TRADE-OFFS BETWEEN REPRODUCTION AND THORN PRODUCTION IN *ROSA MULTIFLORA*

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ABSTRACT

Trade-offs are an important aspect of evolutionary ecology. Our study attempted to offer insight into the trade-off between the production of thorns and the production of reproductive structures in *Rosa multiflora,* an invasive shrub growing at The College of New Jersey. Branches were collected from a total of 30 plants – 10 plants from each of three sites – a lakeshore, an open area, and a forest. Branches were divided into discrete sections and categorized into sections of old, middle and new, with old sections being the innermost regions of the shrub and new sections, the outermost regions. These sections were then analyzed for thorn and fruit densities.

Ratios between the two densities were calculated in each section in order to analyze the occurrence of trade-offs. At the lake and open sites, fruit-to-thorn ratio increased in progression from older, innermost branches to newer, outermost branches, suggesting a fruit-thorn trade-off dependent on position on the branch, which increases fitness by economically allocating thorns to critical areas of the shrub while investing more resources to favor reproduction in the newer, most accessible regions of the shrub. At the forest site there was a relatively constant ratio of buds to thorns, which is attributable to high herbivory rates resulting in increased thorn production at the branch tips due to an induced mechanical defense. Finally, our combined results for all sites showed no relationship between the production of thorns and the production of reproductive structures, indicating lack of a whole-plant trade-off between the productions of the two structures.

INTRODUCTION

Organisms require similar resources for many varied functions that occur simultaneously. When a critical, limited resource is directed to a particular structure, it is termed resource allocation (Harper and White 1974; Abrahamson and Caswell 1982). Because of the importance of the resource, resource allocation trade-offs must occur in which certain structures at different locations on the organism are allocated more of this resource than other structures (Fox and Stevens 1991; Ashman and Baker 1992). Trade-offs can be important drivers of evolution because they influence many of the characteristics and functions of organisms that are subject to natural selection (Carey and Tatar 1995). The trade-offs between these factors ultimately affect the fitness (survival, reproduction) of the organism (Partridge and Harvey 1988; Stearns 1976).

This study addressed the trade-off between the production of thorns and the production of reproductive structures in *Rosa multiflora*, a wild rose shrub that is common in fields, forests, and roadsides. Both thorns and reproductive structures influence the fitness of *R. multiflora,* but there may be limited resources (water, soil nutrients, sunlight) available for both, and therefore a trade-off may occur. The trade-off may be different at various locations on the shrub, even within one branch, depending on the local fitness associated with the trade-off. For instance, while the innermost and most critical areas on the plant may allocate resources to produce thorns, the outermost and most heavily pollinated areas may allocate resources to produce reproductive structures. Such a difference in trade-offs could increase the survival of the shrub by increasing protection at the critical areas of the shrub, as well as increasing its ability to reproduce, by being more readily accessible to pollination and seed dispersal. This combination of increasing survival and ability to reproduce should increase the overall fitness of *R. multiflora.*

Thorns are vital plant structures because they protect the plant from various herbivores (Young 1987; Baur et al. 1991; Bi et al. 1996; Agrawal 2000; Gomez and Zamora 2002). Thorns are a successful form of mechanical defense and assist in the survival of many shrubs, including *R. multiflora*. Shrubs without thorns have a lower chance of survival and therefore have lower fitness when subjected to an environment in which herbivores are present (Gomez and Zamora 2002).

Despite the great benefit in some cases, there can be detrimental factors associated with thorn production. Seeds are encapsulated within the fruit of the shrub, which is eaten by herbivores, who ultimately disperse the seeds through their feces (Lee 1984). Since thorns act as a form of mechanical defense against herbivores and limit their activity on the shrub (Gomez and Zamora 2002), they may also prevent seed dispersal. Thus, the fitness of the shrub may be reduced by its diminished ability to reproduce in this fashion.

Moreover, thorn production can be detrimental to the plant because there is an energy cost associated with growing thorns (Skogsmyr and Fagerstrom 1992). Energy and nutrients allocated to thorn production are unavailable for allocation to the production of reproductive structures. Conversely, the more energy and resources that are allocated to the formation of reproductive structures, the less energy and nutrients are available to the production of thorns.

