

## BRANCHING RESPONSES IN *SILPHIUM INTEGRIFOLIUM* (ASTERACEAE) FOLLOWING MECHANICAL OR GALL DAMAGE TO APICAL MERISTEMS AND NEIGHBOR REMOVAL<sup>1</sup>

PHILIP A. FAY<sup>2,4</sup> AND HEATHER L. THROOP<sup>3</sup>

<sup>2</sup>Natural Resources Research Institute, University of Minnesota Duluth, 5013 Miller Trunk Highway, Duluth, Minnesota 55811-1442 USA; and <sup>3</sup>School of Natural Resources, University of Arizona, 325 Biological Science East Building, Tucson, Arizona 85721-0043 USA

Branching in plants increases plant access to light and provides pathways for regrowth following damage or loss of the apical meristem. We conducted two experiments in an eastern Kansas tallgrass prairie to determine how apical meristem loss (by clipping), apical meristem damage (by insect galling), and increased light availability affected growth, reproduction, and branching in *Silphium integrifolium* (Asteraceae). The first experiment compared clipping with galling. Clipping increased axillary shoot numbers, while galling increased axillary shoot lengths, reflecting different allocation responses among damage types and inhibition of branching by galls. However, total capitulum production was less in all gall/clip treatments than in intact shoots. The second experiment compared clipping with mowing the surrounding vegetation to increase light availability. Mowing increased total leaf, total capitulum, and axillary shoot length and axillary capitulum production in clipped and unclipped plants and in large vs. small shoots. The presence of the neighboring canopy, not of an intact apical meristem, was therefore the stronger limitation on leaf and capitulum production. These experiments suggest that damage and light competition affected both branching frequency and the partitioning of resources among shoots, branches, and leaves. Because *Silphium*'s growth form is widespread, similar responses may occur in other grassland forbs.

**Key words:** *Antistrophus silphii*; apical dominance; Asteraceae; branching; competition; galls; herbivory; Konza Prairie.

Plant branching is a plastic trait that reflects the balance between growth from apical and lateral meristems. This balance is governed by morphological, physiological, and environmental factors, including the number, arrangement, and extent of integration among meristems, the synthesis and movement of plant hormones (Anderson et al., 2001; McIntyre, 2001), and the availability of light, water, and soil nutrients (Paige and Whitham, 1987; Maschinski and Whitham, 1989; Fay et al., 1996; Järemo et al., 1996; Marquis, 1996; Strauss and Agrawal, 1999; Stowe et al., 2000).

Apical dominance is thought to confer greater plant success by increasing access to light in light-competitive environments (Aarssen and Irwin, 1991; Irwin and Aarssen, 1996; Järemo et al., 1996; Huhta et al., 2000) when branching would provide little further access to light or net carbon gain. However, many plants with strong apical dominance maintain dormant lateral meristems and thus the capacity to branch. The dormant meristems are thought to provide a reserve that avoids predictable herbivore damage and thus are available for compensatory growth and reproduction following damage to the apex (Paige and Whitham, 1987; Maschinski and Whitham, 1989; Lortie and Aarssen, 2000). In addition to the potential compensatory response, branching is thought to confer an advantage to plants when light availability is high, because branching would enable plants to maximally exploit the available light (Aarssen and Irwin, 1991).

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<sup>4</sup> Author for correspondence (e-mail: pfay@nrri.umn.edu)

The impacts of apical meristem damage are likely to vary with different forms of damage (Honkanen et al., 1994; Stowe et al., 2000). For example, gall formers that attack apical meristems are likely to cause redirection of growth without actually removing or killing the apex (Weis and Kapelinski, 1984; Fay and Hartnett, 1991; Silva et al., 1996). The effects of galls are likely to differ from those of mechanical removal of the apical meristem, such as might occur from large browsing mammals or chewing insects because of the physiological and morphological integration of insect galls with the plant (McCrea et al., 1985; Larson and Whitham, 1991; Shorthouse and Rohfritsch, 1992). However, both types of apical meristem damage may influence plant growth and reproduction, particularly in light-competitive environments because of the possible changes in branching architecture that are likely to result.

