

Changes in reproduction and architecture in flowering dogwood, *Cornus florida*, after attack by the dogwood club gall, *Resseliella clavula*

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Plants exhibit a range of responses in growth and reproduction to attack by herbivores from loss, to no effect, to overcompensation. We assessed herbivore impact on branch architecture, growth, and sexual reproduction by flowering dogwood, *Cornus florida*, for four years after attack by a specialist stem gall-forming fly, *Resseliella clavula*.

We estimated the immediate and long-term consequences of herbivory for vegetative growth and flower and fruit production on marked shoots that were galled or ungalled at the outset of our study. The response of dogwood trees to herbivory was complex with an initial negative effect on flower and fruit production, followed by compensatory shoot elongation and inflorescence production after three years, and a tendency toward overcompensation after four years. When observations on fruit production were terminated at the end of year three, fruit production on galled shoots was still suppressed relative to ungalled shoots. Attack by the gall-former in the initial year of the study caused an immediate reduction in shoot survival and a 46% decrease in inflorescence and 79% loss in fruit production relative to ungalled shoots. After four years, compensation in both vegetative growth and inflorescence production was detected. A tendency toward overcompensation within the fourth year was indicated by 24% greater shoot elongation and 90% more inflorescence production on galled shoots than on ungalled shoots. Compensation in vegetative growth on surviving galled shoots involved increases in the average length and the number of vegetative modules produced. Reproductive compensation occurred because a greater number of vegetative modules gave rise to reproductive buds on galled shoots than on ungalled shoots in the third and fourth years of the study. Our results suggest that in long-lived species, the initial response of the plant may not be an adequate measure of the impact of herbivores on plant fitness. Responses to herbivores may extend for several years beyond the year of attack, and compensatory or overcompensatory responses may only become apparent after several growing seasons.

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Plant-herbivore theory once held that herbivory always caused a decline in plant fitness (Ehrlich and Raven 1964, Janzen 1979, Strong et al. 1984). However, observations of equal or greater plant growth and reproduction following herbivory, compensation or overcompensation, respectively, conflict with the long-held assumption that herbivores always have negative im-

pacts on plant reproduction (Harris 1973, 1974, Crawley 1987, Paige and Whitham 1987, Maschinski and Whitham 1989, Prins and Verkaar 1992). Nevertheless, the negative effects of herbivores on growth and reproduction have been extensively documented for both herbaceous and woody plants (see reviews by Crawley 1983, 1989, Hendrix 1988, and Marquis 1992).

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Several species of herbaceous plants have exhibited the capacity to compensate in reproductive traits following herbivore damage and to overcompensate in some cases (McNaughton 1983, 1986, Solomon 1983, Argall and Stewart 1984, Paige and Whitham 1987, Benner 1988, Maschinski and Whitham 1989, Michaud 1991; but see Bergelson and Crawley 1992). Some species of herbaceous plants exhibit a decline in reproduction following herbivory, but the response is compensatory when observed over a longer period (Solomon 1983). Other species of herbaceous plants overcompensate by producing more flowers and seeds soon after being damaged when compared to undamaged plants (Inouye 1982, Paige and Whitham 1987, Maschinski and Whitham 1989).

A primary mechanism suggested to account for overcompensation in plants is architectural change (Aarssen and Irwin 1991, Paige 1994, Aarssen 1995). Plant architecture, or the pattern of production of new shoots, branches, and roots can be altered following herbivory (Oppenheimer and Lang 1969, Simberloff et al. 1978, Aarssen and Turkington 1985, Whitham and Mopper 1985, Craig et al. 1986, Paige and Whitham 1987, Strauss 1991). Reproductive overcompensation is not a necessary consequence of architectural change caused by herbivory. Production of cones, flowers, and seeds can be negatively or positively associated with architectural change (negative: Whitham and Mopper 1985, Craig et al. 1986; positive: Inouye 1982, Paige and Whitham 1987).

