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Plant age and attack by the bud galler, *Euura mucronata*

P.W. Price[1], H. Roininen[2], and J. Tahvanainen[2]

[1] Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA and Museum of Northern Arizona, Flagstaff, AZ 86001, USA
[2] Department of Biology, University of Joensuu, SF-80101, Joensuu 10, Finland

Summary. As ramets of the willow, *Salix cinerea* L. (Salicaceae) aged shoot length decreased in the six populations studied in S.E. Finland. Many traits correlated positively with shoot length: basal diameter, number of internodes, internode length, leaf size, and length of growing period. The bud-galling sawfly, *Euura mucronata* (Hartig) Man. (Churchill) (Hymenoptera: Tenthredinidae), responded positively to shoot length or correlated traits, and negatively to ramet age in three forest populations. This herbivore attacked the most vigorous plants in a population, and numbers of attacks declined as ramets aged and senesced. The generality of this kind of herbivore response to plant quality is emphasized.

Key words: *Euura mucronata* – Bud galler – Herbivore – Plant age – *Salix cinerea*

Phenotypic variation in plant populations is being recognized increasingly as a cause for variation in herbivore attack. Observed changes within one genotype have included such characters as seasonal nutrition (e.g., Scriber and Slansky 1981), change in induced defenses (e.g., Haukioja and Neuvonen 1985), natural pruning (e.g., Danell et al. 1985; Danell and Huss-Danell 1985), and plant age (e.g., Craig et al. 1986; Frankie and Morgan 1984). But the generality of inevitable plant phenotypic change due to aging, and correlated traits, and their effects on herbivore populations, do not seem to be adequately recognized. Therefore, we intend in this paper to document one case of plant change with age and the response of a herbivore.

The plant species studied during 1986 was *Salix cinerea* L., and all locations were near Joensuu, in S.E. Finland. It is a clonal willow with a bushy habit. Ramets grow to 4 or 5 m in annual increments which remain recognizeable throughout life because terminal winter bud scars persist as a line in the bark encircling the stem. The plant grows in moist pine forests, lake and river edges, water meadows and bogs. We use the term "shoot: to denote the terminal years growth on a stem.

One of the commonest herbivores on *S. cinerea* is the bud-galling sawfly, *Euura mucronata* (Hartig). Man. (Churchill) (Hymenoptera: Tenthredinidae). Females oviposit on young shoots, piercing through petiole bases into axillary buds, and causing galls to form in the bud. The gall's position on a plant can be recognized easily in late winter and early spring when the swollen dead galled buds are conspicuous on shoots in the absence of leaves. A brief description and life history is given by Pschorn-Walcher (1982), but this herbivore has been studied very little. The galls we studied had been formed on 1985 shoots and persisted into the Spring and Summer of 1986 when we counted them.

Offprint requests to: P.W. Price

Materials and methods

1. Correlates of ramet age

Shoot length changes as plants age were studied in two ways. The first used 25 ramets at Enankoski, an open lakeside site, which were aged by counting the number of growing seasons marked by winter bud scars. For each ramet, growth increments in length per season were measured, and associated with the year in which that growth occurred. Another 25 dead ramets were aged to find the mean age at death of ramets. Checks on age using annual ring counts gave identical results.

The second method was employed in the three forest sites, Rantakyla, Linnunlahti and Ylämylly where *S. cinerea* was an understory shrub, and in three open sites, Mammin Island lakeside, and the water meadow sites of Ukonnummi, and Raivo Bog, where *S. cinerea* was a dominant species. At each site 15 to 25 ramets were aged as above and the length measured of 20 terminal shoots per ramet which grew in 1985. In addition, the number of bud galls per shoot formed in 1985 was counted.