In productive grasslands such as the tallgrass prairie of the North American Central Plains, dominant tall grasses determine light availability to herbaceous dicots ("forbs"; Turner and Knapp, 1996). Many forb species grow with a vertical, unbranched architecture produced by vigorous apical meristems, and the presence of an intact meristem is thus crucial to maintaining access to light in such species. *Silphium integrifolium* Michx. (Asteraceae) is one of these apically dominant forbs. However, *S. integrifolium*'s apical meristems may be galled by *Antistrophus silphii* Gillette (Hymenoptera: Cynipidae) or removed by browsers. These traits make *S. integrifolium* a suitable model system for evaluating branching patterns in response to competition for light and different forms of meristem damage.

We conducted two experiments in natural field populations. One experiment compared the lateral growth responses of *S. integrifolium* to apical meristem galling with responses to mechanical removal of the apical meristem by clipping. The second experiment compared the lateral growth responses of *S.*

*integrifolium* to clipping with its responses to decreased light competition, which was achieved by mowing neighboring vegetation. Through these experiments, we addressed two primary questions: (1) Does apical meristem damage from galling and clipping lead to the same outcomes in terms of shoot growth, branching, and reproduction? (2) Does the presence of neighboring plants that reduce light availability alter the effects of apical meristem removal?

## MATERIALS AND METHODS

**Plant and galler life histories**—*Silphium integrifolium* grows throughout the tallgrass prairies of central North America on deep-soiled sites. *Silphium*'s architecture is typical of many prairie forbs. Plants consist of 20–50 shoots that originate from rhizomes and grow vertically to a maximum of 1 m in height. The rhizomes are strongly woody, typically 4–7 cm long, 1–2 cm diameter, and have a compact branching pattern that makes individual plants (genets) easy to identify. Growth begins in April when rhizome buds produce rosettes that bolt in May. Each shoot supports 15–25 pairs of sessile opposite primary leaves with axillary meristems (Fay and Hartnett, 1991). In the absence of damage, there is no lateral branching, and each apical meristem differentiates into a terminal inflorescence of 1–15 capitula in July, ending shoot elongation. Achenes mature in August and all aboveground parts die back by the end of October.

*Antistrophus silphii* is a small cynipid wasp typically about 5 mm in adult length, and one of eight *Antistrophus* species known from North America (Krombein et al., 1979). All form galls on Asteraceae, most on the genus *Silphium*. On *S. integrifolium*, galls form after female *A. silphii* oviposit into apical meristems during 2–3 wk in May as the shoots bolt (Fay and Hartnett, 1991). The brief oviposition period means there is little variation in the timing of gall formation that might affect subsequent lateral growth, and lateral shoots are not subject to galling because they grow after the oviposition period. Galls are apparent within 2 wk, morphing the meristem into a sphere with final diameter of 1–4 cm. Up to 30 larvae feed within each gall in individual chambers. Larvae overwinter in galls as third instars, pupate in April, and emerge in May.

**Study site**—The experiments were conducted in 1995 at Konza Prairie Biological Station in the Flint Hills tallgrass prairie near Manhattan in north-eastern Kansas, USA (39°05' N, 96°35' W). The study site covered 2 ha and was dominated by Eastern gamagrass (*Tripsacum dactyloides*) and switchgrass (*Panicum virgatum*); forbs present included goldenrod (*Solidago canadensis*) and Baldwin's ironweed (*Vernonia baldwinii*). Konza's climate is temperate and continental, with July mean temperature of 27°C (range 20°–33°C). During this study, April through August rainfall totaled 729 mm, compared to an average of 510 mm (1982–1995). The study site was burned during April in four of the previous five years and in the two years preceding this study. Both experiments used naturally established *S. integrifolium* and naturally occurring *A. silphii* apical meristem galls.

**Field experiments**—**Galling vs. clipping**—Twenty plants were selected, and within each plant two galled and two ungalled shoots that were visually judged to be similar in length and basal diameter were selected. One galled and one intact apical meristem were clipped in the first internode, removing the meristem or gall but leaving the most terminal pair of expanded leaves. This created four experimental shoot classes: intact, clipped, galled, and galled + clipped. Shoots were clipped during the first week of June, when typical shoots are 60–90 cm tall with 10–15 internodes (Fay and Hartnett, 1991). All shoots began the experiment with their original population of axillary meristems; production of additional axillary meristems was possible for intact and damaged shoots. Neighboring vegetation was left intact.

