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The functional resource of a gall-forming adelgid

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Abstract Interactions among shoots within plant modules could allow gall-insects to acquire resources from other plant parts near the feeding sites. As a result, nearby plant parts may act as a “functional resource”, or extended resource base. We tested for functional interconnections between galls and adjacent ungalled shoots in *Adelges cooleyi* Gil. (Homoptera: Adelgidae) on *Picea engelmanni*, Engelmann spruce. Observations of gall and surrounding shoot weights showed that gall weights were twice normal shoot weights, but that surrounding shoot weights were unaffected. Reducing photosynthate availability by covering galls or surrounding shoots with opaque cloth suggested that functional interconnections exist among them; covering galls reduced surrounding current-year ungalled shoot weight, and covering surrounding shoots reduced their weight even further, but neither covering treatment affected gall or gall-insect weight. These patterns suggest that surrounding shoots constitute an extended and flexibly utilized resource base for adelgid galls. Resources made available via functional interconnections appeared to be equally available throughout adelgid galls. No differences were found in gall-insect performance in parts of the gall closer to connections with surrounding shoots compared to more distantly-located gall-insects. Further studies are required to examine patterns of resource movement among unmanipulated galls and shoots. Functional resources may be common features of plant/gall-insect interactions, potentially playing an important role in gall-insect reproductive success and habitat selection.

Key words Gall-insect · Resource availability · *Picea engelmanni* · *Adelges cooleyi* · Plant modular structure

Introduction

A fundamental feature of plants is their modular structure (Whitham and Slobodchikoff 1981; Dirzo and Sarukhan 1984; Watson and Casper 1984; Waller 1986; Tuomi and Vuorisalo 1989). By modular structure, we refer to the repeated morphological subunits of which most plants are constructed (e.g., metamers, White 1979). Within modules, varying degrees of physiological interaction occurs between sinks, or net carbon users, and sources, or net carbon producers (Watson and Casper 1984).

Plant modular structure is becoming recognized as an important factor in plant interactions with herbivorous insects (Mattson et al. 1988; Haukioja et al. 1990; Whitham et al. 1991; Rosenthal and Kotanen 1994; Suomela and Ayres 1994). From the plant's perspective, modular structure may guide responses to herbivory (Haukioja et al. 1990). Physiological interactions within modules may compartmentalize herbivore impacts (Watson and Casper 1984; Marquis 1988, 1991), restricting which sources can be drawn on by damaged plant sinks. In some cases, damage may completely reverse transport patterns, causing damaged sources to become resource sinks (Kirst and Rapp 1974; Larson and Whitham 1991).

Physiological interactions within modules are also important from the insect's perspective because such interactions allow herbivores to acquire resources from other closely integrated plant parts, enlarging their resource base. For example, Larson and Whitham (1991) found that galls formed by the aphid *Pemphigus betae* on narrowleaf cottonwood (*Populus angustifolia*) imported assimilate from adjacent leaves on the same shoot. This helped explain the greater fitness of *Pemphigus* aphids occupying galls at the base of leaves (Whitham 1978; Larson and Whitham 1991), because in this position on the leaf the aphids had best access to the vascular connections with adjacent leaves.

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We suggest that for many kinds of herbivorous insects, physiological interconnections among plant parts create a "functional resource" extending beyond the occupied leaf or shoot. The functional resource could enlarge an insect's resource base and play an important part in insect reproductive success and habitat selection. Gall insects may be especially likely to draw on such an extended resource base. The growth and maintenance of a gall is a metabolically expensive undertaking (Shorthouse and Rohfritsch 1992) which houses, feeds, and protects gall insects for a large part of their life cycle. Vascular parasites and sessile insects may also interact with nearby unattacked parts in a module if their feeding creates a large sink for host resources.

