

# Effects of shoot apex removal in *Lythrum salicaria* (Lythraceae): Assessing the costs of reproduction and apical dominance

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The effects of shoot apex removal may be used to evaluate the cost of apical dominance and the cost of reproduction in plants. Plants that have shoot apices removed may have lateral meristems released from apical dominance and thus, may out-yield undamaged plants (i.e. overcompensate) either in the year of damage, or in the subsequent growing season, reflecting the cost of leaving apical dominance intact. Shoot apex removal may also reduce or prevent reproduction (undercompensation) in the year of damage, leaving more resources stored and available for greater reproduction (overcompensation) in the subsequent season relative to undamaged plants (reflecting the cost of reproduction for undamaged plants in the previous season). These hypotheses were tested using *Lythrum salicaria* L. (Lythraceae) as a study species. The effects of pre-flower (early), post-flower (late), and all-season shoot apex removal were recorded in *L. salicaria* within a natural population. Clipped plants were shorter and more branched than unclipped plants, but failed to outperform unclipped plants (in terms of biomass or reproduction) in either the year of treatment or the subsequent year, indicating no evidence for either a cost of apical dominance or a cost of reproduction in this species. Mean seed mass, however, was greater in pre-flower clipped plants compared with unclipped plants in the year of treatment. The interpretation of these results may involve effects of reduced attractiveness to pollinators (and hence reduced fertilization and seed set) in shorter (clipped) plants. The cost of reproduction may be negligible due to *in situ* photosynthesis of reproductive structures and enhancement of vegetative photosynthesis during reproduction, as reported for other species.

Key words: apical dominance, compensatory responses, *Lythrum salicaria*

## INTRODUCTION

The timing of vegetative tissue damage is considered to be an important factor affecting compensa-

tory responses in plants (McNaughton 1982, Benner 1988, Maschinski & Whitham 1989). Moderate early-season herbivory or simulated herbivory in non-competing plants may lead to overcom-

compensation resulting from disruption of apical dominance and increased growth and reproductive potential from the release of lateral meristems (Harris 1974, Inouye 1982, Amuti 1983, Argall & Stewart 1984, Paige & Whitham 1987, Maschinski & Whitham 1989, Michaud 1991). Such overcompensation can be interpreted as a cost of apical dominance in undamaged plants (Aarssen & Irwin 1991, Aarssen 1995, Chamberlin & Aarssen 1996). However, not all studies of the effects of shoot apex removal have demonstrated overcompensation. Late-season herbivory, in particular, usually leaves insufficient response time in the growing season, resulting in, at best, only compensatory biomass production and usually undercompensatory reproduction in the year of damage.

Few studies of compensatory responses in plants, however, have followed the effects of shoot apex removal into the subsequent growing season. Compared with undamaged plants, damaged plants may be more productive and more fecund in the year following damage for two reasons. First, the effects of disrupted apical dominance and released lateral meristems may be to increase photosynthate production and nutrient uptake in the year of damage, but these resources may be stored below-ground rather than invested in above-ground growth and reproduction in the current year. These stored resources may then be used to support greater above-ground growth and/or reproduction (relative to undamaged plants) in the subsequent year, i.e. "delayed" overcompensation. Second, if reproduction is reduced or prevented by shoot herbivory or clipping, resources that would have been otherwise allocated to fruit set and seed development may be stored below ground and invested in greater reproduction (compared with undamaged plants) in the subsequent year. The greater reproduction for damaged plants in the subsequent year thus represents the cost of reproduction for undamaged plants in the previous year (e.g. Zimmerman & Pyke 1988, Jennersten 1991, Galen 1993, Syrjänen & Lehtilä 1993). Hence, reproduction may show an undercompensatory response in the year of damage, but an overcompensatory response in the subsequent year, resulting in a net response of equal compensation.

We explored these hypotheses using the wetland perennial *Lythrum salicaria* L. (Lythraceae).

This species is a troublesome alien weed in North America where it remains largely unaffected by consumers (Mal *et al.* 1992). The large root stock of this species is the main organ of storage and perennation (Shamsi & Whitehead 1977). The impact of shoot apex removal, including inflorescence removal, as a control measure has not been previously studied. We recorded the effects of pre-flower (early), post-flower (late), and all-season shoot apex removal, on architectural and reproductive components of *L. salicaria* within a natural population. Responses to shoot apex removal were recorded at the end of the growing season in both the year of treatment and in the subsequent year. We tested the following predictions: (i) plants clipped early in the growing season would have overcompensatory growth and/or reproduction in the year of treatment and/or in the subsequent growing season (reflecting a cost of apical dominance in unclipped plants), (ii) plants clipped late in the growing season would display undercompensatory reproduction in the year of treatment, but overcompensatory reproduction in the subsequent growing season (reflecting a cost of first season reproduction in unclipped plants), and (iii) plants clipped periodically all-season would demonstrate only undercompensation due to excessive tissue removal.

## MATERIALS AND METHODS

The study was conducted at the Queen's University Biological Station in a small marshy bay on Lake Opinicon (Leeds & Grenville County, Ontario; 44°33'N, 76°20'W). The wetland was dominated by *Lythrum salicaria*, grasses and sedges, and its size was about 2 ha. Other less common species included swamp loosestrife (*Decodon verticillatus* L.) Ell., cattails (*Typha* spp.), marsh bedstraw (*Galium palustre* L.), water plantain (*Alisma subcordatum* Raf.), common arrowhead (*Sagittaria latifolia* L.), water arum (*Calla palustris* L.), slender blue flag iris (*Iris prismatica* Rush.), bittersweet night shade (*Solanum dulcamara* L.), tufted loosestrife (*Lysimachia thyrsoiflora* Gray) and various ferns and mosses. The edges of the wetland contained a mix of willows (*Salix* spp.), red osier dogwood (*Cornus stolonifera* Michx.), red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Michx.f.), hemlock (*Tsuga canadensis* L.), cedar (*Thuja occidentalis* L.), and alder (*Alnus rugosa* DuRoi.).

