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# Interactions between cottonwood and beavers positively affect sawfly abundance

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**Abstract.** 1. Cottonwood (*Populus* spp.) are the dominant tree type in riparian forests of the western U.S.A. In these riparian forests, the beaver (*Castor canadensis*) is a major ecosystem engineer that commonly browses cottonwood, resulting in distinct changes to plant architecture. Here the hypothesis that beaver herbivory indirectly affects the distribution of a keystone leaf-galling sawfly through architectural changes in cottonwood was examined.

2. It was found that: (a) beaver herbivory of cottonwood results in an increase in average shoot length over unbrowsed cottonwood; (b) sawfly galls were up to 7–14 times more abundant on browsed cottonwood than unbrowsed cottonwood; and (c) sawfly gall abundance was correlated positively with changes in shoot length after beaver herbivory. Together these data show that the individual and combined effects of cottonwood and beaver herbivory increase shoot length, positively affecting sawfly abundance.

3. Because herbivores are a ubiquitous component of most ecosystems, we argue that the indirect effects of herbivory on plant quality, and subsequently other herbivores, may be as important as environmental variation.

**Key words.** Beaver, herbivores, *Populus*, sawfly, trait-mediated indirect effects.

## Introduction

Beaver are the epitome of a keystone species, an ecosystem engineer (Jones *et al.*, 1997), and are a common herbivore of riparian forests. In the western U.S.A., cottonwood riparian forests comprise less than 3% of the landscape, are severely threatened but still contribute disproportionately to overall biodiversity (Noss *et al.*, 1995). In these cottonwood riparian forests the beaver show strong foraging preferences for *Populus* spp. (Bailey *et al.*, 2004). Herbivores represent a ubiquitous component of biological systems whose effects on host-plant quality are diverse. In addition to consuming 10–20% of above-ground net primary productivity, herbivores alter plant quality through induced chemical (Karban, 1992) and architectural changes (Nakamura & Ohgushi, 2003), and by building structures (e.g. ecosystem engineers – Jones *et al.*, 1994, 1997). Through their patterns of foraging, beaver herbivory can result in changes to host-plant chemistry, architecture, and ontogeny that can affect associated arthropod community members (Martinsen *et al.*, 1998).

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Herbivores alter plant quality in a variety of ways resulting in indirect trait-mediated effects on other herbivores (Hunter & Price, 1992). For example, Bailey and Whitham (2003) showed how herbivory of aspen by elk reduced shoot length, and thus negatively affected the distribution of a keystone sawfly. However, interactions where one organism benefits from the effects of another organism may be common (Jones *et al.*, 1997). For example, Nakamura *et al.* (2003) showed how a stem-galling herbivore altered the abundance of plant tissue on willow through gall formation and positively affected the overall abundance of aphids. Martinsen *et al.* (1998) also showed how beaver herbivory of cottonwood induced changes to specific plant phytochemical compounds that attracted and were subsequently sequestered by a Chrysomelid leaf beetle.

Along the Weber River, near Ogden, Utah, U.S.A., narrowleaf cottonwood (*Populus angustifolia*) are a dominant habitat type that supports a diverse community of organisms (Whitham *et al.*, 1999) including beaver and a keystone leaf-galling sawfly (*Phyllocolpa* sp.; Bailey & Whitham, 2003). Linkages between vigorously growing host plants and sawflies' ovipositional preferences are well documented in the literature (Price *et al.*, 1998; Price & Carr, 2000) with both free-feeding and gall-forming herbivores. *Phyllocolpa* sp. is an important insect herbivore in cottonwood riparian forests whose presence results in significant changes to the composition of associated arthropod communities (J. K. Bailey & T. G. Whitham, unpublished). In aspen forests the presence of this sawfly can increase average arthropod richness and abundance two and four times respectively, and have been shown to be an important food item for insectivorous birds (Bailey & Whitham, 2003).

*Populus angustifolia* resprout prolifically after beaver herbivory. This resprout foliage differs in architecture relative to unbrowsed trees and is ontogenetically juvenile (i.e. plant modules that are not yet reproductive). Initial observations showed that sawflies were concentrated on beaver resprout. Because many species, including *Phyllocolpa*, are known to prefer large leaves and vigorously growing tissues (Price & Clancy, 1986; Price, 1991; Price *et al.*, 1998; Price & Carr, 2000), we predicted that the vigorous resprout growth resulting from beaver herbivory would be better habitat for sawflies than comparably aged cottonwood without beaver herbivory.