The energy cost associated with thorn production has been shown through the study of induced mechanical defenses in shrubs. For example, some shrubs have a tendency to increase allocation of nutrients and energy to thorn production, but only in the presence of herbivores, as a consequence of herbivory (Gomez and Zamora 2002). In the absence of herbivory, shrubs tend to produce fewer thorns, indicating that fitness is greater if thorns are allocated economically, and only produced when necessary (Karban 1993; Argrawal 2000; and Gomez and Zamora 2002).

This observation of "thorn production only when necessary" may apply to our study of thorn production on the branches of *R. multiflora.* A major trade-off that led to the greater fitness of the plants that lacked unnecessary thorns in the studies of Karban (1993); Argrawal (2000); Gomez (2002) and Zamora (2002) was the increased ability of the shrubs to produce more reproductive structures (Carey and Tatar 1995). The fitness of shrubs, including *R. multiflora*, relies heavily on their ability to reproduce. It is only when resources are limited (Pyke 1989) or when thorn production must be increased (Karban 1993; Argrawal 2000; and Gomez and Zamora 2002) that less energy and fewer nutrients are allocated to the formation of reproductive structures. Optimally, shrubs should survive easily and therefore allocate fewer resources to structures other than those used in reproduction. It could be said that thorns should be produced only when absolutely necessary in order to maximize fitness.

This study of *R. multiflora* is important to the fundamental understanding of trade-offs. Every organism is subjected to limited resources, such as nutrients and energy. Additionally, every organism has many structures that serve as mechanisms for various functions, which can optimize fitness of that organism, with a balance of trade-offs between the two functions. This study examined two plant structures related to fitness: thorns, which affect survival, and fruits, which affect reproduction. Specifically, the study focused on trade-offs in resource allocation by investigating the relationship between thorn density and fruit density along different sections of branches. The goal of this study was to confirm our hypothesis that there is a negative relationship between the production of thorns and reproductive structures in *R. multiflora.* Furthermore, the allocation of resources to thorns and reproductive structures must occur in such a way that overall fitness is increased. This may be accomplished by a greater allocation of thorn structures to the innermost, crucial areas of the branch while allocating more resources to reproductive structures in the outermost, more accessible areas of the branch.

METHODS

Rosa multiflora branches were collected from three different sites on two separate dates on the campus of The College of New Jersey (TCNJ) in Ewing, NJ, USA. The first collection took place on 1 March 2007 at the perimeter of Lake Sylva at TCNJ. The second collection took place on 22 March 2007 from both an open, sunny site and a forest site, near Green Lane. Branch collection from all sites followed the same procedure. At each site, one branch was removed from each of ten different specimens. The branches were removed objectively by always choosing those that were closest to the bottom of the *R. multiflora* plant and, at the lakeshore site, facing away from the water.

Each branch was separated into 25 cm sections, starting at the base and ending with the tip. Side branches that were growing off the main branch or another side branch were divided into 10 cm sections. The section of the main branch that these side branches originated from was recorded. For each 10 cm or 25 cm section, the number of thorns and fruit were recorded. Thorns or fruit that were visibly damaged or removed were recorded as though they were intact data. These damaged structures were closely examined using a magnifying hand lens.

Analysis of variance (ANOVA) was used to analyze the differences in the ratio of fruits to thorns among different branch sections at each site. Data from each site were analyzed with separate ANOVAs. Regression was used to analyze the relationship between the number of thorns and the number of reproductive structures among individual specimens.

RESULTS

Samples of *R. multiflora* at the lake site produced higher fruit-to-thorn ratios in progressively from old to new sections of branches. These results were statistically significant (Figure 1; ANOVA, Table 1). At the open site, *R. multiflora* also produced higher fruit-to-thorn ratios progressively from old to new sections of branches (Figure 1; ANOVA, Table 2). By contrast, *R. multiflora* at the forest site produced no significant differences in fruit-to-thorn ratios among older or newer branch sections (Figure 1, ANOVA, Table 3).

