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Author(s): Timothy P. Craig, Peter W. Price, Joanne K. Itami

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RESOURCE REGULATION BY A STEM-GALLING SAWFLY ON THE ARROYO WILLOW¹

TIMOTHY P. CRAIG

Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011 USA

PETER W. PRICE

Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011 USA and
Museum of Northern Arizona, Flagstaff, Arizona 86001 USA

AND

JOANNE K. ITAMI

Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011 USA

Abstract. We studied the impact of the stem-galling tenthredinid sawfly, *Euura lasiolepis*, on the growth and branch age structure of the arroyo willow, *Salix lasiolepis*. Normally, as willows age they become less susceptible to galling, but heavy *Euura* galling maintains willows at a young, relatively susceptible juvenile stage. The *Euura* form more galls on long shoots. Long shoots are found on clones with young branches. Heavy galling stunts or kills growth distal to the gall, stimulating sprouting by indefinitely dormant buds located near branch bases. The resulting young branches keep the clone susceptible to further galling. In contrast, increasing branch age of lightly galled clones confers resistance to galling. We term this model of gall-induced resource maintenance the resource regulation hypothesis. Resource regulation is the maintenance or increase of high-quality resources by an herbivore species that impacts immediately subsequent generations of the same herbivore species on the same plant.

Key words: age-related susceptibility; compensatory growth; *Euura lasiolepis*; gall; herbivory; plant-herbivore relations; resource regulation; *Salix lasiolepis*.

INTRODUCTION

When herbivores feed on a plant resource three results are possible: resource quality can decline if there are induced defenses (Green and Ryan 1972, Haukioja and Niemelä 1979, Ryan 1983), resource quality can be unchanged, or resource quality can increase (Mattson and Addy 1975, McNaughton 1976, 1979, 1983, Owen and Wiegert 1976, Montgomery 1980, Owen 1980). A specific case of the last result we term resource regulation, a previously undescribed interaction. We define resource regulation as the maintenance or increase of high-quality resources by an herbivore that impacts immediately subsequent generations of the same herbivore species on the same individual plant. This study tests our "resource regulation hypothesis": high densities of galls formed by the tenthredinid sawfly *Euura lasiolepis* (Smith) maintain high-quality resources on the arroyo willow *Salix lasiolepis* (Benth), and these resources are available to subsequent generations of *Euura*.

NATURAL HISTORY

In northern Arizona the willow *Salix lasiolepis* has a shrubby growth form. An individual willow clone can cover a large area and spreads by layering. A single clone may consist of many different clusters of branch-

es based on "root stocks" connected by underground branches. "Root stocks" are actually perennating stems forming a large mass of branches, living and dead, from which extensive adventitious root systems develop. Branches were found to live no more than 12 yr, although "root stocks" persist for many years. We distinguish between shoots, the actively growing stems with leaves, and branches, the accumulated stems of past years' growth without leaves. Shoots are predominantly produced from buds set the previous year. However, some buds are not activated the year following formation and are indefinitely dormant; we term these dormant buds. They can be activated by any damage to the plant; commonly they sprout very near the base of the branch.

Euura emerge in late May and early June, when shoots are growing rapidly (Price and Craig 1984). Females oviposit through the base of the petiole into the young succulent shoot, laying an egg near the differentiating xylem. Only one or two nodes per shoot are available for oviposition on any day. Larvae feed on the parenchymatous tissue of resulting galls. Galls range in size from 4 to 10 mm; in diameter, and from 10 to 60 mm in length. Adults emerge the following spring, leaving large exit holes.

