REPORTS

THORNS AS INDUCED MECHANICAL DEFENSE IN A LONG-LIVED SHRUB (*HORMATHOPHYLLA SPINOSA*, CRUCIFERAE)

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Abstract. We have experimentally tested under natural conditions the cost and inducibility of thorns in *Hormathophylla spinosa* (Cruciferae), a shrub heavily damaged by ungulates. We first excluded ungulates from 40 shrubs, 20 in each of two years (1992 and 1998), to test for a negative phenotypic correlation between thorn density and seed production. Next, we removed thorns from 20 protected shrubs to compare seed production in thornless shrubs vs. control plants (also excluded from ungulates). Finally, we monitored the change in thorn production for three years in the 1998 ungulate-exclusion experiment to test whether plants growing in an herbivore-free environment would reduce thorn production. Thorns seem to be phenotypically costly for *H. spinosa*, since a negative correlation with percent fruit set was found in both years, and thorn removal in the second experiment enhanced seed production. In addition, thorn density significantly decreased from the first to the second and the third years in shrubs excluded from ungulates in the 1998 experiments. These results suggest that thorns are induced defense in *H. spinosa*.

Key words: Cruciferae; defense, cost of; Hormathophylla spinosa; *induced defenses; mammal herbivory; thorns.*

INTRODUCTION

Plants are defended against herbivores by many different kinds of chemical and/or mechanical traits, which can be constitutive or induced (Karban and Baldwin 1997, Agrawal 1999*a, b*). Most plant traits are thought to have a fitness cost, whether metabolical, physiological, reproductive, or any other kind (Simms 1992, Skogsmyr and Fagerström 1992, Zangerl and Bazzaz 1992, Mauricio 1998, Agrawal et al. 1999, Strauss et al. 1999). Costs of defenses have been proposed as a main factor driving the evolution of induced defenses (Karban and Baldwin 1997, Karban et al. 1997, Agrawal et al. 1999, Agrawal 2000). Resistant plants are more fit in the presence of herbivores, when the benefit of protection against herbivores surpasses the cost of defense production, but are less fit than susceptible plants in enemy-free environments, since costs are expressed, but not the benefit (Karban and Baldwin 1997). By using induced traits, plants occurring in a herbivore-free environment avoid investing in unnecessary, costly defenses (Agrawal et al. 1999). Since damage varies over space and time, plants use damage as a signal to induce resistance traits (Agrawal 1999*a*), and relaxation of these nonconstitutive traits

occurs gradually after the cessation of herbivore attack (Karban and Baldwin 1997, Young and Okello 1998). Induced responses are expected to be more frequent in long-lived plants, since they will probably experience more radical environmental changes during their lifetime than short-lived plant species (Karban and Baldwin 1997).

Costs are not expressed uniformly in all environments, being stronger in environments where resources are limiting (Baldwin et al. 1990, Karban and Baldwin 1997). However, most experiments have been performed under controlled, nonnatural environments, which provide unlimited resources or other unrealistic circumstances and where costs are presumably less intense (Bergelson and Purrington 1996, Karban and Baldwin 1997).

Several kinds of physical traits function as defenses against herbivores (e.g., Cooper and Owen-Smith 1986, Young 1987, Milewski et al. 1991, Gowda 1996, 1997, Obeso 1997, Cooper and Ginnett 1998, Young and Okello 1998, Agrawal 2000). In some plant species, these mechanical defenses are induced, increasing in size and/or number in response to damage (e.g., Young 1987, Bazely et al. 1991, Milewski et al. 1991, Gowda 1997, Obeso 1997, Young and Okello 1998, Agrawal 1999*a*, 2000). Despite this growing empirical evidence, only scarce and equivocal information exists about the costs of these mechanical traits for the plant, and most

such results concern small structures such as trichomes. Whereas no cost of trichome production was found for *Brassica rapa* (Agren and Schemske 1993, 1994), substantial fitness cost associated with the production of trichomes has been found in *Arabidopsis thaliana* (Mauricio and Rausher 1997, Mauricio et al. 1997, Mauricio 1998), *Raphanus raphanistrum* (Agrawal et al. 1999), *Lepidium virginicum* (Agrawal 2000), and *Datura wrightii* (Elle et al. 1999).