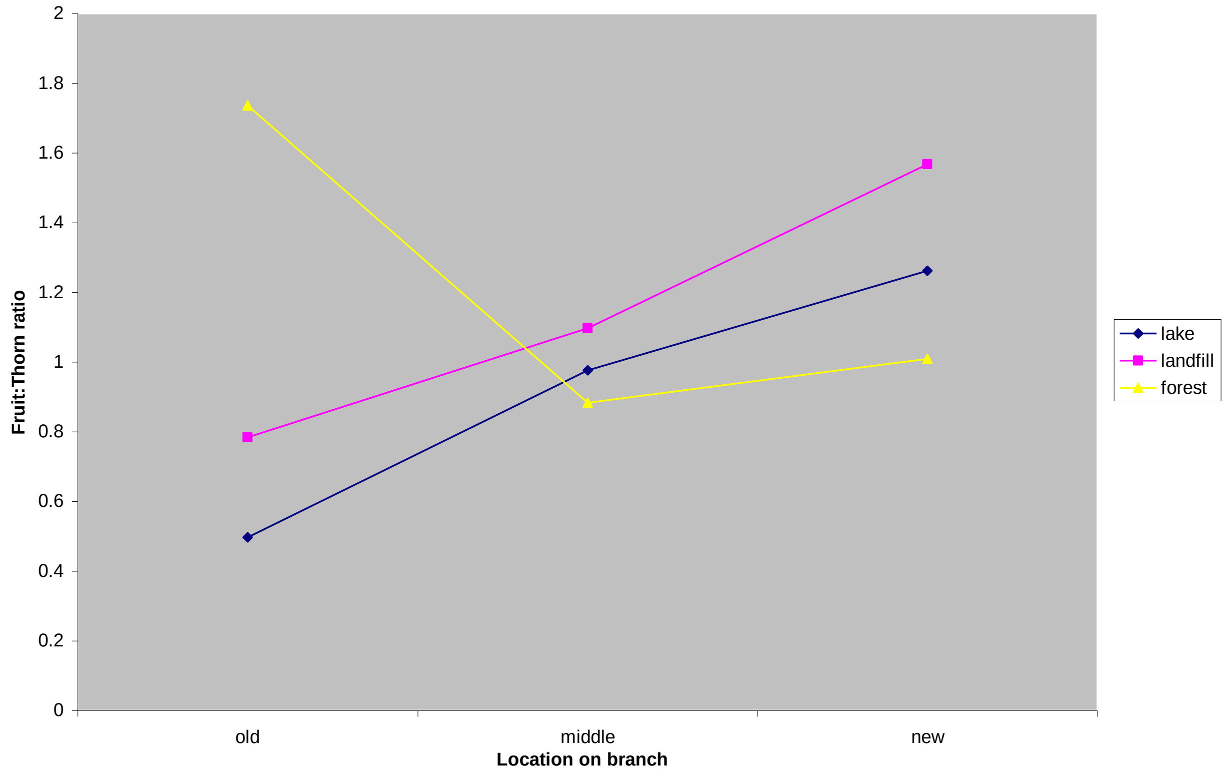

Figure 1. Anova for fruit to thorn ratio for old (innermost), middle, and new (outermost) sections of *Rosa multiflora* branches (n=30).

Lake site

Anova: Single Factor

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Old	8	4.688	0.586	0.024992
Middle	8	8.273	1.034125	0.018216
New	8	10.903	1.362875	0.05648
Side	8	6.852	0.8565	0.205403

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	2.547128	3	0.849043	11.13164	5.53E-05	2.946685
Within Groups	2.135642	28	0.076273			
Total	4.68277	31				

Table 1. Anova single factor for fruit-to-thorn ratios in old (innermost), middle, and new (outermost) sections of *Rosa multiflora* branches at the lake site.

Landfill site

Anova: Single Factor

SUMMARY

Groups	Count	Sum	Average	Variance
old	10	7.839	0.7839	0.147347
middle	10	10.965	1.0965	0.129218
new	10	15.674	1.5674	0.987462

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	3.111126	2	1.555563	3.69192	0.03825	3.354131
Within Groups	11.37625	27	0.421343			
Total	14.48737	29				

Table 2. Anova single factor for fruit-to-thorn ratios in old (innermost), middle, and new (outermost) *Rosa multiflora* branch sections at the landfill site.

Forest site

Anova: Single Factor

SUMMARY

Groups	Count	Sum	Average	Variance
old	10	17.358	1.7358	3.451713
middle	10	8.833	0.8833	0.013826
new	10	10.093	1.0093	0.187224

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	4.234782	2	2.117391	1.739005	0.194801	3.354131
Within Groups	32.87487	27	1.217588			
Total	37.10965	29				

Table 3. Anova single factor for fruit-to-thorn ratios of old (innermost), middle, and new (outermost) sections of *Rosa multiflora* branches at the forest site.