METHODS

This study was conducted on willow clones on the property of the Museum of Northern Arizona, Flagstaff,

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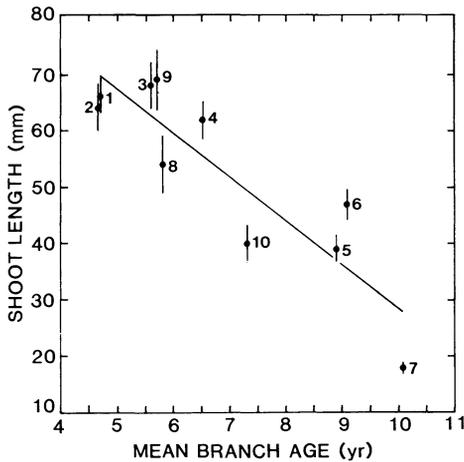


FIG. 1. Regression of mean shoot length (\pm SE) on mean branch age for clones MH 1-10 ($y = 105.04 - 7.63x$, $df = 8$, $r^2 = 0.81$, $P < .001$). Clone identification numbers are given next to the respective points on graph.

Arizona, in 1982 and 1983. All clones except one were on watercourses draining into the Rio de Flag: MH 1-10 were at a spring near the McMillan House, CS 1-2 were at Coyote Spring, MNA 1-7 and NP 4-9 were on Schultz Creek, an intermittent stream. DB 1 was near a building within 100 m of the MH site. Clones were distinguished from each other on the basis of characters such as shoot color, node length, bud color, sex, and time of bud break.

The long-term impact of galling on willow growth was studied by destructively sampling one root stock from each clone MNA 2-4, and two root stocks from MNA 1. Gall densities for past years were determined by censusing prominent gall scars, which are visible for several years following sawfly emergence. The number of winter bud scars between the ground and the shoot was used as an estimate of age; we term this shoot branch age. Ages based on counting scars were compared to ages calculated by counting growth rings and were found to correspond completely. By measuring shoot branch ages for all shoots, we were able to assess the proportion of branches initiated as dormant bud shoots.

We measured the impact of the past 3 yr of galling on current shoot growth and attack rates on CS 1 and CS 2. For 400 shoots on each clone we recorded the cumulative number of galls (1980-1982) on branches on which the shoot grew. For each 1983 shoot the shoot length and the number of galls were recorded.

Ovipositions were censused following the 1983 oviposition season. A random sample of 500 shoots per clone was taken between 17 June and 20 June on MH 1-3, and a 100-shoot random sample was taken on MH 1-10 between 30 June and 5 July. For each shoot, we recorded the number and location of galls, the total length, and the number of nodes. In the fall, 50 shoots

from each clone were sampled to determine mean shoot branch age for each clone.

We measured the influence of 1982 gall densities on 1983 dormant bud shoot production on MH 1-10. Branches were randomly sampled and marked on each clone until 50 dormant bud shoots had been measured, or the whole clone censused. In fall 1983, the 1982 shoot cohort on the marked branches was censused for shoot length and number of galls, and each shoot was classified as living or dead.

Relative reproductive investment on each clone in 1983 was measured by randomly sampling 50 shoots from each clone and counting the number of inflorescence and vegetative buds.

RESULTS

Willow growth patterns

As mean shoot branch age increased, shoots decreased in vegetative growth and increased in reproductive investment. Mean shoot branch age was negatively correlated with mean shoot length in between-clone comparisons on MH 1-10 (Fig. 1). The proportion of inflorescence buds was used as an indicator of investment in sexual reproduction. The proportion of inflorescence buds was positively correlated with mean shoot branch age in between-clone comparisons on MH 1-10 ($y = 7.63 + 3.73x$, $r^2 = 0.52$, $P < .05$, $df = 8$).

Sawfly attack patterns

The probability of a shoot having one or more galls increased with shoot length (Fig. 2). Galled shoots were significantly longer than ungalled shoots (Student's $t = 4.53$, $P < .005$, $df = 8$). The number of galls per node also increased significantly with shoot length in between-clone comparisons (Fig. 3). The number of galls