2. Correlates of shoot length

We regarded shoot length as an index of change with plant age, not necessarily the one used by *E. mucronata* for initiating plant attack. Therefore, other shoot traits were measured to test the extent to which shoot length was a predictor of other plant characters that change with plant age. These traits were the following, and were measured on 1986 shoots on one willow clone in Linnunlahti forest, with sample sizes ranging from 10 to 25 shoots as recorded in the results: height of shoot above ground, shoot length, basal diameter, number of internodes, internode length, diameter of nodes, leaf length and width, petiole length and diameter, and length of growing period. Bud size was not measured as buds are concealed between the shoot axis and petiole and are not available as an oviposition cue until a sawfly

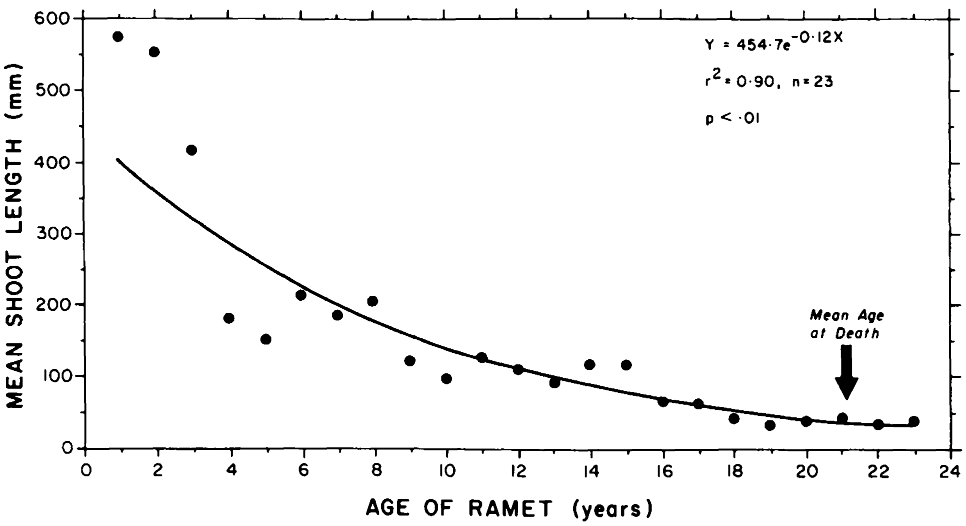

Fig. 1. Relationship between age of ramet and mean shoot lengths for 23 ramets at Enankoski

Table 1. Correlation equations for ramet age (X) and 1985 shoot lengths (Y) for six sites in which *S. cinerea* occurs. r^2 provides an estimate of the per cent variance in Y accounted for by X

Location	Correlation equation	Sample size	r^2	Probability
FOREST SITES				
Linnunlahti	$Y = 262.26 - 12.31X$	25	0.50	<0.01
Rantakyla	$Y = 206.29 - 9.03X$	25	0.75	<0.01
Ylämylly	$Y = 201.12 - 8.74X$	25	0.54	<0.01
OPEN SITES				
Mammin Island	$Y = 257.27 - 10.52X$	25	0.34	<0.01
Ukonnummi	$Y = 131.96 - 5.28X$	21	0.38	<0.01
Raivo Bog	$Y = 310.52 - 16.75X$	15	0.73	<0.01

female has commenced oviposition and pierced the petiole. For each shoot, node position was recorded when measurements were made, so trends from proximal to distal positions on a shoot could be studied.

All tests for pattern used the least square method of correlation (e.g., Snedecor 1956), and the linear equation providing the highest r value was used (of arithmetic, logarithmic, exponential and power function fits).

Results

Age and shoot length

There was a significant exponential decline in shoot length with age of ramet in the Enankoski site (Fig. 1). In the 3 first years growth was over 400 mm per year, then for 12 years it was near 200 declining to 100 mm per year, and in an apparently senescent period from 16 years shoots were less than 100 mm. The mean age at death was 21.4 years.

The same pattern was evident at all other sites (Table 1) although the very early age classes were not available in these populations. In the forest sites, such as Rantakyla, shoot lengths were comparable to the Enankoski willows, going from a mean of about 160 mm at 4 years down to about 40 mm at 18–20 years (Fig. 2).

All age and shoot length relationships were highly significant with age accounting for 34 to 90 percent of variance in shoot length (Figs. 1, 2, Table 1). There is a very predictable pattern to *S. cinerea* ramet growth throughout these areas.