In mid May 1993, 200 small plants and 200 large plants

were selected randomly. Two distinct size classes were used in order to account for any possible effects that plant size may have as a source of variation in the data. Plants with 3–5 main stems from the previous year's growth were considered to be small plants, whereas plants with ten 10–12 old main stems were considered large plants. The average number of old main stems was 4.0 for small plants and 10.3 for large plants. The study plants were generally taller than neighbouring plants (usually grasses and sedges) and hence experienced minimal competition for light.

The experiment was set up as a  $2 \times 4$  full factorial design with two plant size classes by four clipping treatments: pre-flower clipping (3 times), all-season clipping (6 times), post-flower clipping (4 times) and unclipped (controls). For each plant size class, fifty replicate plants were assigned randomly to each clipping treatment (although a few replicates were lost to mortality or damage from unknown causes during the study). The number of old main stems did not differ among the plants assigned to the clipping treatment groups (Model I ANOVA  $F_{3,374} = 1.6$ ,  $P = 0.694$ ,  $r^2 = 0.03$ ). For the pre-flowering and all-season clipping treatments, approximately 3 cm were removed from all shoot tips at each clipping using clipping shears. The first clipping was performed on 26 May, the second clipping on 22 June and the third on 22 July 1993. The pre-flower clipping treatment was then left to flower and set seed for comparison with unclipped control plants. Plants that were clipped all-season were clipped three more times at two-week intervals before harvesting in September.

Flowering began in mid-July for plants assigned to the control and post-flower clipping groups. Inflorescences in *Lythrum salicaria* develop from shoot apices as terminal spikes. Hence, for the post-flowering clipping treatment, shoot tips were clipped at the base of the flowering spike. All open spikes were removed at each clipping. Spikes were clipped first on 9 July 1993 and subsequently thereafter at approximately two-week intervals for a total of four clippings. Hence, the plants in the post-flowering and all-season clipping treatments never set seed in the year of treatment.

During July and August the date of first flower was recorded for each plant. In September, after flowering had finished in both the pre-flower clipping and control plants, fruits on these plants were collected and counted, and seeds were counted from ten randomly selected ripe fruits per plant. In October, after stalks had turned brown, the following data were collected for each plant: height (of the tallest shoot), number of spikes, number of shoot tips, and number of main stems emerging from the base. Above ground parts of each plant were then harvested, dried to constant mass and weighed. Fifty seeds from each plant were randomly selected and weighed to obtain mean seed weight per plant. Fifty randomly selected seeds from each plant were surface sterilized (in a 30% solution of Javex™ bleach with 0.1% Triton surfactant) and allowed to germinate in a sterile petri dish containing filter paper moistened with 3 ml of sterile distilled water. The petri dishes were sealed with Parafilm™ and placed on a greenhouse bench for 30 days with random

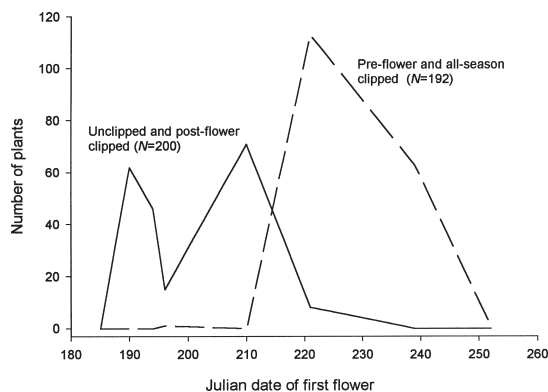


Fig. 1. Date of first flower in *Lythrum salicaria* for plants that were unclipped before flowering began (controls plus post-flower clipping treatment) (solid line) and plants that were clipped before flowering began (pre-flower plus all-season clipping treatment) (dashed line). Small and large plants are pooled.

re-location every 3 days. Normal daylight was about 8 hours in duration and temperature was constant between 20–25°C, day and night. The total number of germinated seeds per dish was recorded after ten consecutive days with no further germination.

Study plants were re-visited at the end of the second growing season (October 1994) and the number of flowering spikes and total number of fruits were recorded for each plant.

A two-way Model I ANOVA was performed for each character to determine the effects due to clipping and plant size. The effects were fixed; hence, the variance-ratio test (or  $F$  test) was determined by effect MS/error MS. The variances for each variable were heterogeneous ( $P < 0.05$ ) using  $F_{\max}$  test on raw data. Square root and logarithmic transformations of the data were applied but variance homogeneity could not be achieved in most cases. Hence, the data were ranked globally and analyzed nonparametrically by an extension of the Kruskal-Wallis test (Zar 1984). Ranking tends to destroy interactions that existed prior to ranking; hence interactions are not interpreted. Since ten different variables were analyzed, the sequential Bonferroni technique (Rice 1989) was used to adjust the per-test type I error rate to hold the experiment wise type I error rate at 5%.