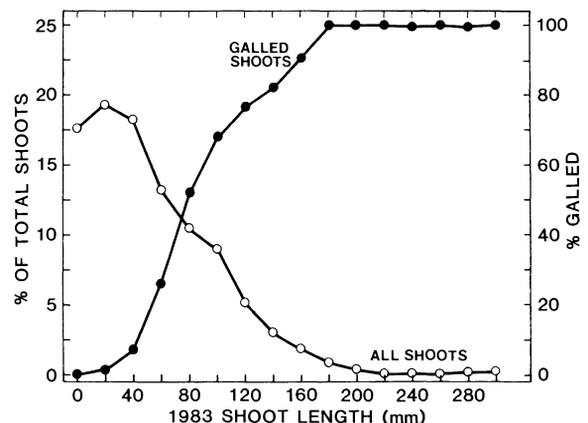


FIG. 2. Pooled sample of all shoot lengths taken from clones MH 1-10. Data were collected 30 June through 5 July 1983, $n = 1230$. \circ percent of shoot lengths that fell in each 20-mm category. \bullet percent of shoots in each 20-mm category that were galled.

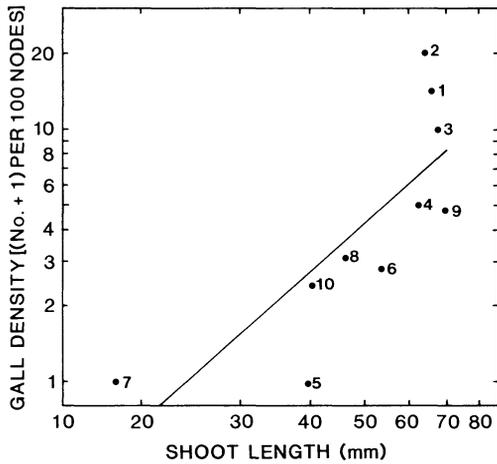


FIG. 3. Regression of mean gall density [(number + 1) per 100 nodes] on mean shoot length for clones MH 1-10 ($\log_e y = 2.92 + 0.0147 \log_e x$, $df = 8$, $r^2 = 0.82$, $P < .001$). Data were collected at the end of the attack period, 30 June through 5 July 1983. Clone identification numbers are given next to the respective points on graph. Logarithmic scales are used.

per node was significantly ($P < .001$) related to increasing shoot length for all within-clone samples, excluding one clone without galls at the MH site. Results for clone MH 2 are shown as an example (Fig. 4).

Gall density was negatively related to mean shoot branch age (Fig. 5) and with the proportion of inflorescence buds ($y = 38.6 - 0.99x$, $r^2 = 0.43$, $P < .05$, $df = 8$). Clones showed a consistent pattern: young clones with long shoots had high gall densities and low numbers of inflorescence buds.

Sawflies had a low tendency to disperse from clones they emerged on. No galls were formed on 14 pots of willow clones placed < 15 m from clones that had large *Euura* populations. Seven other randomly selected, interspersed pots of clones with sawflies bagged on them had large numbers of galls. In > 40 h of behavioral observations on ovipositing sawflies, none was observed to disperse from an isolated clone.

Impact of galls on willow growth

Euura galls either killed shoots or decreased future growth distal to the shoot. Many heavily galled shoots died during the year following oviposition. The 1982 shoots that died in 1983 had approximately twice as many galls as those still living (Fig. 6). Shoots that survived had stunted growth distal to galls for several years. The cumulative number of galls in 1980-1982 was significantly negatively related to both 1983 shoot length and the probability that a shoot had galls in 1983 (Fig. 7).

Heavy galling increased the number of dormant buds that sprouted and consequently lowered the mean shoot branch age of the clone; we term this juvenilization. The number of dormant bud shoots increased with gall density (Fig. 8). Dormant bud sprouts were formed

near the base of the willow, giving the clone a younger branch age structure. These branches produced fast-growing shoots for several years following initiation.

The same clones sustained high attack rates year after year. Gall densities in 1982 were strongly related to gall densities in 1983 on clones MH 1-10 ($\log_e y = 1.02 \log_e x - 0.10$, $r^2 = 0.88$, $P < .001$, $df = 8$). Twelve clones censused yearly from 1980 to 1984 (with clones added in 1982 and 1983), showed significant positive between-year correlations for every combination of years. A significant percentage of the variation in gall density for each year was explained by the gall density in any previous year (Table 1).

