Testing for cost of apical dominance in vegetation: a field study of three species

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Damage to the shoot apex commonly causes release of lateral meristems from apical dominance in plants. This has been shown in some species to promote increased seed and/or biomass production (i.e. overcompensation) by stimulating lateral branching, primarily in plants growing free from competition for light. This may represent a potential fitness cost when apical dominance is left intact in non-competing plants. In this study, shoot apices of three herbaceous species, *Hypericum perforatum* L. (Hypericaceae), *Melilotus alba* Medicus (Fabaceae) and *Ambrosia artemisiifolia* L. (Asteraceae) growing in open habitats were removed in order to determine if a potential fitness cost of apical dominance was evident. We predicted that in such open habitats, where competition for light is relatively weak, there should be relatively little evidence for a potential cost of apical dominance; since there should be relatively little benefit in having apical dominance here, selection should minimize any potential fitness cost of apical dominance, or minimize apical dominance directly. This prediction was supported: all of the species compensated but none overcompensated for shoot apex removal in terms of biomass or flower production.

Key words: competition, herbivory, neighbours, overcompensation, selection, shoot apex removal

INTRODUCTION

Owen and Wiegert's (1976) prediction that plants could benefit from being eaten has encouraged numerous studies on plant responses to herbivory, and vigorous debate in the literature (e.g. Belskey 1986, Verkaar 1988, Whitham *et al.* 1991, Belsky *et al.* 1993). The removal of apical dominance via herbivory of the shoot apical meristem has been considered one of the principal factors responsible for eliciting overcompensatory responses to herbivory (Harris 1974, Maschinski & Whitham 1989, Whitham *et al.* 1991, Aarssen 1995). Apical dominance provides a plant with a meristem reserve as more lateral meristems are produced than actually develop into stems or branches (Phillips 1975, Hsaio & Huang 1989, Cline 1991). If the shoot apex and thus the source of apical control is removed or damaged, growth may resume from this pre-existing meristem supply. Examples of yield increases in
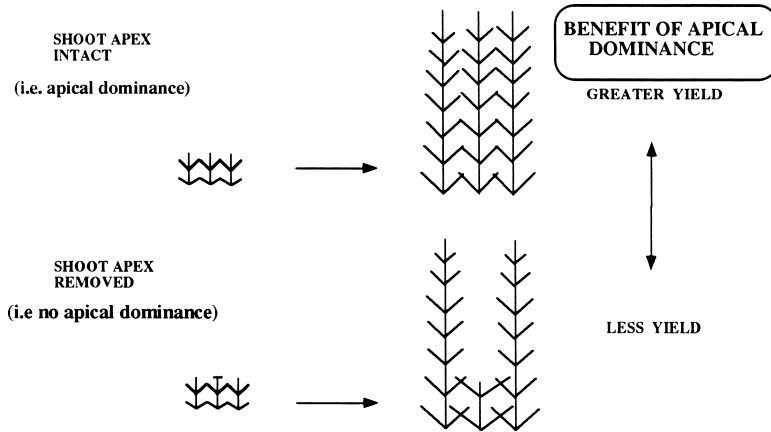
Fig. 1. Schematic illustration of the predicted benefit of apical dominance when in competition with neighbours. Removal of the shoot apex may result in decreased performance since commitment to vertical extension is disrupted while neighbours continue to grow tall.

herbaceous plants following shoot apex removal either alone, or in association with other plant parts, are now common (e.g. Clifford 1979, Tayo 1980, 1982, Inouye 1982, Amuti 1983, Argall & Stewart 1984, Schlichting & Levin 1984, Sheldon 1986, Paige & Whitham 1987, Aarssen & Turkington 1987, Wein & Minotti 1988, Benner 1988, Maschinski & Whitham 1989, Strauss 1991, Mopper *et al*. 1991, Michaud 1991). These data clearly illustrate that removal of biomass (when the shoot apex is included) can result in increased plant biomass and reproduction. The most pressing question now is not can plants benefit from being eaten, but why?

A number of hypotheses for overcompensation following herbivory have been proposed involving the role of natural selection. Most of these (see Owen 1980, 1990, Whitham *et al*. 1991) interpret overcompensation as an adaptive response that has evolved as a consequence of natural selection due to herbivory. Yet, as Harris (1974) notes, "it is difficult to accept that a plant will synthesize with less efficiency than the environment allows until it is "woken up" by an insect chewing at it." One way to address this difficulty is to approach the question of why plants overcompensate by asking first: why do plants have apical dominance? (Aarssen & Irwin 1991).