## Methods

### *Beaver–sawfly association*

To document that sawflies prefer cottonwood resprout caused by beaver herbivory, we censused sawfly galls on resprout (cottonwood ramets that arise from a stump) and adjacent non-resprout (other juvenile cottonwood ramets) growth. Juvenile tissue was surveyed on adjacent beaver resprout and control trees to minimise the effects of age on sawfly gall abundance and directly test the effects of host-plant architecture. Sawfly galls are easily recognisable as longitudinal folds along the leaf-blade margin. In 2001, 50 shoots from 125 narrowleaf cottonwood trees (63 beaver resprout and 62 control) along the Weber River were selected randomly and visually censused for sawfly galls. In 2002, 50 shoots from 52 narrowleaf cottonwood (i.e. 26 beaver resprout and 26 control) were selected randomly and visually censused to confirm the 2001 gall patterns. These data were analysed using a Student's *t*-test.

The observational data from 2001 indicated that more galls were found on beaver resprout and suggested that architectural differences between browsed and unbrowsed cottonwood could be driving these patterns (Price, 1991). Because shoot length is a common mechanism affecting sawfly gall abundance, in 2002 10 shoots from each sample that was surveyed were selected randomly and measured. Shoot length and sawfly gall abundance data were averaged for beaver resprout and control trees, and analysed using Student's *t*-test. Comparison of the relationship between shoot length and gall abundance was carried out using a simple linear regression.

## Results

### *Beaver–sawfly association*

In both 2001 and 2002, we found a close association between beaver and sawflies; beaver herbivory positively affected the abundance of sawfly galls. In both years, sawfly galls were 7–14 times more abundant on beaver resprout growth than on control cottonwood (Fig. 1a; $F_{1,124} = 35.5$, $P < 0.05$; Fig. 1b; $F_{1,51} = 46.6$, $P < 0.05$). Because beaver resprout is more vigorous, having faster growing shoots that are more nutritious with reduced leaf toughness (Martinsen *et al.*, 1998) as compared with unbrowsed cottonwood, it was predicted that gall abundance would be correlated to shoot length.

Overall, there was a positive response of sawfly galls to long shoots regardless of the mechanism driving the variation (i.e. browsed or unbrowsed ramets). However, the independent and combined effects of within-plant variation and beaver herbivory on shoot length were related to gall abundance. The independent effects of unbrowsed cottonwood showed that shoot length explained 30% of the variation in sawfly gall abundance ($F_{1,25} = 10.15$, $r^2 = 0.30$, $P < 0.05$). Similarly, the independent effects of beaver herbivory significantly increased the average shoot length of beaver resprout by three times ($n = 52$, d.f. = 1,51, $F = 101.3$, $P < 0.05$) over control cottonwood shoots. On beaver resprout, shoot length explained 41% of the variation in gall abundance ($F_{1,25} = 16.6$, $r^2 = 0.41$, $P < 0.05$). When both treatments were combined there was a positive relationship between gall abundance and shoot length that explained 61% of the

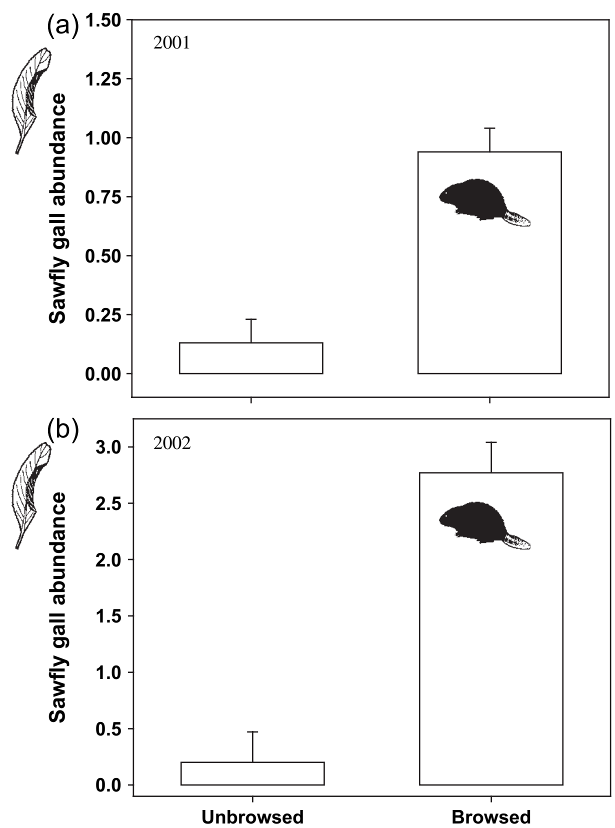


**Fig. 1.** Galls made by sawflies occur significantly more often on beaver-browsed cottonwood than on unbrowsed cottonwood. Sawfly galls are 7–14 times more abundant on resprout cottonwood than control cottonwood. These data were consistent over 2 years of observation (means + 1 SE are shown).

variability in gall abundance as shoot length increased from 5 mm to > 300 mm (Fig. 2; $F_{1,51} = 78.3$, $r^2 = 0.61$, $P < 0.05$).