Continued heavy gall densities resulted in significant juvenilization of a clone, keeping it susceptible to attack. Examination of gall scars on MNA 1-4 showed that two clones (MNA 2 and 3) had heavy galling, and two (MNA 1 and 4) had light galling in each of the previous eight years. Analysis of 65 branches from these clones showed that those clones that had sustained high, consistent attack had much higher proportions of shoots on branches initiated as dormant bud shoots (Table 2). Two clones had been juvenilized by *Euura* galling (MNA 2 and 3).

DISCUSSION

We have constructed a model of how *Euura* galling affects clone growth and consequently maintains consistently high levels of galling (Fig. 9). A willow clone is kept in a juvenilized, susceptible state by heavy galling and is prevented from reaching a mature, resistant state. A heavily galled clone reallocates energy from growth of many older, shorter shoots to fewer, younger, faster-growing shoots, thus increasing resources for *Euura*. In contrast, on a weakly attacked clone, increasing

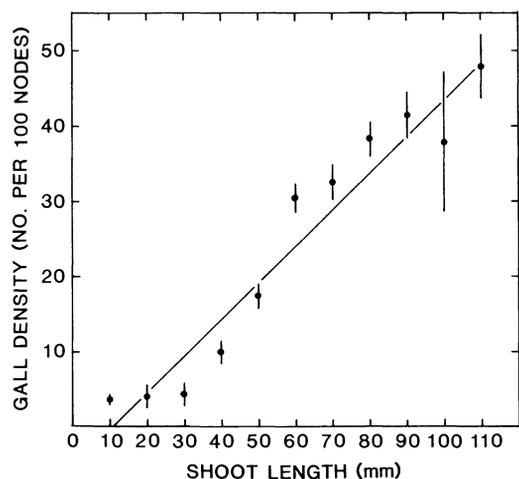


FIG. 4. Regression of mean gall density (number per 100 nodes, \pm SE) on mean shoot length for clone MH 2 ($y = 0.48x - 4.7$, $df = 9$, $r^2 = 0.94$, $P < .001$). Data were collected at the end of the attack period, 17 June 1983. Regression is plotted on shoot length class means, but the same level of significance was obtained from regression on the original data.

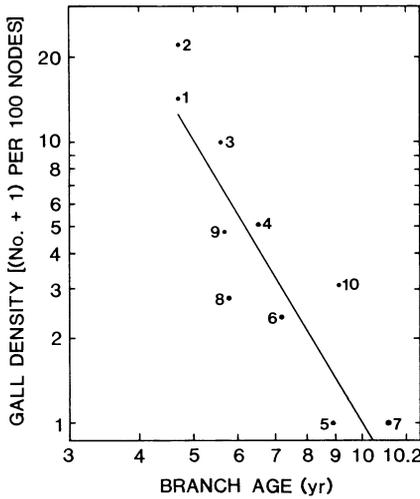


FIG. 5. Regression of gall density [(number + 1) per 100 nodes] on mean branch age for clones MH 1-10 ($\log_e[y + 1] = 17.5 - 3.3 \log_e x$, $df = 8$, $r^2 = 0.77$, $P < .001$). Clone identification numbers are given next to points on graph. Logarithmic scales are used.

shoot branch age leads to less vigorous vegetative growth and a lower rate of sawfly attack. These results agree with the observations of Smith (1970) that "sucker" growth on willows had high gall densities and that galling could be enhanced by pruning to increase this growth.

The initiation of the juvenilization cycle is not understood. We hypothesize that *Euura* must discover a willow in a juvenile state to maintain high-quality resources. It is also not known whether the quantity of high-quality resources is increased or only maintained by galling. These questions can only be answered through long-term experiments.