Architectural changes following herbivory that may lead to compensatory or overcompensatory responses may take place over several growing seasons in woody plants, rather than occurring in the year of attack as reported for herbaceous species. However, there are few studies of herbivore damage that measure multi-year responses in plant growth and reproduction (but see Ericsson et al. 1980, Edwards 1985, Sacchi et al. 1988, Strauss 1991, and Edenius et al. 1993). Initially, branch growth in Scots pine decreased following artificial defoliation, but after four years no differences remained between damaged and undamaged branches indicating that plants compensated for damage (Ericsson et al. 1980), while in *Salix lasiolepis* compensation occurred in the second growing season following attack (Sacchi et al. 1988).

We conducted a multi-year study of the impact of the dogwood club gall, *Resseliella clavula*, on branch architecture, growth, and sexual reproduction in flowering dogwood, *Cornus florida*. We examined three questions: 1) does the dogwood club gall cause a sustained increase or decrease in vegetative growth and sexual reproduction? 2) if not, does the plant's response in growth and reproduction to attack by the herbivore change over time in a manner consistent with the occurrence of compensation or overcompensation? and 3) does architectural change account for any observed compensation or overcompensation?

Methods

The plant species

Cornus florida L. (Cornaceae) occurs as a small understory tree in forests from Connecticut to Florida, grows along fence rows and in old-fields, and is widely planted in horticultural settings. Reproductive buds formed during one growing season produce inflorescences the next spring. Several fruits, each containing one seed, may be produced on an inflorescence. Plants in full sun produce abundant flowers and fruits each year but at the shoot level fruit production in one year may lead to a decreased chance of flowering or fruiting on that shoot in the subsequent year. Vegetative and reproductive buds are morphologically distinct, permitting determination in autumn of flowering rates for the following spring. At bud-break in the spring, dormant vegetative buds on the shoot produced the previous year give rise to one to five shoots, and vegetative buds associated with terminal reproductive buds give rise to two shoots following flowering. Shoots continue to elongate during the course of the summer, producing as many as four internodes, each with dormant accessory buds. After bud-break initiates new growth in spring, accessory buds on new growth tend to remain dormant and produce few, if any, sub-shoots. The regularity of production of shoots with several internodes and the appearance of annular bud scale scars permits year classes of shoots to be clearly delimited so that shoot growth and patterns of branching can be determined.

The insect herbivore

Resseliella clavula (Beutenmuller) (Diptera: Cecidomyiidae) is a univoltine gall-forming fly that attacks shoots of flowering dogwood (Schread 1964, Gagné 1989). Eggs are laid on terminal leaves near the apical bud where the maggots work their way into newly developing shoots, resulting in a club-shaped gall. The gall can be located on an internode in the middle of the shoot or on a terminal internode depending on whether oviposition takes place early or late in the season. Galls contain multiple larvae that feed within the pith of the swollen bud or shoot. The gall occasionally kills shoots, but gall presence may also cause the release of dormant accessory buds resulting in the formation of multiple shoots (Johnson and Lyon 1988). Reproductive buds that develop on shoots in the year of gall formation may be malformed or die.

Gall abundance

We estimated the abundance of *R. clavula* on *C. florida* for both forest edge and interior trees in each year of the study. Five large branches were randomly selected

on each of 30 trees located along the forest edge or in the forest understory. The proportion of modules with galls was recorded from 1988 through 1992. To test for differences in galling rates among years and sites, we performed a repeated-measures analysis of variance on the angularly transformed proportion of shoots galled. We adjusted degrees of freedom of *F*-tests using the Huynh–Feldt epsilon to account for non-sphericity of the variance-covariance matrices (Winer 1971, O'Brien and Kaiser 1985).

Impact on growth, reproduction, and shoot survival

To determine the impact of galling by *Resseliella clavula*, we monitored growth, reproduction, and survival on galled and ungalled shoots of flowering dogwood at the Pace-Steeger Estate, Fluvanna County, Virginia, USA between 1988 and 1991. All trees were located along a natural forest edge bordering a pasture. We randomly selected fifteen trees with trunk diameters between 7.5 and 15.0 cm at a position 40 to 50 cm above ground level. We marked five newly galled shoots on each tree and chose the nearest ungalled shoot of similar size and age to control for differences in insolation and growth potential in different sections of the tree crown. We assumed that shoots selected by *R. clavula* and ungalled twigs differed only in the presence or absence of galls and that no initial differences in shoot vigor were present. We outline analyses to test this assumption later in this section. We will use the term shoot to indicate the sample units marked in 1988, and module to refer to all new vegetative units originating in a given year from each of the shoots. Each October between 1988 and 1991, every newly produced module distal to the initial mark was counted and its length measured. To assess the impact of *R. clavula* on reproduction by *C. florida*, we counted the number of inflorescences and the number of fruit produced on each marked shoot each year from 1988 to 1991 or 1988 to 1990, respectively.