## RESULTS

Flowering time was delayed by about one month in plants that were clipped before flowering began (pre-flower and all season clipping treatments) compared with plants that were unclipped before flowering began (controls and post-flower clipping treatment) (one-way Kruskal-Wallis  $H = 280.3$ ,  $P < 0.0001$ , d.f. = 1, Fig. 1). Plant architecture was

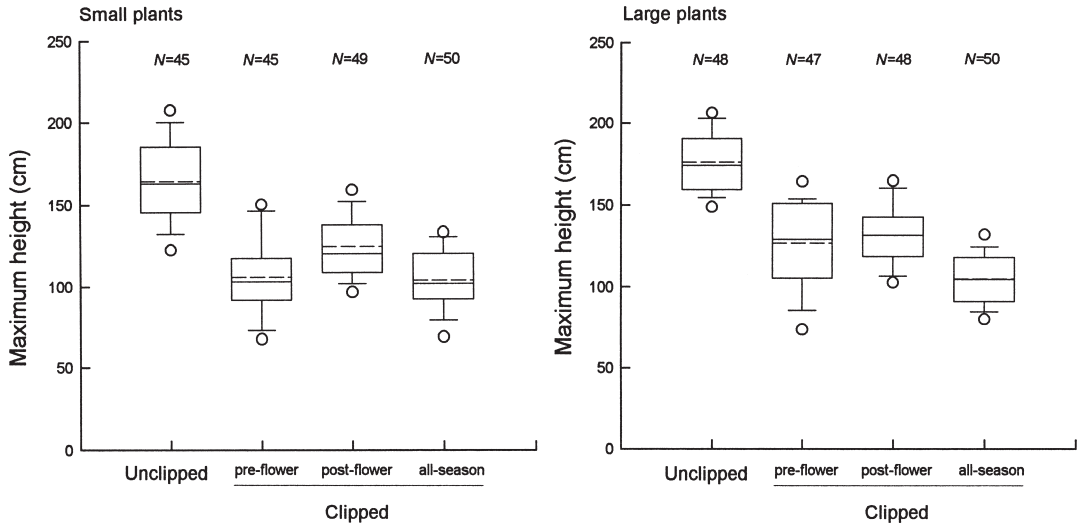


Fig. 2. First-season maximum height of small and large plants of *Lythrum salicaria* for individuals that were unclipped, clipped pre-flowering, clipped post-flowering and clipped periodically all-season. Boxes: 25th and 75th percentiles intersected by the median (solid line); whiskers: 10th and 95th percentiles; dashed lines: the means. *N* = sample size.

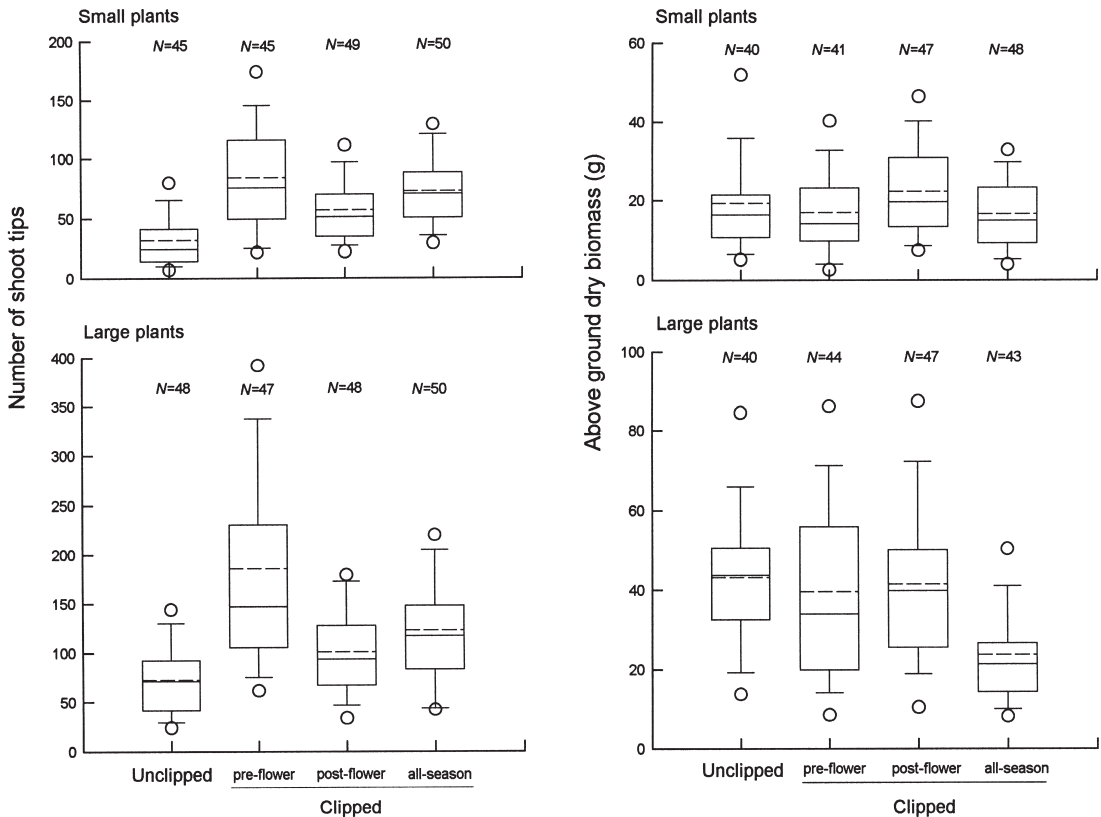


Fig. 3. First-season number of shoot tips in small and large plants of *Lythrum salicaria* for individuals that were unclipped, clipped pre-flowering, clipped post-flowering and clipped periodically all-season. Boxes: 25th and 75th percentiles intersected by the median (solid line); whiskers: 10th and 95th percentiles; dashed lines: the means. *N* = sample size.