Hormathophylla spinosa Küpfer (Cruciferae) is a long-lived, iteroparous, thorny shrub from the Western Mediterranean. We have demonstrated that the many thorns produced by this shrub species act as defenses against ungulates, since they decrease herbivory intensity and enhance female fitness (Gómez and Zamora 2000*a, b*). In fact, in a four-year field study carried out on three different populations in the Sierra Nevada, we found that ungulates exert directional selection for increased thorn production (Gómez and Zamora 2000*a*). However, we also found spatial variation for this defensive trait, since populations with low herbivory pressure are composed of plants with fewer thorns than populations with high herbivory pressure (Gómez and Zamora 2000*a*). In this paper, we experimentally investigate (1) the phenotypic cost of thorns for *H. spinosa* and (2) the ability of this plant species to relax thorn production in the absence of herbivore damage.

The Study System

Hormathophylla spinosa is abundantly distributed in the high mountains from Southern France to Northern Africa. It produces many flowers (482–74 343 flowers/plant each year) every year (Gómez and Zamora 1992, Gómez 1993). Flowers are arranged in inflorescences of 8–20 flowers each, which grow beyond the hemispherical surface of the shrub. This species does not reproduce vegetatively.

In the Sierra Nevada (southeastern Spain), this thorny crucifer is frequently attacked by many different kinds of vertebrate and invertebrate herbivores. Ungulates (mainly domestic sheep *Ovis aries* and Spanish ibex *Capra pyrenaica*, Bovidae; see Gómez 1993, 1994, Gómez and Zamora 1994) feeding only on flowers, green fruits, and ripe fruits, especially reduce *H. spinosa* reproductive output, destroying up to 90% of the potential seeds in some locations and years (Gómez and Zamora 2000*b*).

The secondary branches of *H. spinosa* form small, rigid thorns, usually located at the basal portion of each inflorescence, and associated with bractea. In 1–2 wk the thorns are fully formed. In addition, the lignified stems of some old infructescences stay in plants acting also as thorns. Old thorns remain in these infructescence stems for several years.

Methods

Testing the phenotypic cost of thorns

Ungulate exclusion and thorn-fitness relationship.— This first experiment investigated the putative cost of thorn production by determining the correlation between thorn production and seed set in the absence and presence of herbivores (cf. Simms and Rausher 1989, Baldwin et al. 1990, Simms 1992, Zangerl and Bazzaz 1992, Simms and Tripplett 1994, Mauricio 1998). If thorns are costly, we expected to find a significant negative correlation between thorns and reproduction in the absence of herbivores, since only the cost but not the benefit of displaying thorns is acting.

Before ungulates started to feed on *H. spinosa* but after snowmelt (late May), we marked 40 shrubs in 1992 and 50 in 1998. Twenty randomly selected plants each year were individually excluded from ungulates by covering each with a fence. The fence had 5-cm mesh size to allow the passage of pollinators and thus avoid interference with pollination. At the beginning of the experiment we quantified the density of thorns in each shrub, both experimental and control shrubs, by counting them in four 25-cm^2 quadrats located randomly on the surface of the shrubs (''thorn density'' hereafter). We also determined the size (in cm^3, estimated as height × largest diameter × smallest diameter) of each experimental shrub, to control for the potential effect of size and age in thorn production pattern. In this shrub species, size is strongly correlated with age (Age = 4.926 + 0.018[size]; R^2 = 0.96; P = 0.00001; N = 20; J. Gómez and R. Zamora, *unpublished data*).