According to the 'light competition hypothesis', overcompensation following herbivory is not a consequence of selection from herbivory, but rather an indirect consequence of selection from competition for light (Aarssen & Irwin 1991, Aarssen 1995). Land plants have generally evolved under the influence of intense competition for light. The light environment is commonly considered to invoke the greatest

selection pressure on plant shape (Crawley 1983, Niklas 1988, Kuppers 1989). Plants that overtop neighbours commonly achieve dominance in vegetation (Grime 1979, Givnish 1982, Niklas 1988, Tilman 1988, Wailer 1988, Kuppers 1989, King 1990, Weiner *et al*. 1990). Thus, the primary selection pressure favouring apical dominance may be the maintenance of height in plants that are competing for light. Unless height can be maintained in other ways, the destruction of the shoot apex, leading to a decrease in height due to the removal of potential nodal areas along the main stem (Olasantan 1986) may confer a competitive disadvantage with neighbours (Aarssen & Irwin, 1991) (Fig. 1).

When plants are not crowded or shaded by neighbours, however, the premium on vertical extension that apical dominance imposes may provide no net fitness benefit. Lateral bud inhibition due to the maintenance of apical dominance may even represent a potential fitness cost to a plant when it is growing free from competition for light. Thus, these plants may overcompensate for shoot apex removal as more meristems may be made available for allocation to growth and reproduction, and plants with more branches are usually more fecund (Tayo 1982, Islam & Crawley 1983, Niklas 1988) (Aarssen & Irwin 1991, Fig. 2). The central distinction of the light competition hypothesis is that, if this potential fitness cost exists, it is presumed to be worth paying, provided that descendants generally accrue fitness benefits of apical dominance (Fig. 1) that are disproportionately greater.

The extent to which plant species may enjoy the benefits of apical dominance without incurring any
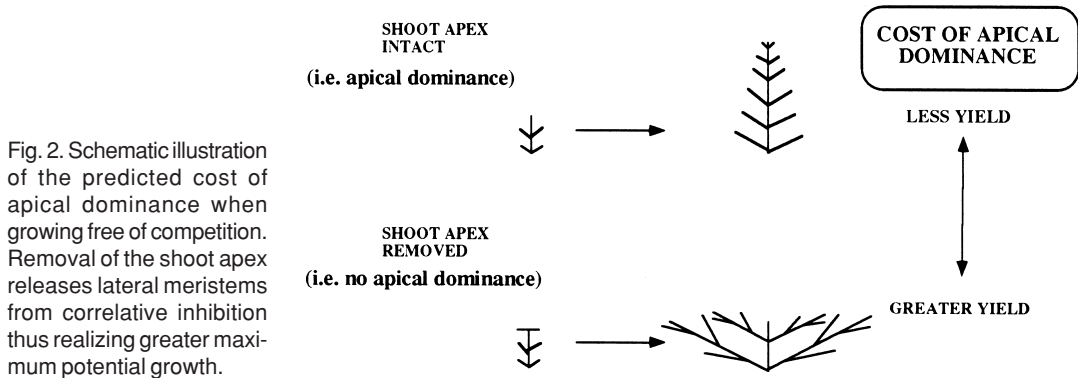
Fig. 2. Schematic illustration of the predicted cost of apical dominance when growing free of competition. Removal of the shoot apex releases lateral meristems from correlative inhibition thus realizing greater maximum potential growth.

costs is unknown. This is likely to depend on both genetic and environmental factors. However, we would predict that ultimately, natural selection should minimize any cost to fitness. Apical dominance may carry a net cost in habitats where there is relatively little benefit of having apical dominance. Accordingly, we predict that in habitats where competition for light is relatively weak (e.g. open, ruderal or impoverished habitats) (Taylor *et al.* 1990), there should be relatively little evidence for a cost of apical dominance (measured as overcompensation following shoot apex removal). This may be a consequence of selection against apical dominance itself, or strong selection against the cost of apical dominance. We tested this prediction by removing shoot apices within natural populations of three common local herbaceous species, *Hypericum perforatum*, *Melilotus alba,* and *Ambrosia artemisiifolia,* and by comparing flower and above ground biomass production with control, intact plants.