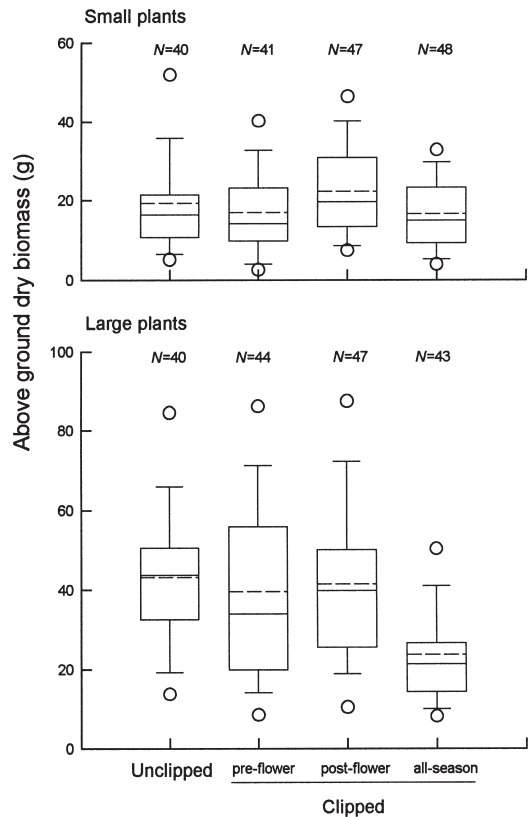


Fig. 4. First-season above ground dry biomass of small and large plants of *Lythrum salicaria* for individuals that were unclipped, clipped pre-flowering, clipped post-flowering and clipped periodically all-season. Boxes: 25th and 75th percentiles intersected by the median (solid line); whiskers: 10th and 95th percentiles; dashed lines: the means. *N* = sample size.

affected by clipping in all treated plants and the effects of clipping were generally independent of plant size. The height of the clipped plants decreased (about 30% overall) (Table 1, Fig. 2). All levels of clipping treatments were significantly different from the control (unclipped plants) according to Dunnett's two-tail test ( $P < 0.05$ ). The number of shoot tips increased (1.6 fold overall) (Table 1, Fig. 3) with clipping and all levels of clipping treatments significantly different from the control according to Dunnett's two-tail test ( $P < 0.05$ ). Total above ground dry biomass was reduced by clipping (about 16% overall) (Table 1),

but the most significant reduction (about 50% overall) occurred in large plants. The significant difference was between all-season clipped plants compared with control plants according to Dunnett's two-tail test ( $P < 0.05$ ) (Fig. 4).

First season reproductive components could only be obtained for unclipped and pre-flower clipped plants, because the other two clipping treatments were not allowed to set seed. Response to clipping was again independent of plant size. Removal of shoot apices had no significant effect on the number of flowering spikes between pre-flower clipped (3 ×) and control plants (Table 1,

Table 1. Results of two-way Model I ANOVAs for effects of clipping and plant size on vegetative and floral characters of *Lythrum salicaria* in the year of treatment. Square root and  $\log_{10}$  transformations did not result in homogeneous variances and re-analyses were performed by globally ranking the raw data and analyzing non-parametrically by an extension of the Kruskal-Wallis test (Zar 1984).

Characters and effects	d.f.	Sum of squares	F	P
<b>Height</b>				
Clipping (C)	3	2 376 526.40	143.0	< 0.0001 <sup>a)</sup>
Size (S)	1	124 486.50	22.5	< 0.0001 <sup>a)</sup>
C x S	3	74 689.60	4.5	0.0041 <sup>a)</sup>
Error	374	2 072 472.60		
$r^2$	0.55			
<b>Number of shoot tips</b>				
Clipping (C)	3	912 770.80	41.8	< 0.0001 <sup>a)</sup>
Size (S)	1	1 012 200.70	139.1	< 0.0001 <sup>a)</sup>
C x S	3	9 590.90	0.4	0.7249
Error	374	2 720 703.90		
$r^2$	0.41			
<b>Above ground dry biomass</b>				
Clipping (C)	3	214 679.68	10.0	< 0.0001 <sup>a)</sup>
Size (S)	1	831 710.87	116.1	< 0.0001 <sup>a)</sup>
C x S	3	89 877.89	4.2	0.0063
Error	342	2 450 315.70		
$r^2$	0.31			
<b>Flower biomass</b>				
Clipping (C)	1	135 844.06	108.5	< 0.0001 <sup>a)</sup>
Size (S)	1	51 219.95	40.9	< 0.0001 <sup>a)</sup>
C x S	1	3 676.23	2.9	0.0885
Error	164	205 301.82		
$r^2$	0.48			
<b>Total number of flowering spikes</b>				
Clipping (C)	1	2 447.01	1.1	0.2917
Size (S)	1	58 714.31	26.8	< 0.0001 <sup>a)</sup>
C x S	1	8 718.16	4.0	0.0475
Error	164	374 044.21		
$r^2$	0.16			

<sup>a)</sup> Effects that remained significant ( $P < 0.05$ ) after application of the sequential Bonferroni technique.

