicated because aphid abundance is a continuous variable. To resolve this, we chose zero and the experiment-wide mean as the two levels of aphid abundance from which we calculated the effect of aphids on thyme, and we estimated the effects of aphids at these two abundance levels from regression equations. We regressed log-transformed aphid abundance on each of the three log-transformed thyme response variables separately for thyme plants with and without competition (fig. 3; table 3). For all thyme variables, aphid abundance had significant negative effects on thyme in the absence of competition, but in the presence of competition, aphid effects on thyme were either not detectable (May flower number, November size) or very weak (May thyme size). (These equations, in themselves, show how competition reduces the effects of aphids on thyme by reducing the per capita effects of aphids, i.e., by reducing the regression slopes.) We then back-transformed these equations to calculate the predicted values for each thyme response variable at both levels of aphid abundance and both with and without competition. This generated variable means for each cell of a 2 × 2 factorial, and from these means we calculated the above-mentioned effect sizes (fig. 4). This descriptive exercise showed that the effects of *Bromus* alone are generally stronger than the effects of aphids alone and that the combined effects of *Bromus* and aphids on thyme are approximately 10% less than would be predicted with additivity under a multiplicative null model. This interaction was especially strong for flower number (figs. 3, 4); in this instance, we see that while aphids alone caused a 68% reduction in flowering, the combined effects of aphids and *Bromus* competition was scarcely larger than the effect of competition acting alone.

The regressions of aphid number on thyme response variables suggest that aphids did not affect thyme plants grown with competition, yet the effect of caging on thyme was equally strong on thyme grown both with and without *Bromus* (i.e., no cage × competition interaction for any response variable; table 2). As a result, the negative effect

**Table 2:** Statistical analysis of the mechanism by which caging reduced thyme size and flower production: ANCOVA of treatment effects on thyme variables with aphid number as a covariate

| | May | | | | November | |
|---|---|---|---|---|---|---|
| | Flowering branches | | Thyme volume ($cm^3$) | | Thyme mass (g) | |
| Effect | $F$[a] | $P$ | $F$[a] | $P$ | $F$[a] | $P$ |
| Chemo | .9 | .4 | **3.1** | **.03** | **3.7** | **.01** |
| Cage | .05 | .8 | .9 | .3 | 3.4 | .06 |
| Competition | **65.2** | **<.0001** | **39.7** | **<.0001** | **57.1** | **<.0001** |
| Aphid | 3.6 | .06 | **8.4** | **.004** | 1.0 | .3 |
| Aphid × comp | **8.6** | **.003** | 3.6 | .06 | **4.2** | **.04** |

Note: Analysis performed on cage, competition (comp), chemotype (chemo; all three are discrete factors), and aphid number (continuous factor). Results for all main effects and significant interactions are shown; significant results in boldface. Results for nonsignificant interactions ($P > .10$) are not shown.

[a] df = 1, 433.

of caging on thyme plants grown with competition was transmitted via some mechanism other than aphids. We hypothsized that the negative effect of caging on thyme grown with *Bromus* was due to an increase in *Bromus* biomass within cages. To test this hypothesis, we repeated our test for cage effects just on those thyme plants with competing *Bromus* but with the addition of *Bromus* biomass as a covariate (table 4). For all three thyme response variables, the effect of *Bromus* biomass was significant. With the addition of this covariate, the effects of caging were no longer significant, indicating that increased *Bromus* biomass within cages was likely responsible for most of the negative cage effect on the thyme plants grown with competition.

With the aphid × competition interaction in the model, the effect of chemotype on flower number was no longer significant. Consequently, the effect of chemotype on flowering was likely due in large part to the differential effects of thyme chemistry on aphids (fig. 4). The fact that the aphid × competition interaction was also significant suggests that the effect of chemotype on flowering was due not only to the effect of aphids but also to the variation in the effect of aphids associated with the presence or absence of competition. We thus conclude that aphids are a source of selection on thyme chemistry because of their differential effects among chemotypes, but the strength of this selection varies as a function of thyme competition with *Bromus*.