**Mowing vs. clipping**—Forty plants were selected and randomly assigned to one of four treatments: intact, clipped, mowed, or mowed + clipped. The mowing treatment reduced the neighboring canopy to 10 cm height in a 0.5-m band encircling each target *Silphium* plant. Other species growing within the

perimeter of the study plants were removed manually. Clipped plants had all apical meristems removed in the second subtending internode. Treatments were applied in mid-June, and mowing was repeated at 2-wk intervals until regrowth of neighboring plants slowed in late July. Light availability for the experimental plants was assessed by measuring photosynthetic photon flux density (PPFD) at 20-cm vertical intervals at peak canopy height (late July) with a 1-m ceptometer (model SF-80, Decagon, Pullman, Washington, USA).

**Plant harvest**—The four target shoots for each plant in the galling vs. clipping experiment, and all shoots in the plants used for the mowing vs. clipping experiment were harvested by cutting shoots flush with the soil in late August. On each shoot, we recorded the number of primary leaves, axillary shoots, and capitula and measured node and axillary lengths. These data were used to derive the shoot height, internode lengths, and primary, axillary, and total leaf and capitulum production for each shoot.

**Statistical analyses**—The galling vs. clipping experiment used a randomized complete block design with plant as the block ( $N = 20$ ), and individual shoots (clipped, galled, galled + clipped, or intact) as the experimental unit ( $N = 80$ ). The mowing vs. clipping experiment used a completely randomized design with plant as the experimental unit ( $N = 40$ ) and shoot responses averaged by plant for analysis, omitting galled shoots (14 galls on 350 shoots). Treatment effects were analyzed with ANOVA using Proc Mixed (SAS 8.2, SAS Institute, Cary, North Carolina, USA; Littell et al., 1996). Means separations were performed using pairwise  $t$  tests among the least squares means. Axillary shoot responses were also compared among shoot size classes based on ranked primary shoot height by mowing (pooled across clip treatments) and clipping (pooled across mowing treatments) with  $\chi^2$  analysis and linear regression. It was necessary to pool clipping and mowing treatments for the size class analysis in order to achieve an adequate sample size for all size classes.

## RESULTS

**Galling vs. clipping**—The clipping treatment (clipped and galled + clipped) increased axillary shoot numbers compared to unclipped control shoots (Fig. 1B, Table 1). Total axillary shoot length was increased in both galled shoot treatments (galled and galled + clipped) compared to the ungalled shoots, and main and total shoot height were reduced in all gall-clip combinations compared to intact shoots (Fig. 1A, B, Table 1). There were no among-treatment differences in mean internode length (Table 1). Treatment effects on leaf and capitula production on the main and axillary shoots (Table 2) generally corresponded with main and axillary shoot lengths (Fig. 1B), and increased axillary leaf numbers offset the decreased primary leaf numbers found across all gall-clip combinations (Tables 1, 2). In contrast, total capitula were reduced across all gall/clip treatments vs. intact shoots, because increased axillary capitula numbers did not fully offset decreased terminal capitula numbers (Tables 1, 2), even though galled + clipped shoots produced greater numbers of axillary and total capitula than did shoots receiving single damage treatments (Table 2).

**Mowing vs. clipping**—Mowing increased light availability at all measured heights in the canopy profile from 20 through 80 cm (mowing  $F_{1,36} = 46.1$ , mowing  $\times$  height  $F_{6,216} = 13.2$ , both  $P < 0.0001$ ; Fig. 2). The clipping treatment caused no differences in the PPFD profile ( $P \geq 0.35$ ). In clipped plants, 96% of shoots produced axillary growth vs. 36% in unclipped plants, with all shoot sizes classes in clipped plants contributing equally to axillary production ( $\chi^2 = 4.7$ ,  $df = 5$ ,  $P = 0.45$ , data not shown). Clipping reduced main shoot height by ~30% (Fig. 3A, Table 1) and decreased primary leaf numbers by ~70% (Tables 1 and 2). There were no among-treatment