We summed data among galled and among control shoots within each tree and examined total growth and reproductive measures to determine if the effect of *R. clavula* on *C. florida* was to suppress growth and reproduction, or if eventual compensation or overcompensation would occur. Total growth and reproductive measures account for the total effect of *R. clavula* on dogwood growth and reproduction through inclusion of zero values for these measures when shoots and resulting modules died in either galled or ungalled treatment groups. We also examined the average growth per module and the averages of growth and reproductive measures per surviving shoot to determine if the plant's response to herbivory is caused by

changes in the architecture of the plant (e.g. number of new modules produced), by changes in the vigor of individual modules, or by a combination of these two mechanisms.

The effects of *R. clavula* on plant growth and reproduction were examined using a fixed-effects model, repeated-measures analysis of variance design that incorporated two treatment factors observed on each subject (tree): 1) the presence or absence of galls in 1988, and 2) year of observation (1988, 1989, 1990, and 1991). Both the main treatment effects and the Year by Gall interaction are important in testing our hypotheses. Significant main effects of galling would most likely indicate suppression if the plant responds as anticipated based on earlier predictions (Schread 1964, Johnson and Lyon 1988). Significant Year by Gall interactions represent a change in plant response to galls over time that could indicate compensation or overcompensation. To determine the negative or positive effects of galling on dogwood growth and reproduction in the year of, and three years following attack, we computed paired *t*-tests to compare each growth and reproductive measure between galled and ungalled shoots. Negative values for *t*-tests indicate that the plant's response to gall presence is suppression, and positive values indicate overcompensation. Because we did not collect data on fruit number in 1991, we compared the difference in fruit production on galled and control shoots in 1990. Results of these *t*-tests will be interpreted as providing evidence for within-year or intra-year suppression, compensation, or overcompensation in reproductive or growth traits on galled compared with ungalled shoots.

Degrees of freedom for *F*-tests for within subjects effects were adjusted using the Huynh–Feldt epsilon to account for non-sphericity of the variance-covariance matrices (Winer 1971, O'Brien and Kaiser 1985). We did not transform the data to stabilize the variances prior to analysis because no assumptions are made about the variance of differences used in paired *t*-tests, and because in repeated-measures analyses of variance, application of the Huynh–Feldt epsilon adjusts for heterogeneity in both the variances and covariances (Winer 1971, O'Brien and Kaiser 1985, Keppel 1991).

To determine if the shoots initially selected by *R. clavula* were more vigorous (had greater potential for growth and reproduction) than the control shoots, we performed regressions for galled or control shoots of the final average module size on the initial average module size for all surviving shoots combined among all trees. We then compared the slopes of these regressions using a *t*-test. If initially galled shoots were more vigorous than ungalled shoots, we would expect the final average size of modules on galled shoots to be greater than for ungalled shoots, after accounting for the initial size of the shoot.

Results

Gall abundance and shoot survival

The proportion of modules galled on dogwood trees differed between years and sites with higher galling rates on trees located on the forest edge compared with the forest interior (Fig. 1; Site - $F_{1,28} = 3.59$, $p = 0.068$; Year - $F_{4,101} = 4.62$, $p = 0.002$). The year by site interaction effect was not significant. Overall, less than 2.5% of modules were attacked by *R. clavula* at our site.

Shoots that were initially galled and control shoots gave rise to new modules that received equal rates of attack by *R. clavula* in subsequent years (Fig. 2; $F_{1,14} = 0.41$, $p = 0.531$). Significantly fewer shoots that were galled in 1988 survived over the four years of observation than control shoots (Fig. 3; $F_{1,14} = 12.47$, $p = 0.003$). Less than 25% of control shoots died while 32% of galled shoots died between 1988 and 1991.