Because so little is known about the real resource base for gall-insects, we sought evidence for functional interconnections between galls and nearby ungallo plant parts, a prerequisite for the existence of a functional resource. We examined the Cooley spruce gall aphid (*Adelges cooleyi* Gil. [Homoptera: Adelgidae]), which galls shoots of Engelmann spruce (*Picea engelmanni* Parry) and other spruces throughout North America (Furniss and Carolin 1980). In previous work with these species (Fay and Whitham 1990), a 75% increase in the size of galled shoots was associated with a 335% increase in the weight of insects occupying the gall. Similar disproportionate increases in the number of gall-insects per gall on larger galled shoots suggested that the development and support of the gall and its occupants required resources originating outside the gall. We tested for functional interconnections between adelgid galls and surrounding ungallo spruce shoots by asking three basic questions:

1. How does the presence of a gall change the weight of surrounding shoots?
2. Is growth of gall insects reduced if nearby shoots are unable to supply resources?
3. Does a gall insect's position in the gall affect its growth, indicating differential access to resources?

Material and methods

Adelges cooleyi life history

Spruce is the primary host for *Adelges cooleyi*, which has a complex, host-alternating life cycle fully described in Cumming (1959). Gall formation occurs during shoot growth in early May. A parthenogenetic, oviparous female (the fundatrix) produces offspring (the gallicolae) that colonize the bases of needles on newly expanding shoots. Groups of gallicolae are enveloped in feeding chambers when neighboring needle bases enlarge and fuse, causing the attacked shoot to assume the pineapple shape typical of adelgid galls (Fig. 1; Johnson and Lyon 1988). Typical *A. cooleyi* galls are 2–4 cm long. Gall formation causes extensive ultrastructural modification of the shoot. Adelgid gall chambers are lined with meristematic epidermal cells that are rich in cytoplasm, starch, and phenols (reviewed by Rohfritsch and Anthony 1992), characteristics of metabolically active tissues (Bronner 1992). Gallicolae feed on these tissues until later stages of development, when they feed on gall vascular tissues. The combination of high metabolic rates and gallicolae feeding suggest that adelgid galls are strong sinks capable of drawing resources from surrounding shoots if functional connections are present.

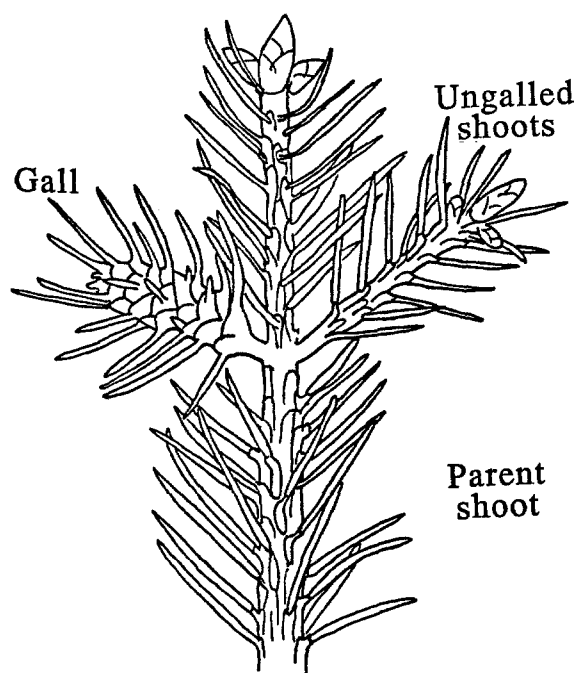


Fig. 1 *Adelges cooleyi* shoot cluster. Each cluster consists of a gall and surrounding current-year ungallo shoots arising from the year-old parent shoot. Galls can form on terminal or lateral current-year shoots

An *A. cooleyi* gall and associated shoots are shown in Fig. 1. We call this a shoot cluster, and focus on this unit as the possible functional resource. The shoot cluster consists of a 1-year-old parent shoot from which arise current year shoots susceptible to gall induction. The functional connections we seek are between the gall and the surrounding shoots in the cluster.

Site

Studies were conducted near Doyle Spring (3050 m elevation) in the Inner Basin of the San Francisco Peaks, north of Flagstaff, Arizona, United States, using the same population of trees studied by Fay and Whitham (1990).