While it is clear from our analyses that the effects of aphids and competing *Bromus* on thyme performance (both size and flowering) interact, we note that our results are somewhat conflicting as to whether they interact specifically on selection for thyme chemotypes (i.e., whether the differential effects of aphids among chemotypes vary with competition); we show that aphids are the mechanism by which chemotype affects flowering, and we show that competition from *Bromus* reduces (or eliminates) the effect of aphids on flowering (fig. 3). Consequently, we should expect to see a chemotype × competition interaction in our original statistical analyses (table 1), but we do not. One explanation for these conflicting results is as follows: were chemotype to affect thyme flowering not only via aphids but also via some other unidentified mechanisms that are not contingent on competition, this second mechanism would reduce the strength of the chemotype × competition interaction, possibly below the level of statistical detection.

## Discussion

A significant finding of our study is the detection of direct and indirect connections between thyme, its *Bromus* competitors, aphid herbivores, and aphid predators (fig. 4). We first comment on the complexities of the structure of the food web centered on thyme. We then analyze the differences in performance among chemotypes. Finally, we discuss how food web structure differs among thyme plants of varying chemotypes and the implications of these different food web structures with respect to natural selection on, and the evolution of, thyme secondary chemistry.

### *Thyme Food Web Structure*

There are significant direct and indirect effects of herbivores and predators on thyme performance. Predators, such as spiders and coccinellids, had strong direct negative effects on aphids, as shown by the four- to sixfold increase of aphids on C, G, and T plants in cages. Interestingly, aphids on L plants were not affected by predator exclusion, perhaps because predators showed chemotype-specific behavior and avoided L plants. Aphids, in turn, had direct negative effects on thyme, as shown by the lower reproduction and size of thyme within closed cages, where aphids were abundant. As a result, predators had a positive indirect effect on both thyme size and flowering via a trophic cascade. It is surprising that this cascade occurred for all chemotypes, despite the fact that we did not detect a predator effect on aphids on L plants. Given that our sample size was particularly low for L plants, it may be that we failed to detect a true cage effect on L plants (i.e., a case of Type I error).

Competition from *Bromus* reduced thyme size. As a result, aphid abundance on thyme plants was reduced by 40% when thyme was adjacent to *Bromus*. This reduction simply reflects the relationship between thyme size and aphid numbers, because competition did not change aphid