Growth and reproduction

Since branching occurred each year, ever-increasing numbers of new modules and inflorescences developed on all surviving shoots leading to a significant effect of year for all total growth and reproductive measures (Table 1A, Figs 4, 5). However, this effect is merely an expected consequence of growth by branching. Additional inter-annual variation in fruit production related to gall attack or growth by branching was also apparent (Fig. 5B).

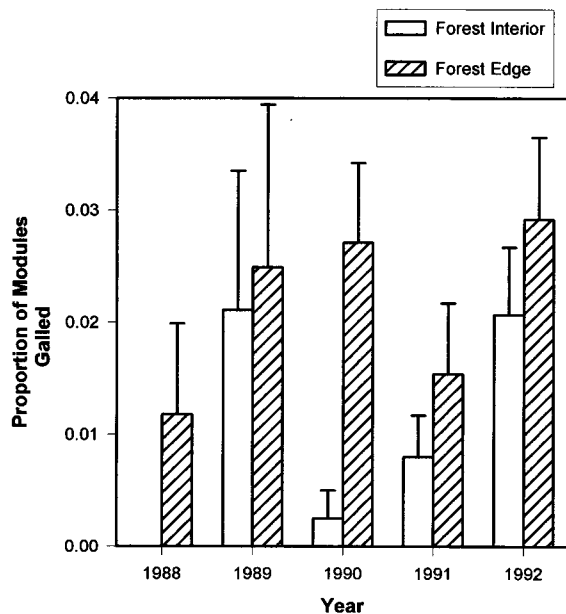


Fig. 1. Proportion of modules galled by the fly *Resseliella clavula* on flowering dogwood trees from 1988 to 1992. Means among trees and one standard error are represented.

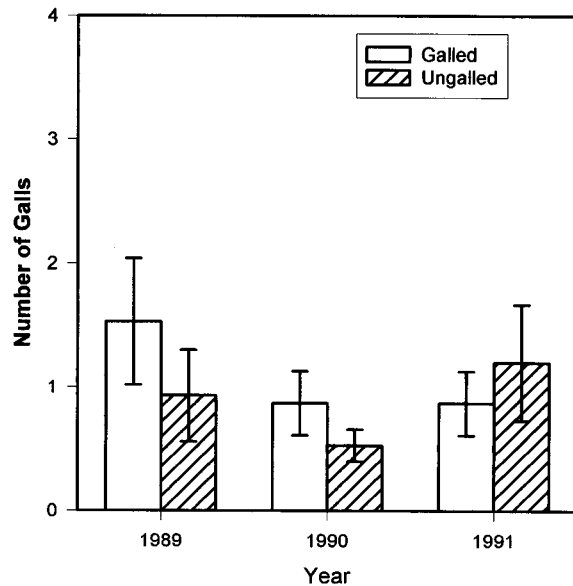


Fig. 2. Gall attack from 1989 through 1991 on new modules originating from shoots originally galled or ungalled in 1988. Means among trees of the number of galls per new module and one standard error are represented.

There was no effect of galls on either total module length, mean length per module, the total number of modules, or the number of inflorescences (Table 1A, Figs 4, 5). However, the number of fruits produced each year was suppressed on galled shoots relative to control shoots, and this suppression was sustained for the three years of observation (Tables 1A, 2, Fig. 5). The number of inflorescences produced on galled shoots was also suppressed in the year of attack, but

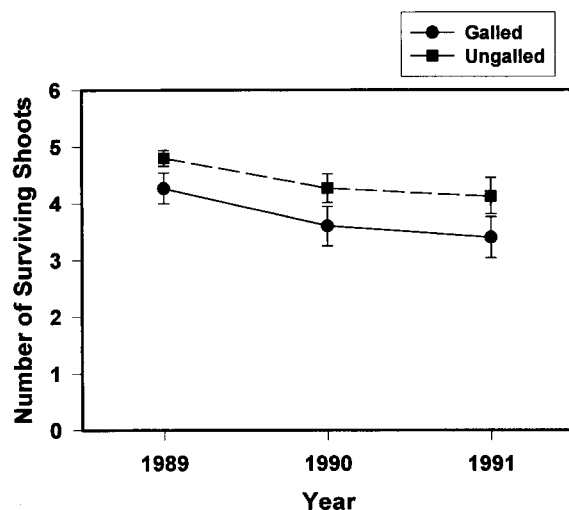


Fig. 3. Number of shoots surviving each year of the five originally galled or ungalled shoots marked on each tree in 1988. Means among trees and one standard error are represented.