## Discussion

### *Indirect interactions*

Although *Phyllocolpa* sp. had a general positive response to long shoots, this study showed that the independent and combined effects of within-plant variation and beaver herbivory are important determinants of sawfly gall abundance. Because beaver herbivory increased overall variation in plant shoot length from ≈ 150 mm on control cottonwood to ≈ 325 mm on resprout, these data suggest that beaver actually engineer part of this pattern. For example, there appear to be more galls on short shoots of beaver resprout than long shoots of unbrowsed cottonwood. Although there is not enough data to analyse this pattern, this would suggest that in addition to shoot length, other factors related to the effects of beaver herbivory also affect the sawfly, such as changes to host-plant phytochemistry.

There are several potential mechanisms that may account for these patterns: first, Martinsen *et al.* (1998) found that phenolic glycosides in beaver resprout were also greater than same-aged control cottonwood. Phenolic glycosides have been shown to be important ovipositional cues for sawflies and thus induced phytochemistry related herbivory may also influence patterns of gall abundance. Second, patch size may also influence sawfly gall abundance. Martinsen *et al.* (1998) showed that populations of a leaf-chewing beetle increased in size as the number of trees cut by beavers increased in a given patch. Although the relationship between patch size and gall abundance was not measured, it is likely that as the number of long shoots increases in a particular patch the number of galls in that patch will also increase.

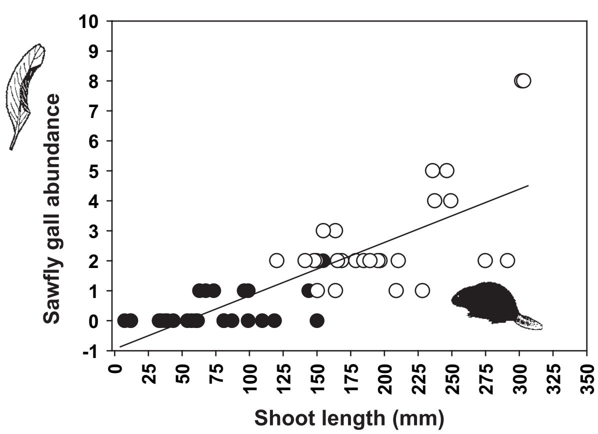


**Fig. 2.** There is a positive relationship between sawfly gall abundance and shoot length. Overall, herbivory (○) increases the variation in shoot length by two times over control cottonwood alone (●). These data demonstrate that the independent and combined effects of within-plant variation and herbivory are important factors affecting the distribution of this sawfly gall.

Although interactions within a trophic level have often been considered unimportant relative to interactions between trophic levels (Hairston *et al.*, 1960), there are at least six major ways that herbivores can indirectly affect the distribution of other community members: (1) selective herbivory can alter plant community composition (Johnston & Naiman, 1990; Bailey *et al.*, 2004); (2) herbivory can affect the chemical composition of the host plant through induction of secondary compounds (Martinsen *et al.*, 1998; Bryant, 1981); (3) herbivory can result in architectural changes in the host plant that alter microclimate and resource quality (Nakamura & Ohgushi, 2003); (4) herbivory can result in changes to the spatial distribution of habitat (Tilman, 1988, 1994); (5) herbivores can build structures such as galls, leaf ties, lodges, etc. (Cappuccino, 1993; Bailey & Whitham, 2003) that can create refuges from predation; and (6) herbivores can interact with other herbivores resulting in novel combinations of the previous factors. This study showed a clear trait-mediated indirect interaction between two important herbivores in a dominant riparian forest system.

Although studies have shown that on average only 20% of the annual net primary productivity in terrestrial systems is consumed (Cyr & Pace, 1993), it is likely that much of the residual annual net primary productivity is affected by herbivory through changes to architecture, chemistry, building of structures, changes to the spatial distribution of habitat, or changes to plant community composition or some combination of these factors. Because herbivores are a component of all ecosystems (Cyr & Pace, 1993; Cebrian, 1999; Polis, 1999), and their effects are common and diverse, we argue that the effects of herbivory on plant quality and subsequently other herbivores may be as important a factor as environmental variation. However, studies examining trophic-level interactions still focus primarily on how changes in environmental conditions (i.e. fertiliser addition, watering experiments, and elevational gradients) can affect host-plant quality and subsequently their interactions with predators and parasitoids (Preszler & Boecklen, 1996; Stiling & Rossi, 1997; Fraser & Grime, 1998; Forkner & Hunter, 2000; Ritchie, 2000).

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