Ten randomly selected inflorescences were labeled in each of the 90 shrubs, and we counted the number of flowers produced and, before seed dispersal, the number ripening to fruit. Thus, as an estimate of the plant's reproductive success, we used the fruit:flower ratio expressed as a percentage (''percent fruit set'' hereafter). Percent fruit set is a good predictor of seed production in *H. spinosa* (inflorescence seed production = −0.005 + [0.258·(% fruit set)]; R^2 = 0.81; P = 0.0001; N = 110 shrubs monitored for 4 yr). In addition, we think that this relative estimate of *H. spinosa* reproductive success is more adequate than any absolute estimate to check energy costs and allocations, because of its relative independence from shrub size. Nevertheless, we also correlated thorn density against flower production of the shrubs, to check whether the potential relationship with percent fruit set could be due to changes in flower production with thorn density rather than to changes in fruit production.

Correlations were evaluated by Spearman rank correlations due to the limited sample size (parametric correlations showed similar results and are not given here). We performed one analysis for each year, with shrubs as sampling units, using the NPAR1WAY procedure in the SAS statistical package (SAS Institute 1997).

Effect of experimental thorn removal on plant fitness.—In a second experiment, we manipulated thorn presence to quantify the reproductive success of shrubs with and without thorns. The logic underlying this

method is that if there is no cost, thornless individuals will have a similar fitness as individuals with thorns in the absence of herbivores. By contrast, if thorns are costly, thornless shrubs will have significantly higher fitness than shrubs with thorns (Simms 1992, Zangerl and Bazzaz 1992, Agren and Schemske 1993, Karban and Baldwin 1997).

To test this, in 1995 we excluded 40 shrubs from ungulates. Thorn size and number was quantified for each shrub. Thus, we randomly selected 20 shrubs, from which we experimentally removed the thorns from ~50% of their surface. After this, we randomly labeled 10 inflorescences. Thorns were removed at the beginning of vegetative growth, just after snowmelt, when they were already determined but not completely formed. Thorn removal was carried out with scissors, taking care not to damage other tissue, whether reproductive or vegetative, in order to avoid side effects due to wounding. In the other 20 shrubs, we left the thorns untouched and labeled 10 inflorescences, as controls. For each of the 40 experimental shrubs we determined the percent fruit set as an estimate of fitness, using the same procedure as explained above. Afterward, differences in the fruit sets between control and thornless plants were analyzed by a one-way ANOVA (GLM procedure, SAS 1997), with arcsine of percent fruit set as the dependent variable, treatment as the fixed factor, and shrub as the experimental unit.

Testing the induction of thorns

We also investigated the inducibility of thorns by measuring the decrease in thorn production when shrubs grew in experimental herbivore-free environments. The logic underlying this method is that, if costly thorns are inducible, shrubs in environments without herbivory will not invest in unnecessary thorns, thus saving the cost associated with their production (Karban 1997, Agrawal 1999a, b, 2000, Agrawal et al. 1999). Thus, we expect a relaxation of this putative induced defense (sensu Young and Okello 1998). The shrubs labeled in 1998 were therefore monitored over a period of three years; 1998, 1999, and 2000; quantifying thorn production and fruit set each year for both control and herbivore-exclusion treatments.

The temporal, between-year relaxation in thorn production in herbivore-free environments was tested by means of a multivariate repeated-measures ANOVA (MANOVAR) employing profile analysis (PROC GLM; von Ende 1993). We used the multivariate approach because data did not exhibit homogeneity of variance ("compound symmetry" assumption), and the within-subject model did not consist of independent orthogonal components ("sphericity" assumption or Huynh and Feldt condition; von Ende 1993), as tested by Mauchly's criterion (Mauchly criterion = 0.864, χ^2 = 6.82, $P = 0.03$, with two degrees of freedom). In this analysis, thorn density per shrub was introduced as dependent variable, environment (ungulate presence
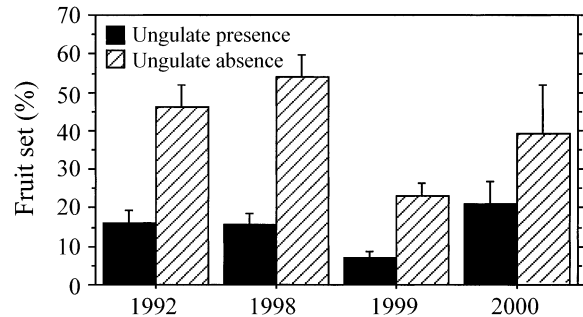