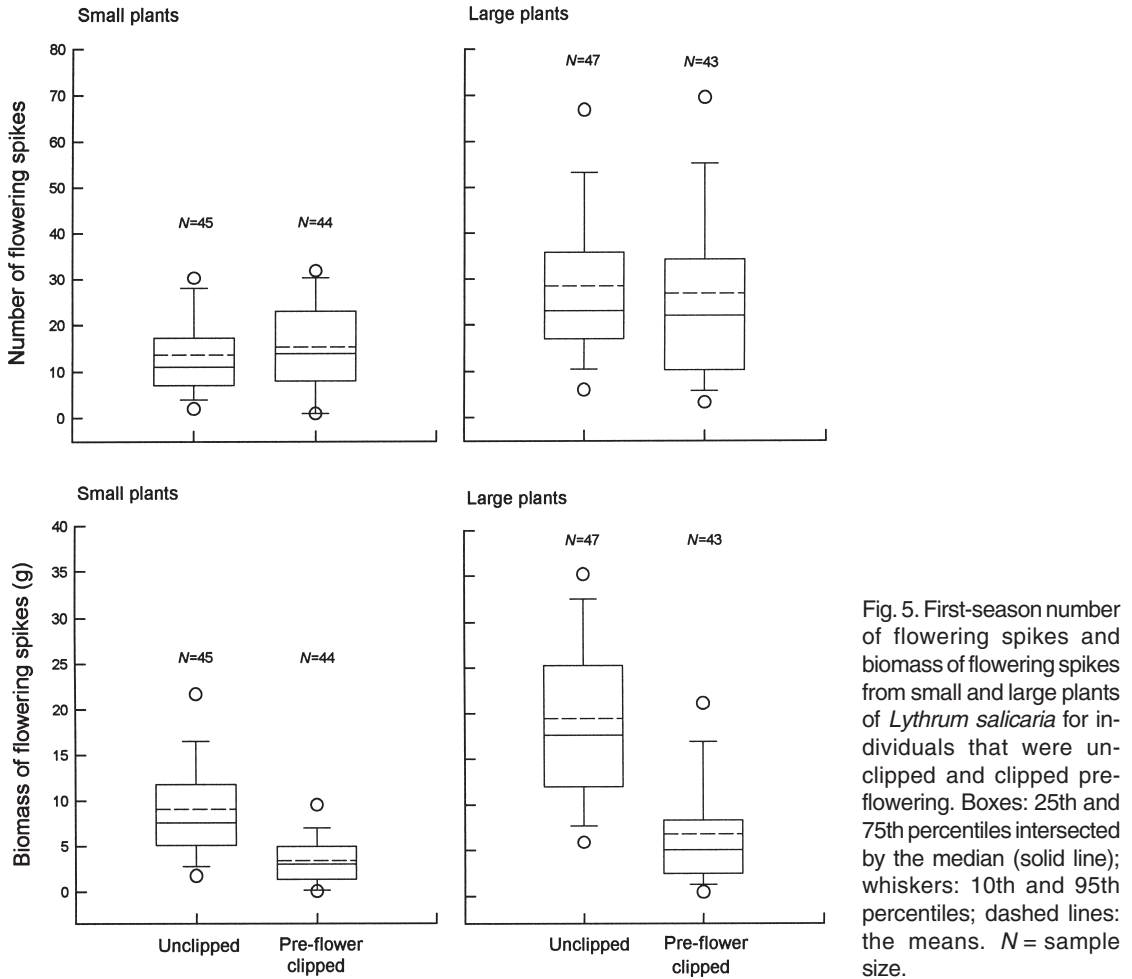


Fig. 5. First-season number of flowering spikes and biomass of flowering spikes from small and large plants of *Lythrum salicaria* for individuals that were unclipped and clipped pre-flowering. Boxes: 25th and 75th percentiles intersected by the median (solid line); whiskers: 10th and 95th percentiles; dashed lines: the means.  $N$  = sample size.

Fig. 5). However, the biomass of the flowering spikes was reduced by clipping (about 60% overall) (Table 1, Fig. 5). Pre-flower clipped plants produced less fruits per plant than control plants (Table 2, Fig. 6). The mean number of seeds per fruit and the total number of seeds per plant were also reduced by pre-flower clipping (Table 2, Fig. 7).

Seed weight was greater, but percent seed germination was lower for pre-flower clipped plants than for unclipped plants (Table 2, Fig. 8). These analyses were based on seeds collected randomly from flowering spikes. Since flowering was delayed in pre-flower clipped plants, the fruits on these plants matured at about the same time as fruits on the top portion of control plants. When analyzed using only seeds from the top portion of

control plants, seeds of pre-flower clipped plants still weighed significantly more than seeds from the top portion of control plants (Model I ANOVA,  $F_{1,148} = 14.9$ ,  $P = 0.0002$ ,  $r^2 = 0.11$ ) (Fig. 8). Hence, the greater seed mass of pre-flower clipped plants was not due to environmental conditions in the later part of the flowering season.

The number of flowering spikes per plant produced in the year following treatment did not differ significantly among treatments (Table 3). The total number of fruits produced per plant in the second growing season differed among the clipping treatments with only marginal statistical significance ( $P = 0.0613$ ) (Table 3); the greatest number of fruits was produced in plants that had received the pre-flower clipping treatment (Fig. 9).

## DISCUSSION

Apical dominance may confer several potential adaptive advantages for a plant (Aarssen 1995). However, apical dominance also limits the number and activity of meristems and hence has the potential to prevent the plant from fully utilizing the available nutrient and photosynthate supply (Harris 1974). This may in turn limit growth and reproduction and, hence, represents a potential cost of apical dominance. This may become a realized

cost in circumstances where the benefits of apical dominance (e.g. tall height to avoid shading by neighbours) are not gained (e.g. uncrowded vegetation) (Aarssen 1995). The potential cost of apical dominance can be expressed in terms of overcompensation following shoot apex removal. In this study, we failed to detect evidence for overcompensation or a cost of apical dominance in *Lythrum salicaria* growing in a natural population.