Table 1. Results of analysis of variance of growth and reproductive attributes of *Cornus florida* in relation to the presence of galls of *R. clavula*. Total values (A) are summed among all shoots marked on a tree and represent tests for compensation and overcompensation. Values per surviving shoot (B) are used to test for architectural changes associated with herbivory.

	Year			Gall			Year × Gall		
	df	F	p	df	F	p	df	F	p
	A. Total values								
Number of modules	1,15	21.32	0.0003	1,14	0.001	0.991	1,15	0.14	0.714
Cumulative module length	1,17	6.38	0.022	1,14	0.28	0.603	1,20	1.54	0.229
Mean module length	1,17	34.10	0.00002	1,14	1.42	0.254	2,24	2.61	0.094
Number of inflorescences	1,19	5.55	0.029	1,14	0.63	0.441	1,19	3.04	0.097
Number of fruit	1,16	4.04	0.062	1,14	7.13	0.018	2,25	1.60	0.222
B. Values per surviving shoot									
Number of modules	1,15	45.03	0.000007	1,14	2.18	0.162	1,16	2.55	0.130
Cumulative module length	1,17	10.88	0.004	1,14	2.84	0.114	2,27	4.77	0.017
Number of inflorescences	1,21	7.38	0.013	1,14	1.98	0.181	2,23	3.59	0.044
Number of fruit	2,23	4.67	0.020	1,14	4.67	0.049	3,38	1.19	0.326

this suppression was not sustained over the four years of observation (Table 2, Fig. 5).

Total module length and mean module length were initially greater on galled shoots than control shoots in 1988, but this pattern was reversed in the second year (1989). On the other hand, the production of inflorescences and fruit was suppressed immediately (Table 2, Fig. 5). By the end of the study, large, but statistically non-significant, increases in total module length, total number of modules, and number of inflorescences were observed on galled shoots (Tables 1A, 2). Total module length and the number of inflorescences on galled shoots exceeded that on control shoots by 24% and 90%, respectively by the fourth year of the study (Figs 4, 5).

Examination of data averaged among modules or among surviving shoots indicates that by the end of the study, surviving galled shoots produced significantly longer modules and more inflorescences than did surviving control shoots, and also tended to produce more modules (Tables 1B, 2).

Comparison of the slopes of the regressions of final average module size on initial average module size indicates that equal-sized galled and ungalled shoots produce similar-sized modules three years subsequent to attack ($t = 0.8836$, $df = 92$, $p = 0.379$; Fig. 6).

Discussion

Attack by the shoot-galling fly *Resseliella clavula* in a single year led to effects on growth and reproduction in flowering dogwood that extended over several years and cannot be interpreted simply as negative or compensatory. Shoot survival and inflorescence and fruit production were immediately suppressed on galled shoots, and growth was suppressed one year after gall formation. After three years, fruit production remained

suppressed on galled shoots, but growth and the production of inflorescences equaled or exceeded that on control shoots.

Measures of total growth and reproduction, which represent the net effect of *R. clavula* on *C. florida*, including factoring in the higher mortality of shoots attacked by *R. clavula*, as well as the tendency of galled shoots to grow and flower more than ungalled shoots, indicate that *C. florida* compensates for damage caused by *R. clavula* within three to four years. In the fourth year, vegetative growth and inflorescence production was greater on galled than on control shoots suggesting a tendency for *C. florida* to exhibit within-year overcompensation for attack by *R. clavula* between shoots on the same plant. However, even after three years, fruit production remained suppressed on galled shoots relative to control shoots. While we did not collect data on fruit production in 1991, since inflorescence production on galled shoots exceeded that on control shoots by 90% in 1991, we project that compensation in fruit production would have occurred. Measures of growth and reproduction averaged among surviving shoots or among individual modules within trees indicate that compensation is achieved because galled shoots produce more and longer modules, and because a greater proportion of these modules produce inflorescences.