Regression analysis of thorns and fruits on the 30 branches collected from all three sites showed no relationship between production of thorns and production of reproductive structures (Figure 2; Regression, Table 4).

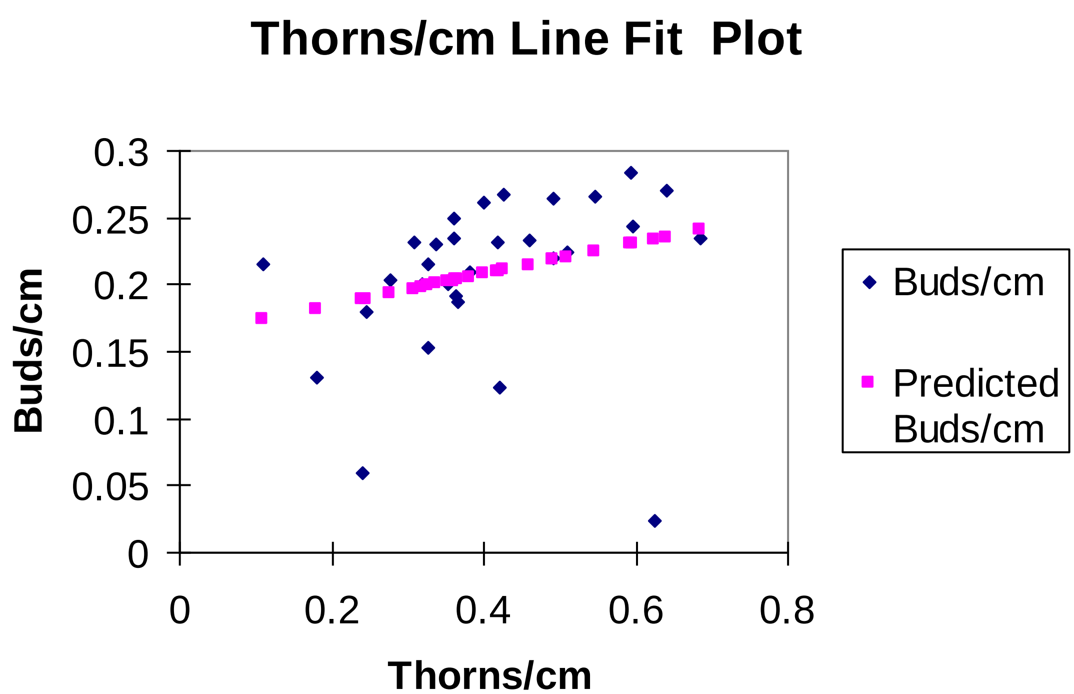

Figure 2. Regression for bud desnity versus thorn density in Rosa multiflora (n=30).

Regression Statistics	
Multiple R	0.270770695
R Square	0.07331677
Adjusted R Square	0.04022094
Standard Error	0.058454497
n	30

Table 4. Regression for fruit density versus thorn density for all collected branches of *Rosa multiflora*.

DISCUSSION

The results show that there was an increase in fruit-to-thorn ratios progressively from the old, innermost sections of branches to the new, outermost ones, at both the lake and landfill sites (Figure 1). A number of different explanations are possible.   Organisms attempt to increase fitness through trade-offs that allow them to survive and reproduce in the most efficient fashion (Williams 1966; Abrhahamson and Caswell 1982; Partridge and Harvey 1988; Ashman and Baker 1992; Karban 1993; Carey and Tatar 1995). If *R. multiflora* shrubs are located in environments subjected to less herbivory and therefore can more easily survive, then they will maximize the production of reproductive structures in plant sections that can lead to high rates of seed dispersal and pollination. In *R. multiflora* these sections are the new, outermost sections of branches. Because of their accessibility, these sections are especially subjected to insect pollination and herbivory by birds and deer, which leads to seed dispersal (Lee 1984).