Clipping reduced plant height (Fig. 2) but increased branching (Fig. 3), associated with the

Table 2. Results of two-way Model I ANOVAs for effects of clipping and plant size on fruit and seed characters of *Lythrum salicaria* in the year of treatment. Square-root, log<sub>10</sub> or arcsin (square root) transformations did not result in homogeneous variances and re-analyses were performed by globally ranking the raw data and analyzing nonparametrically by an extension of the Kruskal-Wallis test (Zar 1984).

Characters and effects	d.f.	Sum of squares	<i>F</i>	<i>P</i>
<b>Fruits/plant</b>				
Clipping ( <i>C</i> )	1	175 750.41	128.8	< 0.0001 <sup>a)</sup>
Size ( <i>S</i> )	1	32 694.72	24.0	< 0.0001 <sup>a)</sup>
<i>C</i> × <i>S</i>	1	5 542.26	4.0	0.0454
Error	171	233 259.93		
<i>r</i> <sup>2</sup>	0.48			
<b>Seeds/fruit</b>				
Clipping ( <i>C</i> )	1	81 563.17	49.3	< 0.0001 <sup>a)</sup>
Size ( <i>S</i> )	1	3 052.22	1.8	0.1762
<i>C</i> × <i>S</i>	1	9 971.68	6.0	0.0151
Error	157	259 562.64		
<i>r</i> <sup>2</sup>	0.25			
<b>Total seeds/plant</b>				
Clipping ( <i>C</i> )	1	148 273.86	133.5	< 0.0001 <sup>a)</sup>
Size ( <i>S</i> )	1	26 213.76	23.6	< 0.0001 <sup>a)</sup>
<i>C</i> × <i>S</i>	1	769.05	0.7	0.4066
Error	157	174 383.72		
<i>r</i> <sup>2</sup>	0.50			
<b>Seed weight</b>				
Clipping ( <i>C</i> )	1	58 912.46	38.7	< 0.0001 <sup>a)</sup>
Size ( <i>S</i> )	1	4 242.67	2.8	0.0971
<i>C</i> × <i>S</i>	1	982.21	0.6	0.4231
Error	148	225 295.98		
<i>r</i> <sup>2</sup>	0.23			
<b>Percent germinated seeds</b>				
Clipping ( <i>C</i> )	1	32 513.90	43.6	< 0.0001 <sup>a)</sup>
Size ( <i>S</i> )	1	4 699.95	3.3	0.0723
<i>C</i> × <i>S</i>	1	7 992.40	5.6	0.0196
Error	148	212 339.84		
<i>r</i> <sup>2</sup>	0.27			

<sup>a)</sup> Effects that remained significant (*P* < 0.05) after application of the sequential Bonferroni technique.

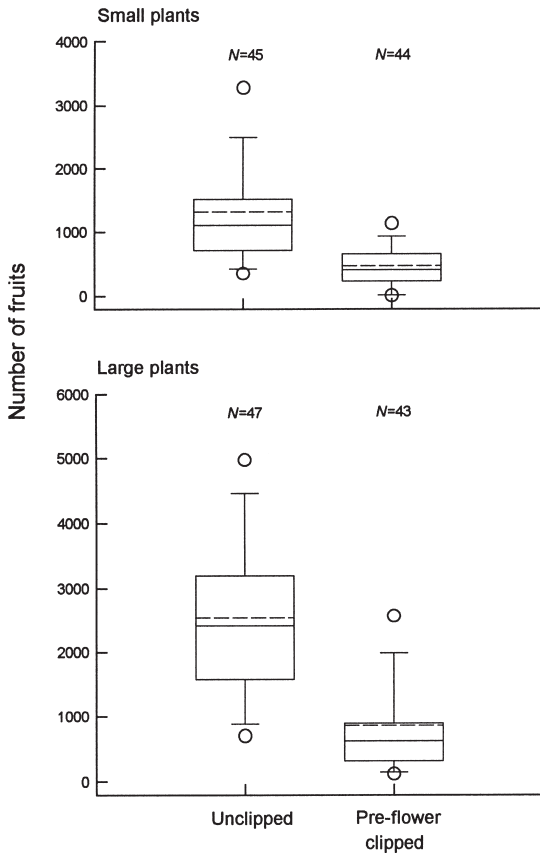


Fig. 6. First-season number of fruits produced by small and large plants of *Lythrum salicaria* for individuals that were unclipped and clipped pre-flowering. Boxes: 25th and 75th percentiles intersected by the median (solid line); whiskers: 10th and 95th percentiles; dashed lines: the means.  $N$  = sample size.

release of lateral meristems from the effects of apical dominance. The branching response was most evident in the pre-flower clipping treatment where plants had the greatest amount of time left in the growing season to respond to clipping. This increased branching, however, was not associated with increased biomass or fecundity (i.e. no over-compensation) in either the year of treatment or the subsequent year. Plants that received pre-flower clipping compensated for shoot apex removal in terms of first-season biomass response (Fig. 4) and number of spikes (Fig. 5), but under-compensated in terms of spike biomass (Fig. 5) and fruit and seed production (Figs. 6 and 7) in the year of treatment. The slightly greater fruit production in the second season for the pre-flower clipped group (Fig. 9) is intriguing but inconclusive owing to the statistical significance of only  $P = 0.0613$ . As predicted, plants that received all-season clipping undercompensated in terms of biomass production (Fig. 4). Hence, clipping shoots at any time in the growing season appears to be detrimental to *Lythrum salicaria* and may help to control the spread of this weed.