The total and mean length of modules on galled shoots was greater than for control shoots at the beginning of our study. This could arise for at least three reasons; 1) our selection of ungalled 'control' shoots was biased toward smaller shoots, 2) *R. clavula* selects more vigorously growing shoots, or 3) *R. clavula* had an immediate stimulatory effect on shoot growth. Because our sampling protocol involved locating galled shoots and the nearest ungalled shoot of the same age, we argue that the initial difference in size of galled and control shoots is unlikely to be due to bias on our part. It is possible that selection of more vigorous shoots

could account for the initial differences in shoot length because oviposition by *R. clavula* females occurs after dogwood shoots have substantially elongated (see Craig et al. 1986, Price 1991). Schread (1964) reported that Felt observed *R. clavula* to select vigorously growing shoots. However, since the average size of modules produced on galled and control shoots at the end of four years did not differ, after controlling for the initial average size of modules, we argue that the initial difference in shoot length should not be interpreted as an initial difference in shoot vigor. Finally, the stimulation of shoot growth by *R. clavula* could account for the initial differences in shoot length between galled and ungalled shoots. Weis and Kapelinski (1984) report that galls of *Rhabdophaga strobiloides*, a gall-midge that attacks willow shoots, causes galled twigs to draw

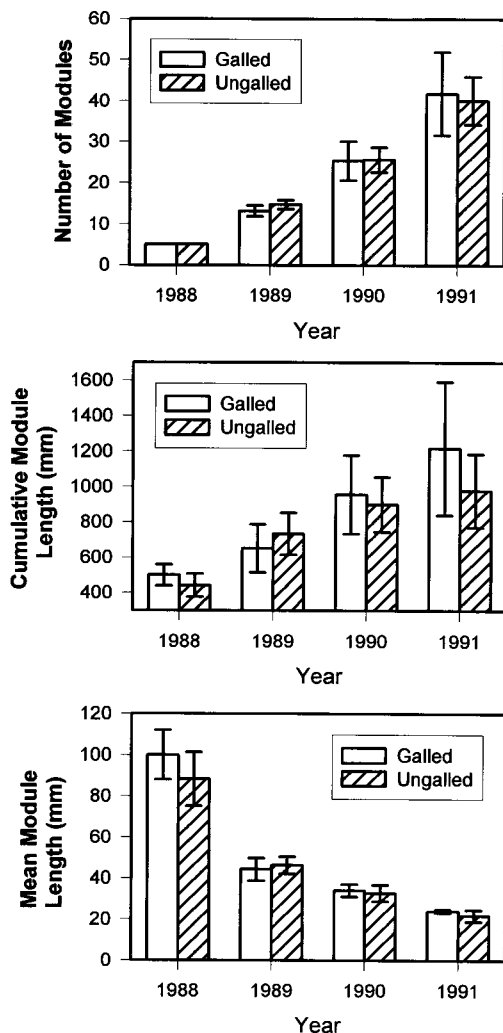


Fig. 4. Mean number of modules (A), total module length (B), and mean module length (C) each year on galled and ungalled shoots. Means among trees and one standard error are represented.