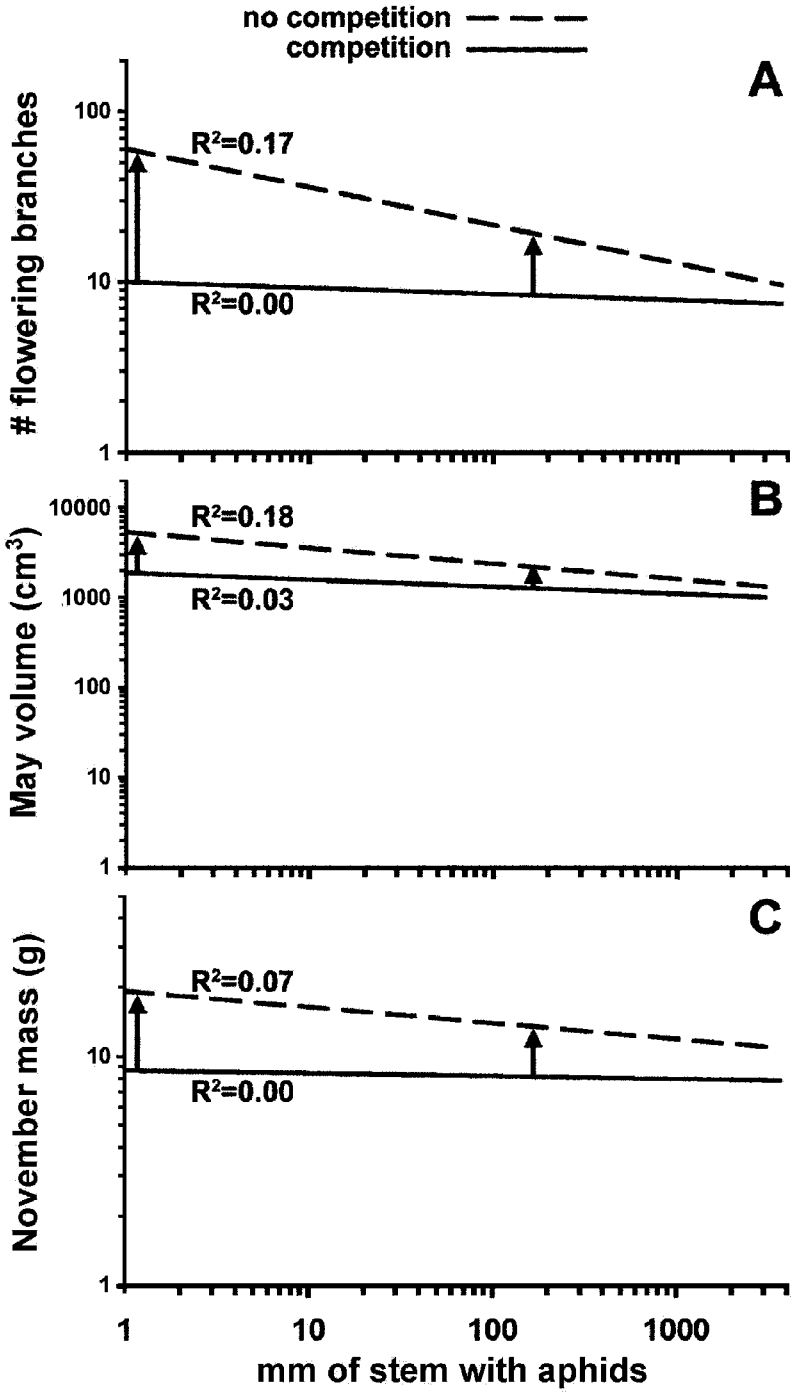


**Figure 3:** Regressions of thyme response variables on aphid abundance (mm of stem with aphids) separately for plants with and without competition. The slopes of each pair of lines were either significantly different ($P < .05$ for flowering [*A*] and November size [*C*]) or marginally so ($P = .0589$ for May size [*B*]). Arrows show the two levels of aphid abundance (0 vs. the experiment-wide mean) under which the effects of competition are compared in figure 4.

**Table 3:** Statistical analysis of the mechanism by which caging reduced thyme size and flower production: regression of aphid number on thyme variables separately for each competition level

| | May | | | | | | November | | |
|---|---|---|---|---|---|---|---|---|---|
| | Flowering branches | | | Thyme volume ($cm^3$) | | | Thyme mass (g) | | |
| Competition level | $F^a$ | $P$ | $R^2$ | $F^a$ | $P$ | $R^2$ | $F^a$ | $P$ | $R^2$ |
| Without competition | **48.9** | **<.0001** | **.17** | **52.6** | **<.0001** | **.18** | **17.0** | **<.0001** | **.07** |
| With competition | 1.2 | .3 | .005 | **8.4** | **.004** | **.03** | .4 | .5 | .002 |

Note: Analysis performed on cage, competition, chemotype (discrete factors), and aphid number (continuous factor). Results for all main effects and significant interactions are shown; significant results in boldface. Results for nonsignificant interactions ($P > .10$) are not shown.

[a] df = 1, 232.

density. As a result, *Bromus* can be seen to have an indirect negative effect on aphids via thyme, mediated by changes in resource abundance and not a modification of interaction between aphids and their host plants.

The relationship between predators, aphids, and thyme depends on whether *Bromus* competitors are present or absent. In the absence of *Bromus*, there is a significant effect of aphid numbers on thyme performance, but this effect disappears in the presence of *Bromus* (figs. 3, 4). This interaction between the effects of aphid herbivores and competing *Bromus* can also be viewed from the perspective of competitor effects: the negative effect of *Bromus* on thyme was lower in the presence of high numbers of aphid herbivores. As a result of this aphid-*Bromus* interaction, predators provided only an indirect benefit to thyme plants growing without competition.

Despite the fact that aphids only affected thyme performance in the absence of competition, we found a significant negative effect of caging on thyme grown both with and without *Bromus*. While the cage effect on thyme grown in the absence of competition reflects the exclusion of aphid predators, the cage effect on thyme growing with *Bromus* was attributable to increased *Bromus* biomass in cages. We did not record *Bromus* herbivores, but it is possible that their exclusion by cages was responsible for this effect.