FIG. 1. Differences in percent fruit set (i.e., ratio of fruit to flowers produced) for plants excluded and nonexcluded from ungulates in 1992, 1998, 1999, and 2000. Figures are means + 1 SE.

vs. absence) was introduced as fixed between-subjects factor, the three years of study as within-subject factor, shrubs as the error term for the between-subjects factor, and the year × shrub interaction was included in the error term for the within-subject factor. If relaxation occurred in one environment more than in the other, we expected a significant environment × time interaction in thorn production. Afterward, we tested whether there were between-treatment differences in thorn production in each year by performing one-way ANOVAs (von Ende 1993).

RESULTS

Testing the phenotypic cost of thorns

Ungulate exclusion and thorn-fitness relationship.— Ungulate herbivory was similarly high during all years. Ungulates ingested 80.1 ± 3.05% (mean ± 1 SE) of the reproductive structures of control shrubs in 1992, 78.2 ± 3.2% in 1998, and 77.9 ± 4.5% in 1999. Consequently, ungulates greatly affected percent fruit set of the shrubs in 1992 ($F_{1,38} = 50.05$, $P < 0.0001$), 1998 ($F_{1,48} = 77.55$, $P < 0.0001$), 1999 ($F_{1,48} = 17.20$, $P = 0.0002$), and 2000 ($F_{1,48} = 10.23$, $P = 0.002$; one-way ANOVAs, Fig. 1). Exclosures were effective, since ungulates did not eat any fruit or flower inside exclosure any year.

There were no statistical differences in thorn density between control and excluded shrubs at the start of both the 1992 (48.0 ± 3.3 vs. 49.5 ± 5.5; $F_{1,38} = 0.06$, $P = 0.81$) and 1998 experiments (39.7 ± 2.7 vs. 43.7 ± 3.5; $F_{1,48} = 0.21$, $P = 0.65$). In addition, thorn density was not significantly related to the size of the shrub in any year (all $P > 0.41$, linear regression analyses).

There was no relationship between thorn density and flower production of the shrubs, irrespective of ungulate presence (1992: $r_s = 0.31$, $P = 0.19$; 1998: $r_s = -0.30$, $P = 0.10$) or absence (1992: $r_s = 0.29$, $P = 0.26$; 1998: $r_s = -0.07$, $P = 0.74$). However, there was a significant negative relationship between thorn density and percent fruit set in shrubs excluded from ungulates both in 1992 ($r_s = -0.507$, $n = 20$ plants, P
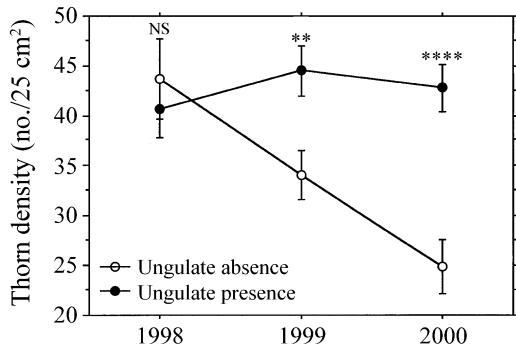
FIG. 2. Between-year differences in thorn density (number of thorns/25 cm^2 ± 1 SE) for plants excluded and nonexcluded from ungulates for 1998, 1999, and 2000. Within-year comparisons done with one-way ANOVAs; NS = not significant, ** $P < 0.01$, **** $P < 0.0001$.