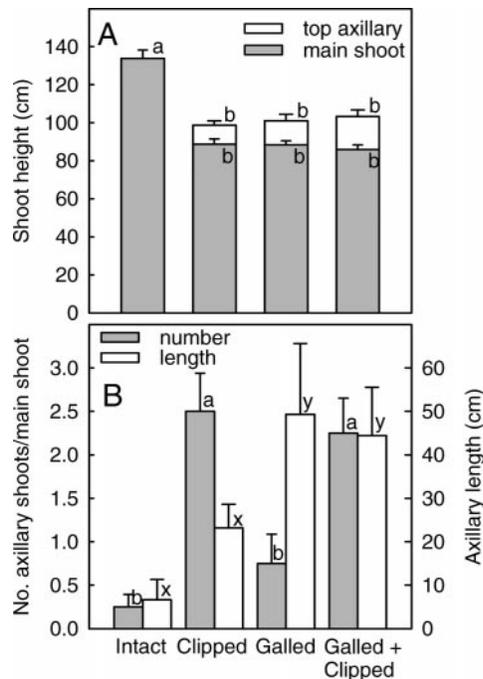


Fig. 1. Shoot and axillary growth in *Silphium integrifolium* main shoots in the galling vs. clipping experiment. Means + 1 SE. (A) Main shoot height; total height including height added by regrowth of axillary shoots from the nearest main node (open). (B) Number of axillary shoots per main shoot and total axillary length per shoot. Letters denote significant ( $P \leq 0.05$ ) differences between means.

differences in mean internode length (Table 2). Clipping increased axillary capitulum numbers and shoot lengths, resulting in equal total shoot height across treatments (Fig. 3A–C, Table 1).

In plants with mowed neighbors, 64% of main shoots produced axillary shoots vs. 58% in plants with unmowed neighbors. Axillary shoot production was more strongly concentrated in larger shoot size classes in plants with mowed neighbors, but did not differ among sizes classes in plants with unmowed neighbors (mowed,  $\chi^2 = 14.7$ , 5 df,  $P = 0.01$ ; unmowed,  $\chi^2 = 4.31$ , 5 df,  $P = 0.50$ ; Fig. 4A), and the larger shoot size classes of plants with mowed neighbors produced longer axillaries with more capitula compared to the large shoots of plants with unmowed neighbors (Fig. 4B, C).

Mowing had no effect on main shoot heights or axillary shoot lengths, but increased axillary shoot and capitulum numbers (Fig. 3A–C, Table 1). The increase in axillary shoot and capitulum numbers was strongest in mowed + clipped plants (Fig. 3B, C, Table 1). Mowing also increased total leaf and capitula numbers (Tables 1, 2).

## DISCUSSION

**Galling vs. clipping**—Both galling and clipping increased *Silphium* axillary growth, but the axillary response was partitioned differently; clipping resulted in many short axillary shoots, galling in a few long axillary shoots, and galling + clipping in many long axillary shoots. Axillary growth is expected after apical meristem damage (Paige and Whitham, 1987; Aarssen and Irwin, 1991; Järemo et al., 1996), but less is known about why the responses would differ in these ways. The mechanism behind the different responses to clipping and

galling may involve two factors. First, galls and meristems are both composed of metabolically active undifferentiated cells (Shorthouse and Rohfritsch, 1992), suggesting that galls may suppress axillaries in the same manner as normal meristems. The increased numbers of axillary shoots after clipping of both normal and galled shoots (Fig. 1B) is consistent with this explanation. Second, the galled shoots may have been more vigorous and therefore produced stronger axillary growth. This possible increased vigor may have been caused by the galls because *Antistrophus* galls enhance *Silphium* water status and leaf photosynthesis rates (Fay et al., 1993). Alternatively, vigorous shoots are often more likely to be galled (Craig et al., 1986; Price, 1991; Throop and Fay, 1999). The combination of increased axillary numbers and length in galled + clipped shoots suggests that galled shoots were initially vigorous shoots, although either reason for increased shoot vigor would yield the same outcome in axillary growth. In the end, these two different kinds of apical meristem damage yielded similar results: equal reductions in total shoot height and capitula numbers among the damage treatments.