In their review of 10 studies factorially manipulating herbivory and competition, Hamback and Beckerman (2003) found two studies showing significant nonadditivity in their effects on plant performance, with one interaction being antagonistic and the other being synergistic. Our results thus bolster the notion that herbivory and competition can act nonadditively, but a predictive understanding of where and when such higher-order effects are likely to occur or whether such an interaction is likely to be additive or nonadditive is still to be achieved.

### *Performance of Individual Chemotypes*

The thyme chemotypes studied showed evidence of differential performance, as measured by both size and reproduction (fig. 2; table 1). The most clear-cut pattern was that plants of the phenolic C showed significantly higher fitness (i.e., reproduction and biomass) than those of the nonphenolic G, with the other chemotypes (phenolic T and nonphenolic L) having intermediate values. This pattern of a phenolic outperforming a nonphenolic is consistent with the results of an earlier, common-garden experiment performed within 50 m of this study (Thompson et al. 2004). A smaller size and reduced flowering of G chemotypes also matches earlier results obtained in laboratory conditions, which included a general lack of repellency of G plants to herbivores (Linhart and Thompson 1995, 1999) and the relative lack of G allelopathic effects on several plant competitors (Tarayre et al. 1995; Y. B. Linhart, P. Gauthier, and J. D. Thompson, unpublished data). The effects of chemistry are more complicated than a simple phenolic versus nonphenolic comparison. For example, G and L differed in their repellency to aphids, perhaps because the changing chemistry of L, which begins life as a phenolic C or T (see "Methods"), made it essentially a "moving target" (sensu Adler and Karban 1994). Differences in performance between C and T are not readily explainable in this fashion but underscore the individuality of the compounds in different chemotypes, even in comparisons of similar isomers (Bais et al. 2002).

### *Implications of Food Web Structure for Selection on Thyme Chemotypes*

The four thyme chemotypes do not show differential growth or flowering with respect to the effects of competition from *Bromus* (i.e., no chemotype × competition interaction). Although we do not detect differential resistance among chemotypes to the effects of competition, this does not imply that monoterpenes as a group have no influence on thyme fitness via allelopathic effects on competitors. Elsewhere, we have documented that thyme-derived monoterpenes reduce the growth of potential thyme competitors (Tarayre et al. 1995; Ehlers and