METHODS

The study was conducted at the Queen's University Biological Station in Frontenac County, Ontario (44°34′02″N, 76°21′52″W). One study site was located in an undisturbed, abandoned sand quarry, about 4 ha in size (the quarry site), in which individuals of the annual *Melilotus alba* Medicus (Fabaceae) and the perennial *Hypericum perforatum* L. (Hypericaceae) the two most common species, were selected for study. (Nomenclature follows Gleason & Cronquist 1991). Plants in the quarry site were widely spaced and rarely shaded by neighbours. The annual *Ambrosia artemisiifolia* L. (Asteraceae) was studied in an adjacent habitat, approximately 0.5 ha in size, consisting of a recently tilled held of sandy loam (the disturbed site). *Ambrosia artemisiifolia* comprised over 90% of the plant cover with the remaining species made up of mostly

grasses. All three species were selected due to availability within open habitats, and their generally upright growth form, with normally one main stem and numerous unexpanded axillary buds below the shoot apex. Clipping treatments were applied when the plants were young with vigorously elongating shoots and no evidence of lateral bud growth (see below).

The quarry site was marked out with 60 randomly placed 3×3 metre quadrats to assist in relocating study plants. Study plants were selected from 45 of the most visibly homogeneous quadrats in terms of soil moisture and neighbour abundance. 100 shoots of *Hypericum perforatum,* and 100 individuals of *Melilotus alba* approximately 10 cm in height (which had not yet branched) were randomly selected from the 45 quadrats (2 to 3 plants per species per quadrat). As genets of H. perforatum were indistinguishable from ramets, only one shoot was selected for shoot apex treatment from the most closely associated shoots in each quadrat in an effort to minimize the chances of sampling the same genet more than once.

For both *Melilotus alba* and *Hypericum perforatum,* fifty plants were randomly assigned to each of the two clipping treatments, i.e. clipped and unclipped. Using a razor blade, the shoot apex as well as 2 unexpanded and 2 expanding leaves, constituting the top 0.5–1.0 cm of each plant, were removed from the fifty plants in the clipped group on May 27, 1990. The fifty plants in the unclipped group were left to grow with the shoot apex intact. As neighbouring plant canopies did not overlap in the quarry, neighbours were not removed. Plants were harvested on July 22nd, 1990 (eight weeks after the clipping treatment), by which time flowering in both species was complete, and seed production had begun.

In the disturbed site, fifty individuals of *Ambrosia artemisiifolia,* that had not yet branched and were approximately 15 cm tall height with 7 internodes along the main stem, were randomly selected. Twenty-five plants were randomly assigned to each of the two clipping treatments, i.e. clipped and unclipped. Shoot apices were removed from the clipped group (on July 26, 1990) using the method described above for the quarry site. Since some plants had close neighbours, these were clipped periodically at ground level within a 0.5 m radius around study plants. All plants were harvested on Sept. 20th, 1990 (eight weeks after the clipping treatment) after flowering was completed.

Plant height, number of primary and secondary branches and length of the longest three primary and secondary branches were recorded at harvest for all three study species. The number of flowers produced was also recorded. Above ground biomass was harvested, dried, and weighed for *Hypericum perforatum* and *Ambrosia artemisiifolia*, but not for *Melilotus alba* due to the unanticipated large size of these plants. Statistical comparison of treatment and control means were performed with the Wilcoxon Rank Sums Test using Procedure NPARlWAY of SAS Institute, Inc. (1988).

RESULTS

Responses to shoot apex removal were similar for *Ambrosia artemisiifolia, Hypericum perforatum* and *Melilotus alba* (Table 1). Removal of the shoot apex decreased main stem height and primary branch number in all three species, but had no effect on secondary branch production, such that more secondary branches per primary branch were produced. Clipped plants also produced longer primary branches and longer secondary branches than unclipped plants. Shoot apex removal had no effect on above ground biomass or flower production (Table 1).

DISCUSSION

According to the light competition hypothesis (Aarssen & Irwin 1991), overcompensatory response to

Table 1. Mean (+ *S.E.*) values for characters measured on *Hypericum perforatum* L., *Melilotus alba* Medicus and *Ambrosia artemisiifolia* L. in control plants and in plants with the apex removed (treatment). *Z*-values and *P*-values are from the Wilcoxon Rank Sums test for the effect of treatment.