The old, innermost sections of branches are relatively inaccessible and therefore the production of fruit and buds in these areas would not favor reproduction, but only reduce the availability of resources that could serve other biological functions, such as defense (Harper and White 1974; Abrahamson and Caswell 1982; Fox and Stevens 1991; and Ashman and Baker 1992). Therefore, high numbers of fruit and buds in the old, innermost sections would not increase fitness. Moreover, defense is favored in the old, innermost sections of branches because these are crucial to the shrub's survival. Should the shrub be subjected to herbivory on these sections, the survival of the shrub is greatly at risk. Damage to the shrub's old, innermost branches entails a much higher threat to its survival than damage of the new, outermost branches, which are relatively expendable. This is because more energy, time and resources must be allocated to the regeneration of the thick, innermost branches. Additionally, if the innermost sections of branch are damaged, the outermost sections of branch are jeopardized because their ability to obtain nutrients is greatly reduced or eliminated.

Increased fruit-to-thorn ratio toward branch tips in plants from the lake and open sites also may occur because plants tend to maximize the allocation of resources to reproductive structures. Only after herbivory has damaged a plant does it allocate more resources to the production of thorns as an induced mechanical defense (Young 1987; Agrawal 2000; Gomez and Zamora 2002). This indicates that fruit and buds are initially produced on branches before thorns, so new sections of branch should have a higher fruit-to-thorn ratio than older sections.

Finally, the lake and landfill sites were suspected to have experienced only minimal herbivory by deer because of their location. Since both sites are near roads and not very secluded, deer probably do not cause much thorn production on branch tips as an induced mechanical defense, which keeps the fruit-to-thorn ratio high at these sites. Although these sites probably experience normal bird and insect densities, these organisms do not cause much damage to plants as deer, and thus induced thorn production should still be minimal at the lake and open sites.

At the forest site, in contrast to the lake and open sites, fruit to-thorn-ratios did not increase progressively from the old, innermost sections of branches to the new, outermost sections of branches, in contrast to the lake and open sites (Figure 1). Although unexpected, this observation can be explained. The shrubs in different sites were not subjected to the same environment nor the same levels of herbivory. Fitness is known to vary among individuals in different environments (Williams 1966; Stearns 1976; Partridge and Harvey 1988; Fox and Stevens 1991; Ashman and Baker 1992; Carey and Tatar 1995), and often can be attributed to different levels of attack by natural enemies (Young 1987; Skogsmyr and Fagerstrom 1992; Karban 1993; Agrawal 2002; Gomez and Zamora 2000).

Deer were likely to have been more abundant at the forest site because of its more secluded location. Indeed, high frequencies of deer have been observed in forested areas at The College of New Jersey. Higher frequencies of herbivory by deer at the forest site may cause even the new, outermost, sections of branches to produce high thorn densities as a result of induced mechanical defense. As previously noted, these sections are the most accessible and also bear the highest fruit densities. Therefore, deer more readily focus on these areas as targets for herbivory. This, of course, will heavily damage these sections of branches and inevitably lead to an increase in thorn production as a consequence of induced mechanical defense (Young 1987; Agrawal 2000; Gomez and Zamora 2002). Although there are no data to support the observation that there is a higher frequency of deer predation at the forest site, the observation must be noted. A useful future study would quantify the frequency of deer and herbivory by deer predation at the lake, open, and forest sites.

This study produced results that do not support our hypothesis that an overall, whole-organism trade-off has occurred between the production of thorns and the production of fruit

(Figure 2), at least according to the measures used here. Trade-offs are primarily associated with resource allocation (Harper and White 1974; Abrahamson and Caswell 1982), so the biomass of biological structures is the component which primarily determines the necessity for trade-offs (Williams 1966; Fox and Stevens 1991; Ashman and Baker 1992). The present study measured numbers of thorns and fruit, without taking into account their size, and thorns clearly vary in size. It is possible that thorn size, but not number, is increased as an induced mechanical defense (Young 1987). An excellent follow-up to this study would be to obtain data on the size and mass of thorns in different sections, rather than simply to record thorn numbers.

Trade-offs are an essential factor in determining the fitness of an organism. In order to gain optimum fitness, resources must be allocated as economically and efficiently as possible. In the case of *Rosa multiflora* and other shrubs, overall fitness is increased by allocating resources to thorn production in crucial areas as well as areas subjected to high levels of herbivory. However, in the absence of predation and in more expendable and accessible areas, allocation of resources to produce reproductive structures is favored.

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