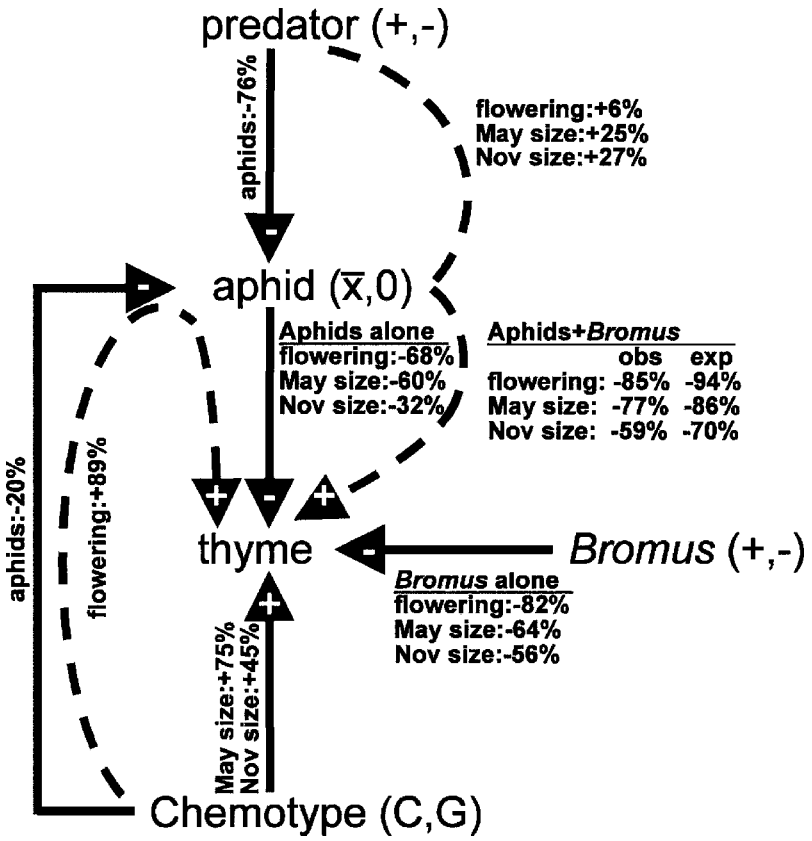


**Figure 4:** Summary of predator, *Bromus*, and chemotype effects on thyme and aphids. Effects are transmitted from the base of the arrow to the head of the arrow. Solid lines represent direct effects. Dashed lines represent indirect effects. The sign of an effect is shown within the arrowhead. Effect sizes (next to arrows) are calculated from back-transformed treatment means shown in figures 1 and 2, except for the indirect effects of predators on thyme that are taken only for thyme plants grown without competition (see text for details). The effects of aphids on thyme are calculated from regression equations of thyme variables regressed on aphid number. Effect sizes are calculated from comparisons of the predicted values for thyme variables with aphid number set to 0 and those with aphid number set to the experiment-wide mean. Because aphid effects interacted with competition, these values were calculated from separate regression equations for thyme plants grown with and without competing *Bromus* (see fig. 3). The combined effect of aphids and *Bromus* we observed (*obs*) are presented next to the expected (*exp*) effects for additivity under a multiplicative null model.

Thompson 2004; Y. B. Linhart, P. Gauthier, and J. D. Thompson, unpublished data). What our current results do suggest is that in the current setting such beneficial actions of secondary chemistry via allelopathy did not differ among the thyme chemotypes we investigated.

The differences in flowering among thyme chemotypes were attributable to variation in aphid abundance (fig. 4). Yet we also saw that this effect of aphids was highly dependent on the presence or absence of competing *Bromus*, and in fact there was no detectable effect of aphids on thyme flowering in the presence of competition (fig. 3*A*). While we found an indirect effect of cages on all thyme plants, our analyses suggest that predators provided only an indirect benefit to thyme via removal of aphids on thyme plants grown without competition. Consequently, whether aphid herbivores affect thyme fitness and select for C chemotypes and whether predators affect thyme fitness by regulating aphid abundance depend largely on the presence or absence of competition with *Bromus*.

In contrast to the above results for thyme flowering, the differences in plant size among thyme chemotypes were not due to the effects of either herbivory or competition. The factors responsible for the chemotype effect on thyme size are not identifiable at this time. There may be inherent differences in the costs of producing these molecules (Gershenzon 1994). In any case, it is noteworthy that the mechanisms by which chemotype influences thyme performance differ between flowering and size, despite the fact

**Table 4:** Statistical analysis of the mechanism by which caging reduced thyme size and flower production: ANCOVA of treatment effects on thyme variables with *Bromus* biomass as a covariate (for competition only)

| | May | | | | November | |
|---|---|---|---|---|---|---|
| | Flowering branches | | Thyme volume ($cm^3$) | | Thyme mass (g) | |
| Effect | $F^a$ | $P$ | $F^a$ | $P$ | $F^a$ | $P$ |
| Cage | 1.2 | .3 | .4 | .5 | 1.9 | .2 |
| Grass | **6.5** | **.01** | **4.5** | **.04** | **9.3** | **.003** |
| Cage × grass | 2.1 | .2 | 1.4 | .2 | **4.0** | **.05** |

Note: Analysis performed on cage, competition, chemotype (discrete factors), and aphid number (continuous factor). Results for all main effects and significant interactions are shown; significant results in boldface. Results for nonsignificant interactions ($P > .10$) are not shown.

[a] df = 1, 229.

that reproduction and size are often observed to be highly correlated (Harper 1977; Crawley 1997).

### *Conclusions: Evolutionary Questions in a Community Ecology Setting*

The factors that influence the maintenance of genetic variability are usually thought of as evolutionary issues. For example, variability in plant chemistry is implicitly thought to involve adaptation and is studied from that perspective. Conversely, the possible influences of predators and herbivores on plant-plant competition are usually considered to be ecological issues. In this study, we combine the two approaches to ask what happens when we study the effects of variation in one presumably adaptive trait in multiple ecological settings. Specifically, how might our understanding of the evolution of this trait be affected by a diversity of interactions that includes competition, herbivory, and predation?