Observations on gall and shoot growth

One sign of interactions between galls and surrounding shoots would be reduced end-of-season shoot weights for surrounding shoots. To test for effects of galls, shoot clusters ($n=108$) bearing usually one, but up to four galls were collected from seven trees in late July 1988 when current-year shoots were fully mature and just before gallicolae emergence. Each individual gall or shoot in the cluster was oven-dried and weighed. Paired ungallo shoot clusters ($n=108$) were also collected from the same whorl as the galled cluster. These pairs were visually matched at the time of collection to have similar sized parent shoots and to have as similar as possible configurations of current-year growth. The dry weights of the individual galls and shoots in galled and ungallo shoot clusters were used to determine how shoot weight was changed by galling and how galls affect weights of surrounding shoots.

Gall and shoot weights were analyzed separately by ANOVA (Proc GLM, SAS Institute 1989). The tree from which the shoot cluster pairs were collected was used as a blocking factor. Not all shoot clusters had the same number of shoots, so the analyses of terminal and lateral shoot weight data were unbalanced, and least squares means were calculated and graphed.

Experimental shading of galls and shoots

To experimentally expose possible functional connections between galls and surrounding shoots, sink-source balances within the shoot cluster were disrupted by covering galls or shoots with opaque cloth to inhibit photosynthesis. We covered either galls or shoots, rather than destructively manipulating sink-source relationships, to avoid disrupting vascular connections in the shoot cluster. Covering the surrounding shoots should inhibit their ability to provide resources to support gall and gallicola growth. In contrast, covering the gall should increase gallicola dependence on resources from surrounding shoots. In each of six trees, 15 shoot clusters were chosen and randomly assigned to have (1) the gall covered, with parent+ungalled shoots exposed, (2) the parent+ungalled shoots covered, with the gall exposed, or (3) uncovered controls. Shoots and galls were covered with two layers of nylon cloth; a black layer against the shoots, and a white layer on the outside to minimize heating the shoots. Covering treatments started in early June 1988 when gall formation and normal shoot expansion were nearly complete, and ended in late July just as galls were beginning to dehisce and gallicolae were beginning to emerge. By the end of the experiment needles were noticeably chlorotic, indicating that covering had affected their physiological processes. At this point galls were dissected, gallicolae counted, and shoots, gall tissue, and gallicolae were oven-dried and weighed. These data were used to calculate end-of-season means for current-year ungalled shoot weight, parent shoot weight, individual gallicola weight, and the total gall weight including gallicolae.

This experiment used a randomized complete block design, with tree as a blocking factor and the whorl where each cluster was located as a covariate. Gallicola weights were log-transformed for analysis. Means from untransformed data are graphed.

Gallicola numbers and growth within defoliated galls

If interconnections occur between galls and surrounding shoots, there may be a gradient of insect performance in the gall, where more or larger insects occupy chambers at the base of the gall, closer to connections with surrounding shoots (e.g., Larson and Whitham 1991). The gradient in insect numbers or performance may be increased if the photosynthetic surface area of the gall is reduced. In early June 1987, 40 galls were defoliated by shaving needles flush with the body of the gall. Care was taken that chambers containing the gallicolae were not damaged. Each defoliated gall was paired with a similar-sized intact gall from the same whorl, for a total of 80 galls.

The galls were collected in late July 1987 just before gallicola emergence and preserved in 70% ethanol. Galls were then dissected by fourths (i.e., basal fourth→apical fourth), the number of chambers and gallicolae counted, and gallicolae weighed after ov-

en drying. From these data we calculated the number of gallicolae per chamber and individual gallicola weight for each fourth of the gall.

This experiment used a split-plot design, with gall (defoliated vs intact) as the whole plot experimental unit and position in the gall as the subplot experimental unit. Gallicola weights were log-transformed for analysis. Means and standard errors from the untransformed data are presented in the figures.