**Mowing vs. clipping**—Axillary growth responded strongly to clipping, much like in the galling vs. clipping experiment, producing capitula that otherwise would not have formed had the apical meristem remained intact (Lortie and Aarssen, 2000). Clipping equalized the shoot size hierarchy in terms of axillary growth, so that most shoots in clipped plants produced axillary growth regardless of their size class. In contrast, mowing of neighboring plants strengthened the shoot size hierarchy, increasing the allocation of resources to axillary reproduction among larger shoots (Fig. 4B–C). The opposing allocation responses to clipping vs. mowing demonstrate the conflicting adaptive pressures that shape the plasticity in *Silphium* branching responses (Bonser and Aarssen, 2003).

The mowing treatment increased total leaf and capitulum numbers for both clipped and unclipped plants. This result was not consistent with previous studies (Aarssen and Irwin, 1991), which predicted that clipped plants should fare better than unclipped plants with mowed neighbors, and unclipped plants should have fared better than clipped plants with intact neighbors. So in the end, the presence of the neighboring canopy altered the effects of apical meristem damage, but not in the ways expected by theory (Aarssen and Irwin, 1991). However, the difference between theory and the observed results is not likely due to unmet assumptions of the light competition hypothesis. *Silphium* apical meristems have a high likelihood of damage from galls and deer browsing, while laterals are not galled and lateral damage from other sources has not been noted.

The responses in leaf numbers to mowing and clipping may partly explain the unexpected outcomes. In plants with mowed neighbors, increased axillary leaf numbers in mowed + clipped plants were offset by decreased primary leaf numbers in mowed unclipped plants, resulting in equal total leaf numbers and, therefore, presumably equal ability to provide fixed carbon to construct capitula. Similarly in unmowed clipped plants, axillary leaves made up for lost primary leaves. The decreased primary leaf numbers with clipping reflects increased leaf abscission. The basis for this interpretation is that clipping reduced main shoot length by ~20%, caused no change in internode length (and therefore in leaves per centimeter of shoot), yet leaf numbers decreased by 70%. The increased leaf abscission suggests that clipping the apical mer-

TABLE 1. Analysis of variance *F* statistics for growth characteristics of *Silphium integrifolium* shoots in the galling vs. clipping and mowing vs. clipping experiments.