One possible result is that all these interactions are orthogonal, that is, independent, of one another. If that is the case, then an understanding of the effect of chemistry in relatively simple laboratory conditions might be a good predictor of its performance in field conditions. Conversely, if the effects of specific plant chemical features change among various ecological settings, then a reductionist perspective is not permissible: one must accept the importance of higher-order interactions and recognize that chemical and other types of phenotypic variation depend on the specific set of multitrophic interactions within which they are situated.

On the basis of past work in this system, we expected to observe an influence of chemotype on the interactions of thyme with the community of organisms in which it grows (Linhart and Thompson 1995, 1999). This past work with thyme, as well as studies from other systems (e.g., van Dam and Hare 1998; Siemens et al. 2002; Glawe et al. 2003), supports the notion that chemical variation in plants can be maintained both by the relatively simple diversifying selection scenarios associated with predictable performance in alternative niches (e.g., Spiess 1977) and also as a result of combinations of different biotic and abiotic challenges to plant growth and reproduction, which select for differing or sometimes opposing chemotypes. In such an evolutionary model, which might be thought of as multidirectional selection, chemotype variation among populations, or within populations over time, is attributable to variation in the combination and intensity of these diverse selective agents.

In the past, these models of selection were based on the implicit assumption that variation in chemotype selection was due to variation in the abundance of the selecting agents but that the strength of selection imposed on plant chemistry by an herbivore or competitor was a relatively fixed quantity. Our current results modify this evolutionary model by illustrating that the effects of diverse selective agents are not, in fact, stable. The same biotic interaction that may provide strong selection under one set of conditions (e.g., aphid herbivory in the absence of plant competition) may provide little or no selection under an alternate set of conditions (e.g., aphid herbivory in the presence of plant competition). While many studies have shown nonadditivity, ours is one of the few (but see Agrawal 2004) to explicitly test for and document nonadditivity in selection from multiple factors. Such nonadditivity may produce extremely fine-grained spatial and temporal mosaics of selection.

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# Appendix from Y. B. Linhart et al., "A Chemical Polymorphism in a Multitrophic Setting: Thyme Monoterpene Composition and Food Web Structure"

## (Am. Nat., vol. 166, no. 4, p. 000)

**Table A1**
Means of thyme response variables

| Chemotype, caging | Comp | May | | November |
|---|---|---|---|---|
| | | Flowering branches | Thyme volume ($cm^3$) | Thyme mass (g) |
| Geraniol: | | | | |
| No | No | 3.31 (.19) | 8.35 (.11) | 2.73 (.12) |
| No | Yes | 2.12 (.20) | 7.43 (.17) | 2.07 (.13) |
| Yes | No | 2.48 (.28) | 7.40 (.24) | 2.40 (.15) |
| Yes | Yes | 1.79 (.21) | 6.84 (.27) | 1.62 (.18) |
| Linalol: | | | | |
| No | No | 3.40 (.35) | 8.54 (.18) | 2.88 (.12) |
| No | Yes | 2.41 (.48) | 7.62 (.33) | 2.38 (.32) |
| Yes | No | 3.07 (.34) | 7.86 (.37) | 2.76 (.21) |
| Yes | Yes | 2.02 (.34) | 7.22 (.33) | 1.98 (.21) |
| Carvacrol: | | | | |
| No | No | 3.89 (.23) | 8.57 (.12) | 3.04 (.11) |
| No | Yes | 2.66 (.28) | 7.89 (.26) | 2.56 (.13) |
| Yes | No | 3.27 (.35) | 8.44 (.29) | 2.91 (.20) |
| Yes | Yes | 2.22 (.40) | 7.83 (.27) | 2.08 (.23) |
| Thymol: | | | | |
| No | No | 3.63 (.15) | 8.38 (.13) | 2.92 (.10) |
| No | Yes | 2.11 (.18) | 7.63 (.12) | 2.36 (.09) |
| Yes | No | 2.80 (.25) | 7.86 (.18) | 2.89 (.09) |
| Yes | Yes | 2.00 (.19) | 7.43 (.16) | 2.21 (.10) |

**Note.** Means ($\pm 1$ SE) of log-transformed May thyme flowering and volume and November thyme mass for chemotype, predator effects on thyme (caging), and competition (comp).