Results

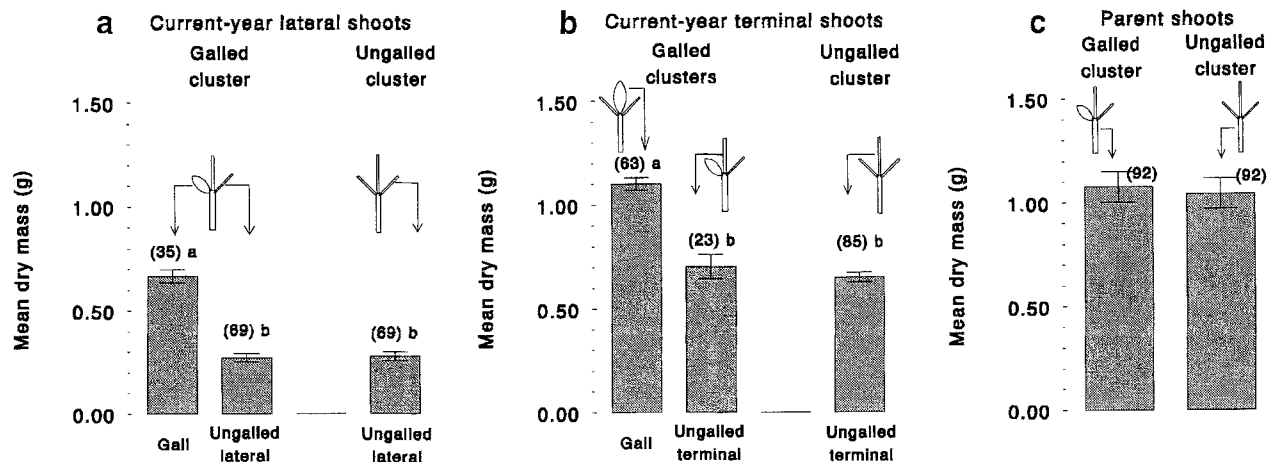
Observations on galls and shoot growth

Conversion of a shoot to a gall roughly doubled its weight (lateral shoots: $F_{2,92}=60.30, P<0.0001$, Fig. 2a; terminal shoots: $F_{2,83}=70.85, P<0.0001$, Fig. 2b). However, the presence of a gall in a shoot cluster had no effect on weights of surrounding shoots in the cluster (all $P>0.30$, Fig. 2a-c).

Experimental manipulation of galls and shoots

Both covering treatments reduced ungalled shoot weights compared with uncovered controls ($F_{2,55}=14.36, P<0.0001$, Fig. 3a), indicating that current photosynthate had become a limiting resource. Covering the gall to increase its sink strength while leaving ungalled+parent shoots exposed reduced surrounding current-year ungalled shoot weight by 22% ($P=0.0369$) compared with controls. Covering the current-year un-

Fig. 2a-c Shoot and gall weights (mean±SE) from shoot clusters containing an *A. cooleyi* gall and from ungalled clusters. **a** Weights of lateral shoots from galled vs. ungalled shoot clusters. Galled lateral shoots are compared with neighboring ungalled laterals, and with lateral shoots from an ungalled cluster. **b** Weights of terminal shoots from galled vs. ungalled clusters. Galled terminal shoots are compared with ungalled terminal shoots from other galled clusters, and with terminal shoots from ungalled clusters. **c** Weights of parent shoots from galled vs. ungalled clusters. Samples sizes in parentheses. Different letters denote significantly different means based on *t*-tests of least squares means generated by GLM (SAS Institute 1989)