Plant response	Galling vs. clipping experiment				Mowing vs. clipping experiment			
	Factor	df	<i>F</i>	<i>P</i>	Factor	df	<i>F</i>	<i>P</i>
Internode (cm)	Galling (G)	1,45	1.2	0.2786	Mowing (M)	1,36	2.3	0.1377
	Clipping (C)	1,45	0.6	0.4327	Clipping (C)	1,36	3.1	0.0856
	G × C	1,45	2.1	0.1526	M × C	1,36	0.3	0.5757
Main shoot (cm)	Galling	1,45	127.7	0.0001	Mowing	1,36	0.7	0.4203
	Clipping	1,45	124.4	0.0001	Clipping	1,36	21.0	0.0001
	G × C	1,45	99.7	0.0001	M × C	1,36	1.0	0.3289
Total height (cm)	Galling	1,45	20.0	0.0001	Mowing	1,36	0.4	0.5446
	Clipping	1,45	39.5	0.0001	Clipping	1,36	1.5	0.2281
	G × C	1,45	37.0	0.0001	M × C	1,36	0.6	0.4543
Axillary shoots (n)	Galling	1,45	0.2	0.6799	Mowing	1,36	6.1	0.0187
	Clipping	1,45	38.8	0.0001	Clipping	1,36	40.6	0.0001
	G × C	1,45	1.6	0.2193	M × C	1,36	0.1	0.7149
Axillary shoot length (cm)	Galling	1,17	6.3	0.0223	Mowing	1,36	0.7	0.4182
	Clipping	1,17	0.2	0.6523	Clipping	1,36	24.6	0.0001
	G × C	1,17	0.6	0.4355	M × C	1,36	0.5	0.4858
Primary leaves ( <i>N</i> )	Galling	1,45	52.7	0.0001	Mowing	1,36	1.3	0.2620
	Clipping	1,45	34.3	0.0001	Clipping	1,36	119.3	0.0001
	G × C	1,45	29.0	0.0001	M × C	1,36	1.4	0.2468
Axillary leaves ( <i>N</i> )	Galling	1,17	5.6	0.0303	Mowing	1,36	2.9	0.0967
	Clipping	1,17	2.2	0.1607	Clipping	1,36	35.1	0.0001
	G × C	1,17	0.0	0.9587	M × C	1,36	1.5	0.2282
Terminal capitula ( <i>N</i> )	Galling	1,45	18.6	0.0001	Mowing	1,36	3.2	0.0835
	Clipping	1,45	33.3	0.0001	Clipping	1,36	33.9	0.0001
	G × C	1,45	18.6	0.0001	M × C	1,36	3.2	0.0835
Axillary capitula ( <i>N</i> )	Galling	1,45	4.6	0.0366	Mowing	1,36	3.9	0.0550
	Clipping	1,45	4.6	0.0366	Clipping	1,36	6.5	0.0150
	G × C	1,45	0.1	0.7597	M × C	1,36	1.1	0.3071
Total leaves	Galling	1,17	1.1	0.3177	Mowing	1,36	4.1	0.0494
	Clipping	1,17	0.2	0.6400	Clipping	1,36	1.8	0.1839
	G × C	1,17	1.1	0.3141	M × C	1,36	0.5	0.4910
Total capitula	Galling	1,45	3.8	0.0563	Mowing	1,36	6.7	0.0140
	Clipping	1,45	10.0	0.0028	Clipping	1,36	0.8	0.3767
	G × C	1,45	14.2	0.0005	M × C	1,36	0.0	0.9520

istem imposed a substantial stress relative to the small amount of shoot tissue removed. Leaf abscission results when carbon gain does not offset leaf maintenance costs (Fitter and Hay, 1987; Ackerly, 1999), and its occurrence suggests that available resources were better invested in branch growth than in main shoot leaf maintenance.

There are several possible indirect effects of the mowing or clipping treatments that were not accounted for but may have

influenced plant growth responses. First, the mowing treatment may have increased soil moisture availability to the study plants via reduced uptake by the surrounding mowed plants (Fahnestock and Knapp, 1994), which might have enhanced *Silphium*'s branching response to mowing. Second, the timing of our treatment applications also may have affected the outcomes (Whitham et al., 1991). For example, clipping took place several weeks after gall formation, but if done coincident

TABLE 2. Growth *Silphium integrifolium* shoots in the galling vs. clipping experiment and the mowing vs. clipping experiment. Values are means with SE in parentheses. Letters represent significant difference among treatment in pairwise comparison tests.