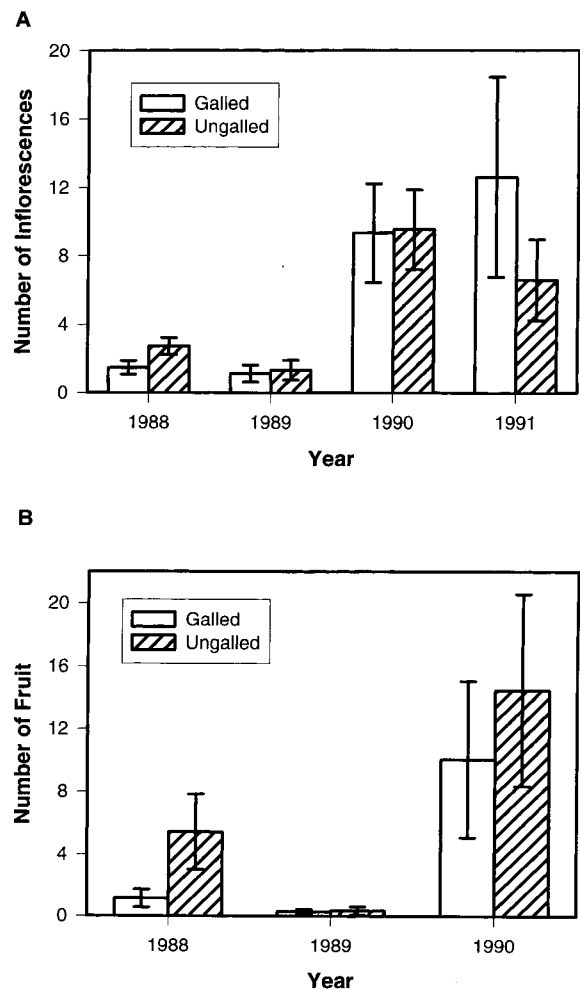


Fig. 5. Numbers of inflorescences (A) and numbers of fruits (B) produced each year on galled and control shoots. Means among trees and one standard error are represented.

photosynthate from other plant parts stimulating the growth of galled twigs.

How do galled shoots compensate for the initial negative effects of the stem-gall? Altered branching patterns are generally associated with herbivores that destroy apical buds or kill the shoots they attack. Bud and shoot death results in reduced apical dominance and stimulates increased lateral or basal shoot production through release of dormant buds (Oppenheimer and Lang 1969, Whitham and Mopper 1985, Craig et al. 1986, Paige and Whitham 1987, Aarssen and Irwin 1991, Strauss 1991, Aarssen 1995). Architectural change in *C. florida* in response to gall presence, measured as the total number of modules on surviving shoots, was not solely responsible for the compensatory growth observed in our study. Both increased elongation of modules, combined with the production of a slightly greater number of modules, was required on galled shoots to offset the loss in growth caused by the higher

Table 2. Results of paired *t*-tests for suppression of growth and reproduction on galled shoots in comparison to control shoots in 1988 and for overcompensation by galled shoots in 1990 and 1991. Total values (A) are summed among all shoots marked on a tree and represent tests for suppression, compensation, and overcompensation. Values per surviving shoot (B) are used to test for architectural changes associated with herbivory. Dashes indicate tests not performed because they are redundant or data were unavailable. Suppression of growth or reproduction by galling should result in large negative *t*-values, while overcompensation should result in large positive *t*-values for cumulative measures. All tests were performed with 14 degrees of freedom. One-tailed significance levels are indicated with asterisks (+ = $p < 0.1$, * = $p < 0.05$, ** = $p < 0.01$).

	Growth	Year	Number of modules	Module length (total)	Module length (mean)
A)	Total	1988	–	1.84*	1.84*
		1991	0.85	0.95	2.95**
B)	Per surviving shoot	1991	1.60 ⁺	2.19*	–
	Reproduction	Year	Number of inflorescences	Number of fruits	
A)	Total	1988	–3.20**	–1.93*	
		1990	–	–1.77*	
		1991	1.61 ⁺	–	
B)	Per surviving shoot	1990	–	–1.10	
		1991	2.06*	–	

mortality observed among galled shoots. The greater number of inflorescences observed on galled than on control shoots in 1991 was more likely the result of a higher proportion of modules producing inflorescences on galled shoots rather than merely a consequence of galled shoots producing more modules. Perhaps architectural change combined with an ability by *R. clavula* to stimulate shoot growth underlies the ability of galled shoots on *C. florida* to compensate by the third year and overcompensate in the fourth year compared with the initial negative effects of the gall. Our results contrast with other plant species where an increase in module number alone follows attack by herbivores that damage or destroy apical meristems (Inouye 1982, Whitham and Mopper 1985, Craig et al. 1986, Edenius et al. 1993).

Our study showed consistent responses by *C. florida* to stem-gall impact in both vegetative and reproductive traits, but these responses occurred at different rates. The initial suppression of reproduction was immediate, occurring in the year of stem-gall formation. The suppression of growth was lagged, occurring in the year following attack. Intra-annual compensation in vegetative growth and inflorescence production occurred in the third and overcompensation in the fourth year following gall formation, respectively. However three years after gall formation, fruit production remained suppressed. While we project that fruit production will eventually compensate for the earlier suppression caused by *R. clavula*, its occurrence will lag behind compensation in growth and flowering by at least one year.