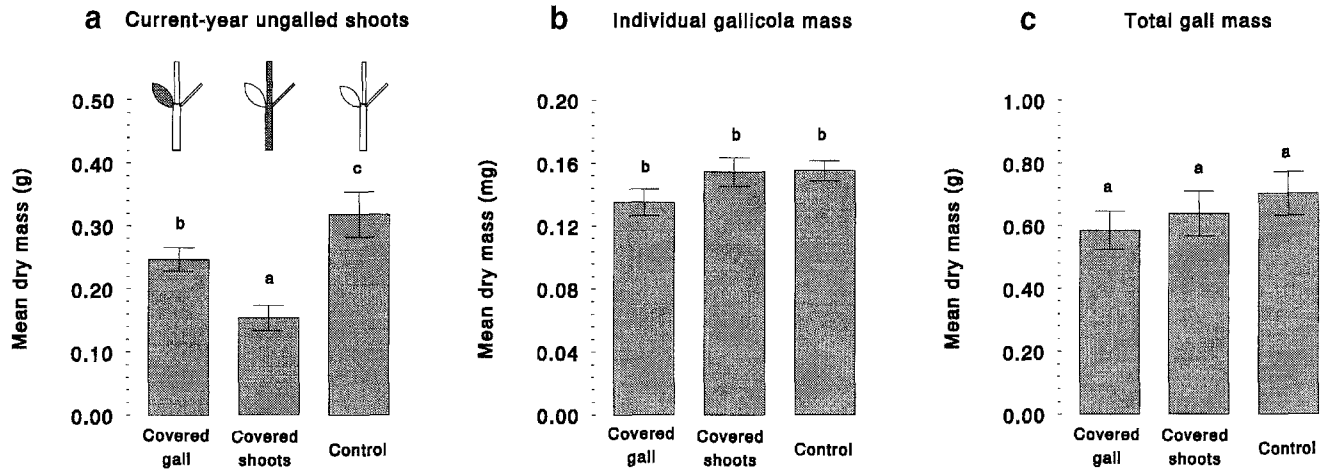


Fig. 3a–c Shoot and insect weights from the shoot covering experiment: **a** ungalged new shoot weight; **b** individual gallicola weight; **c** total gall weight including the gallicolae. Differences between means denoted as in Fig. 2

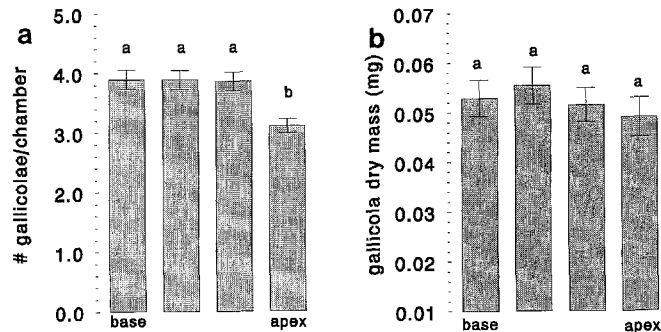


Fig. 4a, b Gallicola distribution and body weights (mean±SE) from different segments of *A. cooleyi* galls: **a** number of gallicolae per gall chamber and **b** individual gallicola dry weight from gall base to gall apex. Differences between means denoted as in Fig. 2

galled+parent shoots to reduce their source capacity while leaving the gall exposed reduced surrounding current-year ungalged shoot weight by 50% compared with controls ($P < 0.0001$). Neither covering treatment affected the weight of the gall or its occupants (total gall weight $P = 0.4828$; gallicola weight $P = 0.1252$, Fig. 3b–c). These patterns suggest that functional interconnections exist between the gall and current-year ungalged shoots.

Gallicola numbers and growth within galls

Removing photosynthetic needles from galls had no effect on gallicola distributions ($P > 0.27$) or body weights ($P > 0.50$), so all galls were pooled for further analysis. There were slightly fewer gallicolae per chamber in gall apices than at the gall's base, closest to potential connections with other shoots ($F_{3,269} = 14.63$, $P < 0.001$, Fig. 4a). Gallicola body weights were equal in all parts of the gall ($F_{3,270} = 1.05$, $P = 0.3720$, Fig. 4b). These results suggest

near equal resource availability for gallicolae throughout the gall.

Discussion

The shoot-covering experiment revealed functional connections between adelgid galls and current-year ungalged shoots. Gall and gall-insect growth was maintained at the expense of current-year shoot weight via these functional connections, suggesting these shoots constitute a functional resource for the gall. Since gall size is correlated with reproductive success (Fay and Whitham 1990; Ozaki 1993), the functional resource could potentially play an important role in the ultimate success of the gall's occupants.