= 0.03, Spearman rank correlation) and 1998 (r_s = −0.616, n = 20 plants, P = 0.007). In both years, thorns explained >20% of the variability in the response variable ($R^2 > 0.21$, according to a simple linear regression). The correlation between percent fruit set and thorn density, although positive, was not significant when ungulates were present ($P > 0.1$, Spearman rank correlations).

Effect of artificial removal of thorns on plant fitness.—Percent fruit set was significantly higher in shrubs from which thorns were removed (57.6 ± 5.2%) than in control shrubs (33.7 ± 5.6%, $F_{1,38}$ = 5.43, P = 0.02).

Relaxation of thorn production

The profile analysis demonstrated that both factors, ungulate presence (Wilks' λ = 0.843, $F_{1,48}$ = 8.92, P = 0.004) and time (Wilks' λ = 0.751, $F_{2,47}$ = 7.79, P = 0.001; MANOVAR), significantly affected thorn production of the experimental shrubs. Most importantly, the slopes of the response curves against time differed significantly between ungulate-excluded shrubs and control shrubs (Interaction term Wilks' λ = 0.700, $F_{2,47}$ = 10.04, P = 0.0002; MANOVAR). Whereas thorn density remained similar in control shrubs throughout the three study years, it significantly decreased (linearly) in excluded shrubs from the first to the second and the third experimental year (Fig. 2). As a consequence, thorn density was significantly different between these two groups of shrubs both in 1999 ($F_{1,48}$ = 8.069, P = 0.007) and 2000 ($F_{1,48}$ = 23.318, P = 0.0001, one-way ANOVA).

Furthermore, the significant negative correlation occurring between thorn density and percent fruit set for excluded shrubs during the first year of the experiment (1998) disappeared during the second year (r_s = −0.172, n = 20 plants, P = 0.492) and third year of ungulate exclusion (r_s = −0.337, n = 20 plants, P = 0.173).

DISCUSSION

The negative phenotypic correlations between thorn production and percent fruit set, found in both years with two different groups of shrubs excluded from ungulates, show that shrubs with higher thorn density had lower female fitness than shrubs with lower thorn density in an ungulate-free environment. Although we did not account for male fitness or for lifetime fitness (something very difficult to get in this system), our results are consistent with the idea that thorn production is costly for *H. spinosa*. The absence of positive effect of thorns on plant fitness when ungulates were present can be due to several reasons. We have reported elsewhere that thorns benefit plant seed production, but there is important variability in this relationship, the effect of thorns on fitness being significantly positive only when ungulate damage is very intense (Gómez and Zamora 2000a). Furthermore, sample size was not large in this study, thereby leading us to use nonparametric tests, and thus, although the relationship between thorns and fitness was positive, the limited sample size might have precluded any significant effect.

The significant increase in fruit production after experimental thorn removal, up to 58% more fruits in thornless shrubs than in control shrubs, also suggests that thorns may be costly to the plant. The correlation between thorn removal and fruit production might also be due to shrub compensation against tissue removal. However, we believe that this possibility is very unlikely in our system, since we injured as little tissue as possible, and because as far as we know, plants usually compensate by producing tissue similar to that damaged (Strauss and Agrawal 1999).