Resources increasing with herbivory

The hypothesis that herbivory increases or maintains resources has been suggested before in terrestrial systems. Mattson and Addy (1975) and Peterman (1978) propose that plant-herbivore interactions are mutualistic in forest ecosystems in long-term cycles; however, in their systems resources are not available to immediately subsequent generations of the herbivore population. Owen and Weigert (1976), and Owen (1980) propose that herbivores can be mutualists in the short term by increasing the rate of nutrient cycling or by altering plant growth form. None of these studies has documented how resources change for subsequent generations of the herbivore population. McNaughton (1976, 1979, 1983) hypothesizes that moderate levels of herbivory may result in an overcompensatory regrowth, resulting in increased primary production. He found that grazing by migratory ungulates in the Serengeti ecosystem in Africa increases primary production of grasses. This benefited grazers that followed in the grazing cycle, not the herbivore population that initiated the resource increase. Dyer and Bokari (1976) hypothesize that grasshopper grazing stimulates plant regrowth. However, Detling and Dyer (1981) found that grass growth was reduced by grasshopper crop exudate and salivary gland extract. They suggest that rapid regrowth following grasshopper grazing would be maladaptive for the plant, since the grasshoppers would continue grazing.

In contrast to the interactions proposed in other terrestrial systems, we find no evidence for mutualism in the willow system; the plant gains no benefit from herbivory. Galls do not increase primary productivity (as in McNaughton 1983), nor do they cause beneficial changes in growth form (as in Owen 1980). Rather, the willow is kept in a juvenile growth form by herbivory,

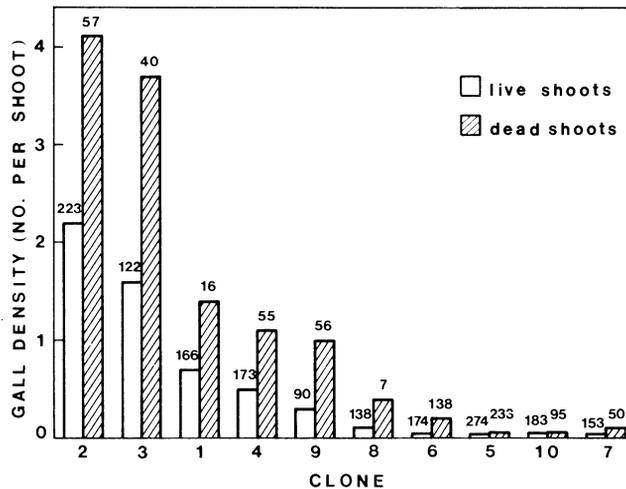


FIG. 6. Comparison of galling density (mean number of galls per shoot) on shoots that subsequently died and on shoots that remained alive, from shoot cohorts initiated in 1982. Measurements were taken in fall 1983 on clones MH 1-10. The dead shoots had significantly more galls than the live shoots (Wilcoxon paired-sample test, $P < .005$, $n = 10$). The numbers above the bars represent sample sizes for each category.

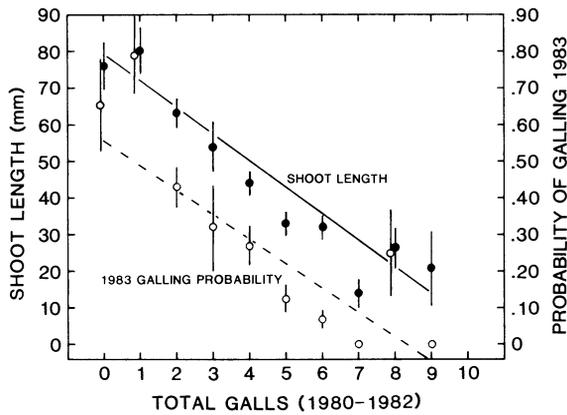


FIG. 7. Relationship between mean shoot length (\pm SE) and cumulative number of galls (1980–1982) on branches with shoots in 1983 ($y = 79.2 - 7.47x$, $df = 9$, $r^2 = 0.88$, $P < .001$), and relationship between probability of a 1983 shoot being galled and the cumulative number of galls (1980–1982) on branches with shoots in 1983 ($y = 63.9 - 7.74x$, $df = 9$, $r^2 = 0.75$, $P < .001$). Samples consist of 800 shoots from clones CS 1 and CS 2. Samples from the two clones were combined since there were no significant differences between clones in gall density or shoot length, in contrast to clones at the MH site.

thereby preventing it from reaching maturity with high sexual reproduction and vegetative spread. Although herbivory does stimulate production of vigorous vegetative shoots, these do not compensate for photosynthetic area lost through shoot stunting and death. The compensatory growth is more susceptible to further galling, increasing herbivore impact. This contradicts McNaughton's (1983) expectation that plants should be adapted to minimize the effects of chronic herbivory.