There are two possible reasons for the lack of evidence for a cost of apical dominance. Overcompensation in biomass and fruit production may have been absent in pre-flower clipped plants because: (i) unclipped plants of *Lythrum salicaria* are not constrained by apical dominance in their ability to fully utilize the available nutrient and photosynthate supply (i.e. there is no potential cost of apical dominance in this species). Similar re-

Table 3. Results of two-way Model I ANOVAs for effects of clipping and plant size on total number of flowering spikes and total number of fruits per plant for *Lythrum salicaria* in the year following treatment (second season). Data were square-root transformed prior to analysis to achieve homogenous variances.

Characters and Effects	d.f.	Sum of Squares	$F$	$P$
<b>Total number of flowering spikes</b>				
Clipping ( $C$ )	3	11.50	1.952	0.1210
Size ( $S$ )	1	159.87	81.383	< 0.0001
$C \times S$	3	2.44	0.413	0.7435
Error	339	665.92		
<b>Total number of fruits</b>				
Clipping ( $C$ )	3	1 091.90	2.48	0.0613
Size ( $S$ )	1	9 489.50	64.55	< 0.0001
$C \times S$	3	771.90	1.75	0.1565
Error	339	49 835.30		



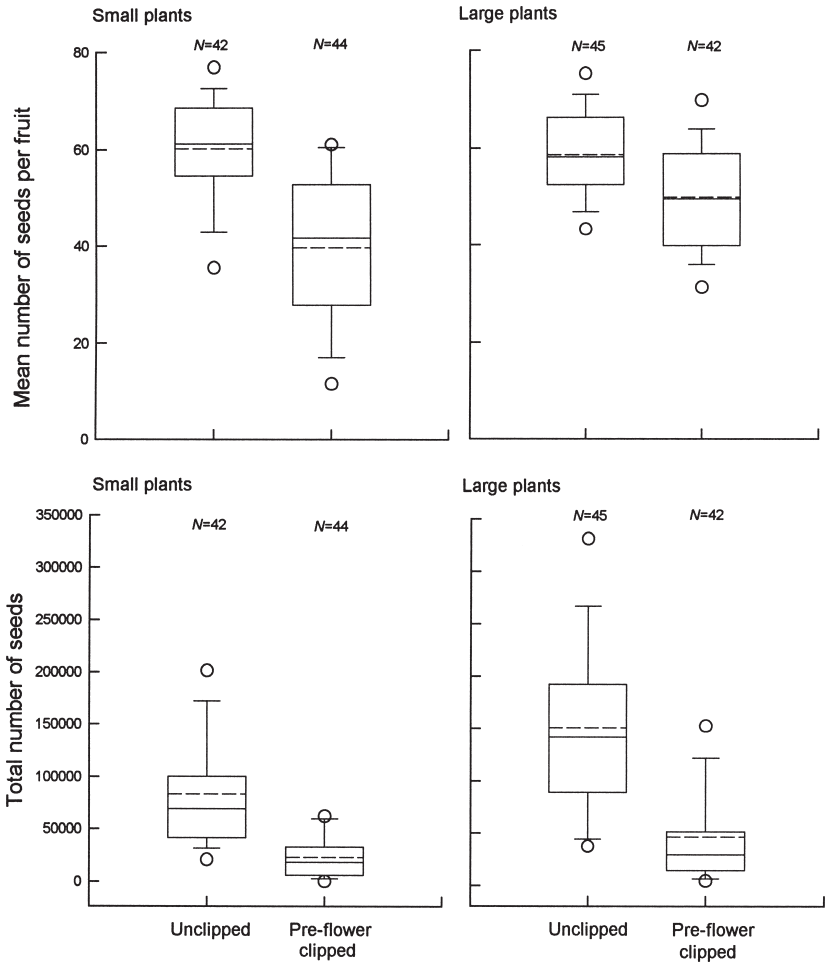


Fig. 7. First-season number of seeds per fruit and total number of seeds produced by small and large plants of *Lythrum salicaria* for individuals that were unclipped and clipped pre-flowering. Boxes: 25th and 75th percentiles intersected by the median (solid line); whiskers: 10th and 95th percentiles; dashed lines: the means.  $N$  = sample size.

sults have been reported for other species (Irwin & Aarssen 1996), and (ii) the clipping treatments prevented the plants from realizing benefits of apical dominance. Apical dominance generally maximizes plant height in upright species which may be important in attracting pollinators (Donnelly *et al.* 1998). Hence, the shorter height of clipped plants in the present study may have reduced pollinator visitation thus resulting in lower fertilization and seed set. Lower fertilization may have made more resources available per fertilized ovule, which may account for the greater mean seed mass in pre-flower clipped plants (Fig. 8). Alternatively, the later flowering time in pre-flower clipped plants may have left insufficient time to mature as many fruits and seeds as were produced by unclipped plants. The reason for re-

duced germination rate of seeds from pre-flower clipped plants (Fig. 8) is unclear, but previous studies have also shown reduced germinability (reflecting presumably stronger dormancy) in larger seeds of some species (e.g. Thomas *et al.* 1979).