Shoot clusters appeared to provide a larger resource base for adelgid galls than would be available were galls functionally independent. For example, in unmanipulated shoot clusters (Fig. 2), extra resources were necessary to support the extra weight of a gall without reducing surrounding shoot weights. The extra resources might come from stored reserves or, more likely, from current photosynthate. Considerable photosynthetic surface area is present in the shoot cluster. A modest increase in shoot cluster photosynthetic rate could probably supply the required photosynthate, and would be continuously stimulated by the gall's heavy metabolic demands (Kozłowski et al. 1991; Shorthouse and Rohfrisch 1992). We believe this is the primary expression of the functional resource in unmanipulated shoot clusters. Stored reserve use would be suggested had galls reduced parent shoot weights (Fig. 2). Since stored reserves play a minor role in conifer shoot growth (Sprugel et al. 1991), and would be depleted by primary growth and unavailable for continued support of the gall (Zimmermann 1971), their role in support of the gall appears small.

The shoot-covering experiment suggested varying reliance of *A. cooleyi* galls on resources from other shoots. Covered galls grew at the expense of neighboring shoots, but uncovered galls were independent of covered shoots. Barriers to carbon flow can restrict which sources supply a sink (Marquis 1988, 1991), however, such barriers

were not evident within the shoot cluster. This flexibility in resource supply provided by the shoot cluster may be a previously unrecognized benefit for adelgids of a gall-forming life history (Price et al. 1987a).

Several studies have identified functional interconnections whereby galls were supported by nearby plant parts, suggesting these interconnections are common features of plant/gall-insect interactions. Defoliation experiments showed that gall-midge (*Rhabdophaga strobiloides*) galls on *Salix chordata* drew resources from adjacent ungalled twigs (Weis and Kapelinski 1984). Radiolabeling experiments have traced the patterns of assimilate flow from surrounding parts into galls (Kirst and Rapp 1974; Larson and Whitham 1991). The lack of apparent barriers to resource acquisition within *A. cooleyi* galls (Fig. 4) suggest they were tightly integrated with resource supplies. These studies suggest that functional interconnections between galls and shoots may involve normally-occurring physiological mechanisms, manipulated by the galls to their own benefit (Weis et al. 1988).

Ecological importance of functional resources

Because evidence is accumulating for the common existence of functional resources (Weis and Kapelinski 1984; Larson and Whitham 1991), we suggest some broader implications of the functional resource for plant/gall-insect interactions. For example, an enlarged resource base enabled by a functional resource might be the mechanism underlying gall-insect preference for large leaves or shoots (Whitham 1978; Price et al. 1987b,c; Caouette and Price 1989; Price 1989; Fay and Whitham 1990; Kimberling et al. 1990; but see Clancy et al. 1993; Fay and Samenus 1994). *A. cooleyi* galls occur more frequently and contain more, larger gallicolae in upper whorls of spruce (Fay and Whitham 1990). There are more neighboring shoots near upper-whorl galls compared to galls located lower in the tree (P. Fay, personal observation), suggesting upper-whorl galls have a larger supplemental resource supply available.

The functional resource for a gall-insect might also help explain differences in galling site selection among gall-insect species sharing a host plant. For example, pairs of galling sawfly species on the willow *Salix lasioides* co-occurred more frequently on larger compared to smaller shoots (Fritz et al. 1987). Larger shoots might promote species co-occurrence by providing larger functional resources, alleviating resource competition between species.

Conclusions

Experimental manipulation of spruce shoots indicated the presence of functional interconnections between adelgid galls and surrounding shoots, consistent with the presence of a functional resource meeting the metabolic demands of the gall and its occupants. The case for a

functional resource for *A. cooleyi* requires additional study to verify resource movement via these connections under unmanipulated conditions. We encourage further studies to search for functional resources and underlying mechanisms in other insect species. If the functional resource concept proves widely applicable, it may provide a common basis for understanding gall-insect performance and habitat selection.

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