Increases in resources as the result of herbivory have been documented in marine systems. Montgomery (1980) found that grazing by the blue damselfish, *Microspathodon dorsalis*, maintained the red alga *Polysiphonia* in an early, rapid growth phase that was highly productive. Simberloff et al. (1978) argue that a root-boring isopod, *Sphaeroma terebrans*, on mangroves benefits the mangrove because it induces more roots

TABLE 1. The proportion of variation (r^2) in gall density that is explained by gall density in each previous census year. Twelve clones (MNA 1–7, NP 4, 5, 7, 8, 9) were sampled in all years (1980–1984). In 1982 BD 1 was added, and in 1983 CS 1 and CS 2 were added.

Current year	Earlier years			
	1980	1981	1982	1983
1981	0.39*			
1982	0.52***	0.69***		
1983	0.71***	0.56***	0.98***	
1984	0.66***	0.60***	0.87***	0.91***

* $P < .05$, *** $P < .001$.

TABLE 2. Comparison of gall densities averaged over three years, with the corresponding percentage of branches that arose from dormant bud shoots (juvenilized branches). Clones differed significantly in the proportion of branches juvenilized ($\chi^2 = 393.74$, $df = 3$, $P < .001$).

Clone	Ave. gall density, 1980–1982 (no. galls/100 shoots)	% of shoots arising from juv. branches
MNA 2	83.6	61.2
MNA 3	69.8	60.5
MNA 1	18.6	8.9
MNA 4	1.0	2.0

to grow than it destroys. They did not emphasize that the isopod may have benefited isopods more than the plant by generating more resources for attack (offspring often feed on roots in which they develop [Rehm and Humm 1973]). Resource regulation similar to that found in the *Euura-Salix* interaction may be occurring in these systems. However, feedback between *Euura* attack and resources is tighter than that discussed in other systems cited: resources are maintained on an individual plant, and they are available to the offspring of the herbivores that caused the increase in resources.

Lack of defense by the willow

Our study showed no evidence of induced defenses against sawflies by the willow, even though the herbivore has a large impact on growth and reproduction. Bryant et al. (1983) hypothesize that rapidly growing shade-intolerant trees (such as willows) are selected to respond to herbivory with fast, heavily defended regrowth. In Alaska they found that juvenile regrowth produced in response to snowshoe hare browsing contained large amounts of secondary metabolites, which inhibited browsing for 4–5 yr. Lack of induced defenses may result from the galling habit. In *Euura* the gall tissue on which the larvae feed (i.e., undifferentiated parenchyma; Price and Craig 1984) is no higher in phenol glycosides than leaves, bark, or cambium (P. Evans, *personal communication*). The galls appear to have circumvented one defense of the willow, and no specific inducible chemical defense appears to have evolved.

The regrowth in response to damage seems maladaptive since it leaves the clone susceptible to further attack. We hypothesize that the regrowth response is adapted to other, stronger selective pressures. The stimulation of dormant meristems by damage is common among trees and shrubs that invade disturbed sites (Bryant et al. 1983). It may be a general response to damage in *Salix lasiolepis*, and not a specific response to *Euura*. *Salix lasiolepis* often grows in steep canyons, where it is frequently disturbed by floods. Rapid regrowth is adaptive in response to flood damage when competition for light and space is high.