Although phenotypic data have to be viewed cautiously since environmental covariances between the trait and fitness may cause the phenotypic covariance to differ in both sign and magnitude from the underlying genotypic covariances (Simms 1992, Mauricio 1998), we believe that these two independent results provide some evidence that thorns, a mechanical defensive structure deterring large mammals in many plant species (Gowda 1996, 1997, Cooper and Ginnett 1998), can be costly for *H. spinosa*. The life history of *H. spinosa*, a long-lived (up to 80-yr-old) iteroparous shrub, makes it highly impractical to gather information on its genetic variation. Nevertheless, phenotypic benefits and costs in themselves provide valuable information about the adaptive value of phenotypic variation in plant defense (Agrawal 1999b, 2000), and other studies have also reported phenotypic correlations as strong evidence of the cost of defenses (see, e.g., Baldwin et al. 1990, Karban 1993, Gianoli and Niemeyer 1997, Agrawal 2000). As far we know, our study is the first to provide data on the cost of a mechanical defense against vertebrate herbivores.

Several nonexclusive proximate reasons can explain why mechanical structures like thorns are costly for *H.*

spinosa. This species needs to produce its thorns every year, each time the shrubs produce new inflorescences, since they are directly grown on to the inflorescence stems. This constant production could be an important factor increasing the resource-based cost of these structures, because the shrub has to divert resources to new thorns every year. In addition, thorns in *H. spinosa* are located at the basal portion of the inflorescences (see *The study system*), which highly precludes the possibility that thorns can contribute to their own growth. Moreover, in many plants the cost of a trait depends on the environmental context (Zangerl and Bazzaz 1992, Elle et al. 1999), with the allocation theory predicting more intense trade-offs under resource limitation (Bergelson and Purrington 1996). In this respect, in contrast to most studies which usually investigate costs in controlled environments, we have quantified the cost of thorns not in the greenhouse but in the harsh environment which *H. spinosa* and its herbivores inhabit, the Mediterranean high mountains.

Our most important finding was that thorn density steadily decreased when ungulates were excluded from plants. This result suggests that thorns in *H. spinosa* are plastic structures that can be induced by ungulate herbivory and relaxed after damage cessation (see Obeso 1997 and Young and Okello 1998 for similar results). We surmise that the same factor that confers a high cost to thorns, the necessity of their yearly production, also provides the plant with the ability to regulate the amount of thorns needed depending on the level of herbivory the previous year. By allocating to the defense only when needed, the plant may save resources for growth and reproduction. In fact, the decrease in thorn production over time occurring in the ungulate-excluded shrubs resulted in a concomitant decrease in the cost of thorns, since the negative phenotypic correlation between thorns and fitness disappeared in 1999. This empirical result supports the idea that induction is a major mechanism to save cost of resistance traits (Karban et al. 1997).

For an induced defense to be adaptive, it must be positively correlated with fitness in an environment with high herbivory pressure but negatively correlated with fitness in the absence of herbivores if the trait is costly (Agrawal et al. 1999) or not correlated at all if the trait imposes no cost to the plant (Dudley 1996, Roy et al. 1999). As far we know, defensive characters have been reported as adaptive plastic traits for only three plant species (Baldwin 1998, Agrawal 1999*a*, 2000). *Hormathophylla spinosa* thorns have been shown to be a defense against ungulates in the Sierra Nevada, decreasing damage and subsequently increasing plants fitness in those populations with high herbivory pressure (Gómez and Zamora 2000*a*). Since the induced phenotype has a higher fitness in an environment with strong herbivory, whereas the noninduced phenotypes have a higher fitness in an environment with low herbivory, thorns in *H. spinosa* could be con-

sidered adaptive plastic traits (Dudley 1996, Dudley and Schmitt 1996, Agrawal 1999*b,* Agrawal et al. 1999, Roy et al. 1999). This suggests that the higher thorn density we found in shrub populations suffering heavy ungulate damage (see Gómez and Zamora 2000*a*) is a consequence of the ability of this long-lived plant to induce thorn production when ungulate damage is intense rather than a constitutive adaptation to local damage regimes.

In conclusion, our experiments suggest that thorns, a defensive trait against ungulate herbivory, are costly for *H. spinosa*. More importantly, this study has demonstrated that thorns are plastic traits that can be induced under strong herbivory damage and relaxed in herbivore-free environments.

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