The effect of herbivory would ideally be measured in terms of effects on plant fitness (Hendrix 1988). In the case of annual or biennial plants, assessment of lifetime

seed production yields a measure that is considered a reasonable proxy for fitness (Kinsman and Platt 1984, Paige and Whitham 1987, Simms and Rausher 1987, Maschinski and Whitham 1989). For perennial herbaceous and woody plants, herbivore effects on plant reproduction have been measured, generally, for one year, with the assumption that such effects may be extrapolated over the lifetime of the plant (but see Sacchi et al. (1988) and Strauss (1991) for assessment of traits that extended two and three years, respectively).

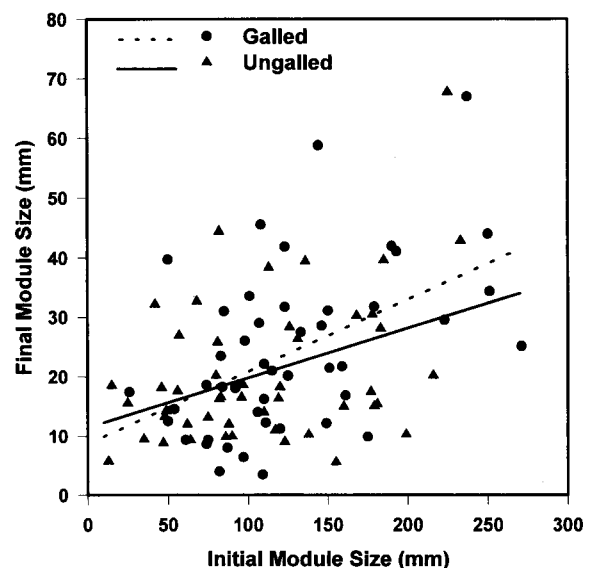


Fig. 6. Regression of final average module length on initial average module length for surviving galled (final = 0.121 [initial] + 8.72, $R^2 = 0.241$, $n = 48$, $p = 0.0004$) and ungalled (final = 0.0836 [initial] + 11.39, $R^2 = 0.156$, $n = 48$, $p = 0.0054$) shoots.

Still other studies examine both sexual traits and vegetative biomass as reflected by rhizome or root biomass to determine whether herbivores affect both current reproduction as well as potential for future growth and reproduction (Hartnett and Abrahamson 1979, Abrahamson and McCrea 1986, Cain et al. 1991, Fay and Hartnett 1991, Wise and Sacchi 1996). Our study represents an attempt to determine the ongoing, rather than solely the immediate, impact of herbivores on woody plant reproduction. Our results indicate that the initial suppression of annual reproduction in *C. florida* caused by *R. clavula* may be offset by compensation in annual reproduction on galled shoots at least five years after gall formation. It is also conceivable that seed production on shoots attacked by *R. clavula* would eventually exceed that on shoots not attacked. However, such overcompensation within individual years would take at least several more years and would never compensate for the delay in reproduction caused by *R. clavula*. Therefore, we contend that the net impact of herbivores on reproduction in woody plants is likely to be negative, although the lifetime impact will be less than expected based on the initial impact of the herbivore. Given that immediate reproductive response of flowering dogwood to *R. clavula* was negative and over time appeared to be compensatory, is this insect abundant enough to elicit an adaptive response by the plant in the population we studied (Belsky 1986, Crawley 1987, Belsky et al. 1993)? Surveys of gall abundance over four years suggest that the low levels of attack by *R. clavula* would be insufficient to induce such strong responses by the plant. However, we would argue that the impacts we observed at the shoot and module level may be manifested as large effects at the whole plant and population levels in several flowering dogwood populations we have observed in both Florida (EFC) and Virginia (CFS), where the dogwood club galler exceeded 25 to 50% of all shoots. The reproductive response was negative, but strongly suggestive that compensation occurred over time. We suggest that the relationship between *C. florida* and *R. clavula* is not mutualistic, but the impact of the club gall on dogwood is far more complex than can be simply classified as either negative or positive.

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