Galling/clipping experiment Plant response	Intact	Clipped	Galled	Galled + clipped
	Internode length (cm)	6.78 (0.28) <sup>A</sup>	6.46 (0.24) <sup>A</sup>	6.42 (0.17) <sup>A</sup>
Primary leaves ( <i>N</i> )	11.88 (1.17) <sup>A</sup>	2.88 (0.99) <sup>B</sup>	1.75 (0.43) <sup>B</sup>	1.38 (0.40) <sup>B</sup>
Axillary leaves ( <i>N</i> )	4.00 (1.15) <sup>A</sup>	9.00 (2.06) <sup>A</sup>	12.17 (3.85) <sup>B</sup>	17.58 (2.82) <sup>B</sup>
Terminal capitula ( <i>N</i> )	3.44 (0.66) <sup>A</sup>	0.00 (0.00) <sup>B</sup>	0.50 (0.26) <sup>B</sup>	0.00 (0.00) <sup>B</sup>
Axillary capitula ( <i>N</i> )	0.00 (0.00) <sup>A</sup>	0.56 (0.39) <sup>B</sup>	0.56 (0.26) <sup>B</sup>	1.31 (0.51) <sup>C</sup>
Total leaves	12.67 (2.91) <sup>A</sup>	11.29 (2.68) <sup>A</sup>	13.67 (3.67) <sup>A</sup>	19.23 (2.91) <sup>A</sup>
Total capitula	3.44 (0.66) <sup>A</sup>	0.56 (0.39) <sup>B</sup>	1.06 (0.46) <sup>B</sup>	1.31 (0.51) <sup>B</sup>
Mowing/clipping experiment Plant response	Intact	Mowed	Clipped	Mowed + clipped
	Internode length (cm)	6.51 (0.32) <sup>A</sup>	6.19 (0.21) <sup>A</sup>	7.31 (0.47) <sup>A</sup>
Primary leaves ( <i>N</i> )	15.70 (1.16) <sup>A</sup>	18.23 (1.12) <sup>A</sup>	5.07 (1.29) <sup>B</sup>	5.03 (0.71) <sup>B</sup>
Axillary leaves ( <i>N</i> )	1.70 (0.91) <sup>B</sup>	2.98 (0.82) <sup>B</sup>	14.20 (2.81) <sup>A</sup>	22.00 (4.35) <sup>A</sup>
Total leaves	17.40 (1.67) <sup>B</sup>	21.21 (1.24) <sup>A</sup>	19.28 (2.27) <sup>B</sup>	27.03 (4.78) <sup>A</sup>
Total capitula	2.11 (0.55) <sup>B</sup>	4.28 (0.79) <sup>A</sup>	1.43 (0.51) <sup>B</sup>	3.50 (1.23) <sup>A</sup>

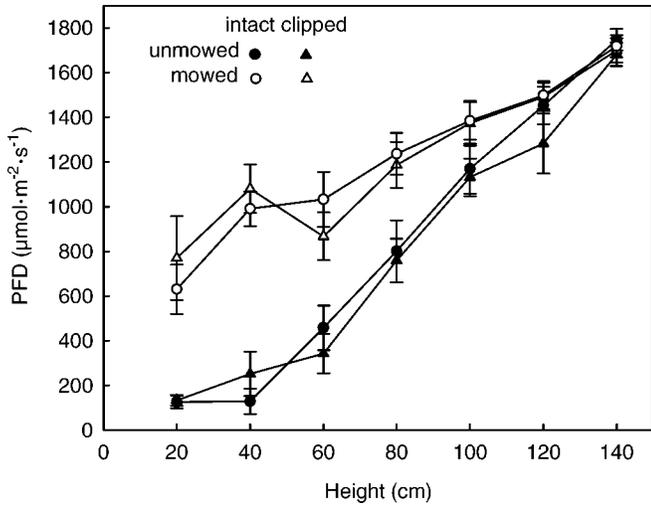


Fig. 2. Vertical profile of photosynthetic photon flux densities (PPFD, means  $\pm$  1 SE) in *Silphium integrifolium* plants in the mowing vs. clipping experiment.