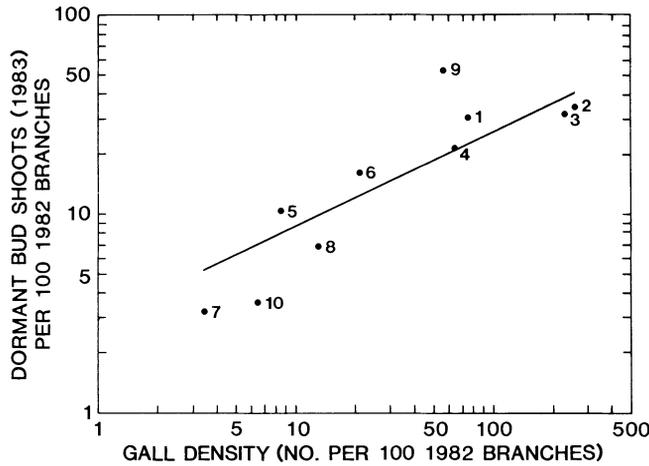


FIG. 8. Regression of number of 1983 dormant bud shoots per 100 1982 branches on number of galls per 100 1982 branches, for clones MH 1-10 ($\log_e y = 1.1 + 0.47 \log_e x$, $df = 8$, $r^2 = 0.79$, $P < .001$). The number of dormant bud shoots and the 1982 gall densities were divided by the number of 1982 branches to standardize the samples from clones of different sizes. Clone identification numbers are given next to the respective points on graph. Logarithmic scales are used.

Age-related susceptibility

Host susceptibility is age-related in other systems. Waloff (1968) found that several species of insects on Scotch broom, *Sarothamnus scoparius*, reached peak abundances on plants 3-6 yr old, then declined. Frankie and Morgan (1984) noted that populations of the cynipid gall wasp, *Disholcaspis cinerosa*, declined as

their live oak hosts, *Quercus* spp., aged. Washburn and Cornell (1981) suggest that the change in host phenology as "sucker" growth aged was partially responsible for the local extinction of the cynipid gall wasp, *Xanthoterus politum*. Our system differs from these studies because heavy galling prevents willow maturation to a nonsusceptible age on heavily galled clones.

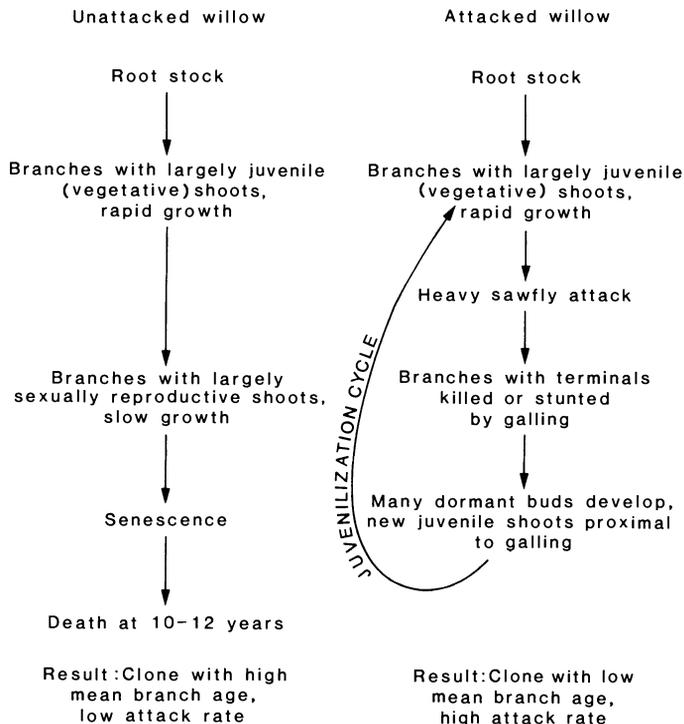


FIG. 9. Diagrammatic representation of the "resource regulation hypothesis." Summary of how willow age structure is changed by sawfly attack, and the mechanisms involved in resource regulation.

We have found that *Euura lasiolepis* changes the growth of *Salix lasiolepis* so that high-quality resources are maintained; these are available to subsequent *Euura* generations. We do not believe our system to be unique: whenever successive generations of herbivores utilize the same individual plant they should be selected to maintain their resources. The possibility of resource regulation exists wherever herbivores have a large repeated impact on individual plant resources with age-related susceptibility, in the absence of relevant induced defenses.

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