	H. perforatum		*M. alba*		*A. artemisiifolia*	
	control N = 44	treatment N = 50	control N = 49	treatment N = 47	control N = 19	treatment N = 23
Main stem height (cm)	144.5 (0.3)	26.5 (0.1)	84.0 (2.9)	27.8 (1.4)	35.1 (1.3)	12.8 (1.7)
Z	6.40		− 8.42		5.03	
P	0.0001		0.0001		0.0001	
Number of primary branches	10.2 (0.5)	4.1 (0.4)	21.4 (0.8)	5.5 (0.3)	17.1 (0.7)	8.9 (0.7)
Z	7.35		− 8.46		5.10	
P	0.0001		0.0001		0.0001	
Number of secondary branches	14.9 (1.1)	16.1 (1.2)	40.0 (3.5)	47.8 (4.8)	45.8 (8.7)	47.2 (6.0)
Z	− 0.58		1.09		− 0.77	
P	0.562		0.275		0.441	
Number of secondary branches per primary branch	1.5 (0.1)	4.5 (0.3)	1.8 (0.2)	9.1 (0.8)	2.5 (0.4)	5.2 (0.4)
Z	− 7.08		7.81		− 3.85	
P	0.0001		0.0001		0.0001	
Primary branch length (cm)	5.1 (0.5)	16.1 (0.9)	18.5 (1.2)	33.9 (1.93)	21.3 (1.8)	27.7 (1.1)
Z	7.33		5.73		− 2.94	
P	0.0001		0.0001		0.0032	
Secondary branch length (cm)	1.1 (0.1)	2.2 (0.2)	2.1 (0.1)	5.3 (0.6)	5.9 (0.9)	10.9 (0–9)
Z	5.5		6.61		− 3.3	
P	0.0001		0.0001		0.0001	
Above ground dry biomass (g)	3.2 (1.7)	2.7 (0.9)			11.6 (1.8)	11.9 (2.1)
Z	− 0.43				0.52	
P	0.667				0.602	
Number of flowers	39.8 (3.2)	43.9 (3.9)	63.5 (4.3)	54.8 (4.9)	65.1 (9.6)	52.9 (4.7)
Z	− 0.26		− 1.90		0.57	
P	0.794		0.057		0.569	

herbivory is a consequence of the disruption of apical dominance following shoot apex removal and should be interpreted as an indirect consequence of selection from competition for light (Fig. 1), not as a trait that has evolved as an adaptive response to herbivory (Aarssen & Irwin 1991, Hjalten *et al*. 1993, Aarssen 1995). Inherent to this hypothesis is the assumption that apical dominance carries a potential fitness cost when plants are grown free of competition and this is reflected by overcompensation following shoot apex removal (Fig. 2). We predicted however that in natural vegetation where competition for light is relatively weak, evidence for a potential cost of apical dominance (overcompensation) should be minimal since we would expect strong selection against any cost, or against apical dominance itself.

The results of this study confirm our prediction. For the three species growing in the open habitats, the removal of the shoot apex altered the architecture (i.e. lengthened branches), but this did not translate into increased plant performance relative to plants with the shoot apex left intact. Shoot apex removal did not increase branch production, a response commonly associated with strong apical dominance, resulting in no change in the production of reproductive meristems. Consequently, all three species compensated for shoot apex removal in terms of flower and above ground biomass production, but did not overcompensate.

These results have two possible interpretations. Firstly, following our prediction above, the lack of overcompensation may imply that apical dominance was either weak or it did not incur any potential cost. Alternatively however, apical dominance may have been so strong that it was quickly reestablished in subtending lateral shoots following decapitation of the main stem, thus restricting overcompensatory growth. The increased secondary branch production in clipped plants is difficult to interpret since it cannot be easily explained by basipetal auxin transport coming down from the main shoot apex. These conflicting interpretations underscore a fundamental unresolved question: How is the strength of apical dominance measured? Further research is required to address this and other important questions in the ecology and evolution of apical dominance in plants: Are there other fitness benefits of apical dominance in addition to its role in competition for light (Aarssen 1995)? Can selection minimize the potential fitness cost of apical dominance while maintaining the ben-

efit? Is such selection more likely in some habitat types than in others? Can selection adjust the plasticity of apical dominance? Is there genetic variation for this plasticity? Are patterns of apical dominance affected by selection from herbivory (associated with benefits from having apical dominance disrupted), and how does this interact with selection from competition (associated with benefits of having apical dominance left intact)? In researching these questions, several factors may need to be taken into account in measuring responses to shoot apex removal in plants, including nutrient level, timing of shoot apex removal and the age of the plant at harvest.

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