We predicted that plants clipped late in the season (post-flowering) and thus prevented from setting fruit would have greater fruit production than unclipped plants in the following season, reflecting the cost of reproduction for unclipped plants in the previous season. However, there was no difference in inflorescence or fruit production among treatments in the year following treatment (Fig. 9). Other studies have also shown that the cost of reproduction may be negligible due to *in situ* photosynthesis of reproductive structures and enhancement of vegetative photosynthesis during

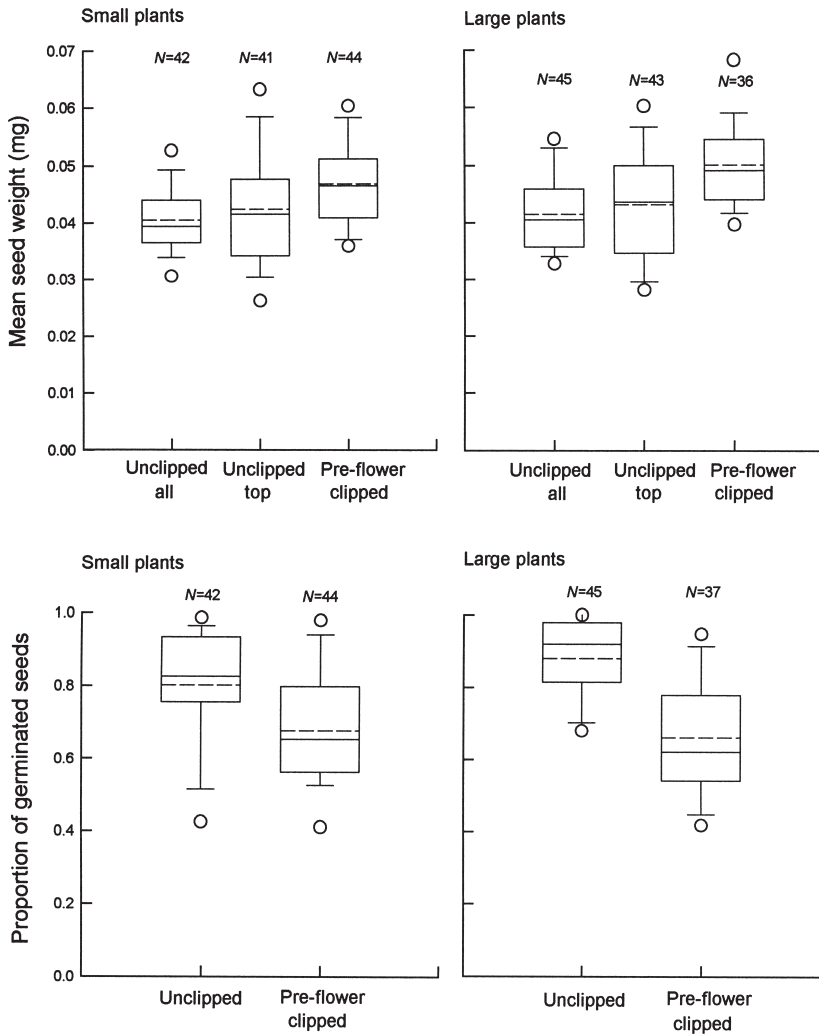


Fig. 8. First-season mean seed weight and proportion of seeds germinated from small and large plants of *Lythrum salicaria* for individuals that were unclipped and clipped pre-flowering. Boxes: 25th and 75th percentiles intersected by the median (solid line); whiskers: 10th and 95th percentiles; dashed lines: the means.  $N$  = sample size.

reproduction (Reekie & Bazzaz 1987). Further studies are required to establish whether these factors play a role in explaining the present results for *Lythrum salicaria*.

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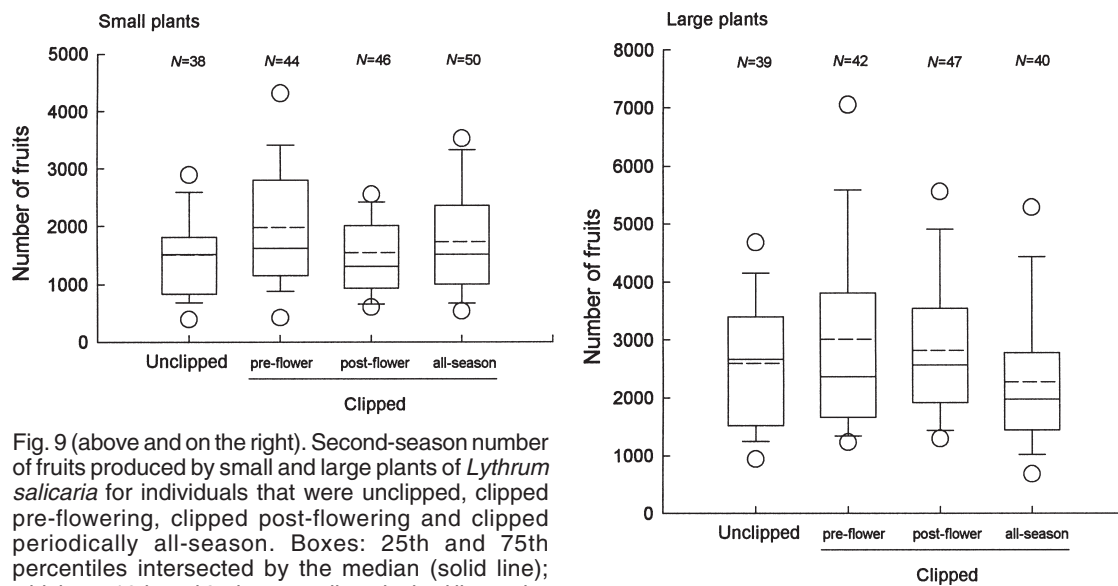


Fig. 9 (above and on the right). Second-season number of fruits produced by small and large plants of *Lythrum salicaria* for individuals that were unclipped, clipped pre-flowering, clipped post-flowering and clipped periodically all-season. Boxes: 25th and 75th percentiles intersected by the median (solid line); whiskers: 10th and 95th percentiles; dashed lines: the means.  $N$  = sample size.

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