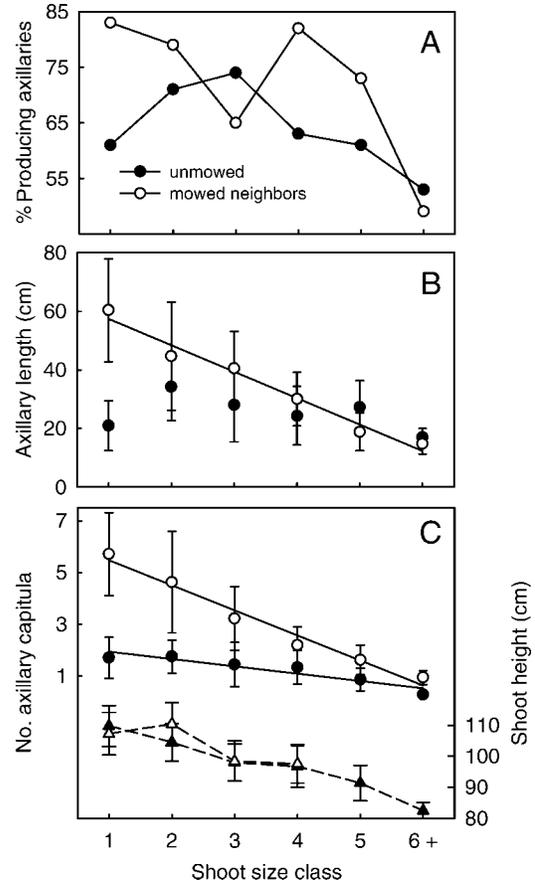


Fig. 4. Axillary production and growth by shoot size class in mowed and unmowed *Silphium integrifolium*, clipping treatments pooled; means  $\pm$  1 SE. (A) Frequency of axillary shoot production. (B) Mean axillary shoot length,  $y = 13.14 - 1.41x$ ,  $P < 0.0001$  (mowed);  $P = 0.76$  (unmowed). (C) Mean number of axillary flower heads (solid lines)  $y = 1.49 - 0.19x$ ,  $P = 0.0003$  (mowed),  $y = 0.67 - 0.08x$ ,  $P = 0.0007$  (unmowed); mean main shoot height for each size class (broken lines).

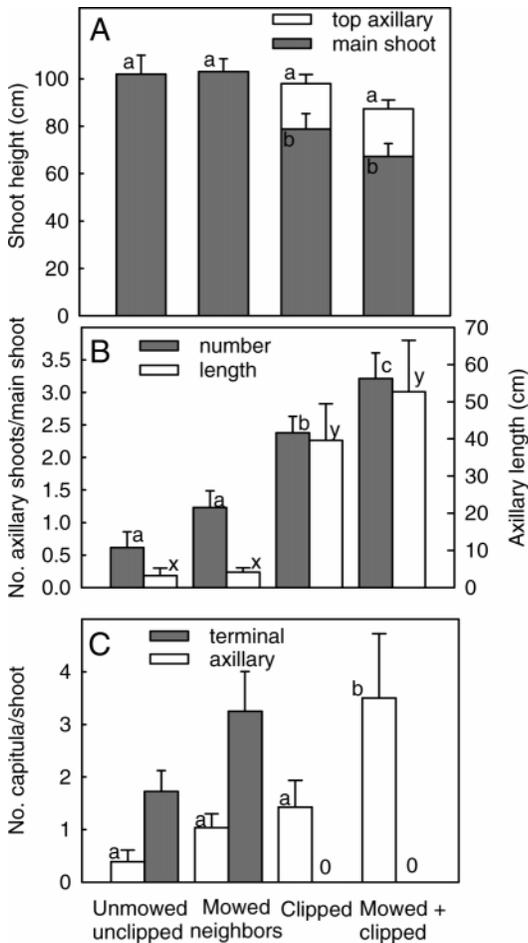


Fig. 3. Shoot and axillary growth in *Silphium integrifolium* in the mowing vs. clipping experiment, means  $\pm$  1 SE. (A) Main shoot height; total shoot height after regrowth of axillary shoots from the nearest main node. (B) Number of axillaries per shoot and total axillary length per shoot. (C) Number of terminal and axillary inflorescences per shoot.

with gall formation, additional axillary growth may have occurred. Earlier mowing might have a similar effect. Third, in the galling vs. clipping experiment we cannot be certain that individual shoots were functionally independent. However, resource transfer among shoots would likely lessen growth differences among shoots (Hartnett and Bazzaz, 1983), making these results conservative indicators of treatment responses. Finally, more detailed fitness estimates like achene numbers, mass, or germination rates may have responded differently than axillary numbers, length, and capitulum production (Irwin and Aarssen, 1996), and longer duration experiments would be needed to assess the true fitness consequences of meristem damage.

In conclusion, these experiments suggest that *Silphium* has considerable plasticity in response to damage and aboveground competition. Damage stimulates branching, but the form of damage may affect how resources are allocated among individual branches, and galls are a unique form of damage that shares some characteristics with intact apical meristems. *Silphium's* growth responses that may maintain access to light in light-competitive environments involve not only regulation of branching patterns, but also regulation of other aspects of resource allocation within the plant, including the manner in

which resources are partitioned among branches and to leaf maintenance. *Silphium's* architecture is common among grassland forbs, and therefore impacts of competition and varying forms of meristem damage on allocation to branching may be a broadly significant factor in influencing light competition among neighboring plants.

## LITERATURE CITED

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