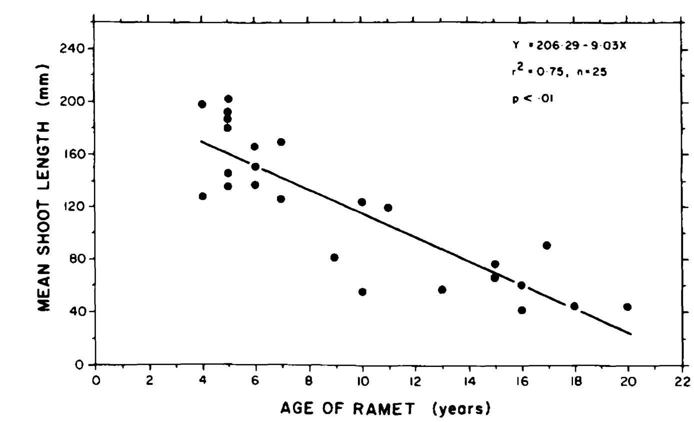

Fig. 2. Relationship between age of ramet and mean shoot length for 25 ramets in Rantakyla forest

Correlates of shoot length

All shoot traits measured were correlated significantly with shoot length (Table 2), with shoot length accounting for 71 to 93 percent of variances in the trait. In every case the size of the part or number of parts per shoot increased with shoot length, and longer shoots grew longer in the season. In addition, shoot position was highly predictable

Table 2. Correlation equations for 1986 shoot length (X) and 10 other shoot characters (Y) for a willow clone in the Linnunlahti forest

Shoot character (Y)	Correlation equation	Sample size	r^2	Probability
Height of shoot above ground (mm)	$Y = 5.14\ X + 397.80$	10	0.79	<0.01
Basal diameter of shoot (mm)	$Y = 0.01\ X + 1.10$	25	0.90	<0.01
Number of internodes	$Y = 0.06\ X + 7.58$	25	0.93	<0.01
Mean internode length (mm)[a]	$Y = 0.06\ X + 2.05$	25	0.91	<0.01
Mean diameter of node (mm)[a]	$Y = 0.003X + 1.31$	10	0.71	<0.01
Mean leaf length (mm)[a]	$Y = 0.24\ X + 18.04$	25	0.88	<0.01
Mean leaf width (mm)[a]	$Y = 0.09\ X + 14.19$	25	0.80	<0.01
Mean petiole length (mm)[a]	$Y = 0.03\ X + 4.49$	25	0.83	<0.01
Mean diameter of petiole (mm)[a]	$Y = 0.002X + 0.88$	10	0.85	<0.01
Days of growth from June 15	$Y = 0.10\ X - 4.44$	25	0.88	<0.01

[a] Means per shoot were calculated from the three middle nodes or internodes per shoot

Table 3. Correlation equations for 1986 shoot positions (X) on stems that grew in 1985, and 3 shoot characters (Y) for a willow clone in the Linnunlahti forest. Shoot positions were numbered from 1 for the terminal shoot, to sequentially higher numbers for the more proximal positions on a 1985 stem. Means are for all shoots on 10 1985 stems (101 shoots total)

Shoot character (Y)	Correlation equation	Sample size[a]	r^2	Probability
Mean shoot length (mm)	$Y = 144.94 - 7.20X$	14	0.55	<0.01
Mean shoot diameter (mm)	$Y = 2.29 - 0.05X$	14	0.41	<0.01
Mean number of leaves	$Y = 14.60 - 0.37X$	14	0.55	<0.01

[a] i.e., there were 14 shoot positions on 1985 stems

Table 4. Regression equations for relationships between ramet age (X) and mean shoot length per ramet (X) and mean number of galls per shoot (Y) in forest sites

Site	X	Regression equation	Sample size	r^2	Probability
Linnunlahti	Age	$Y = 1.28 - 0.39\ \ln X$	25	0.22	<0.05
	Shoot Length	$Y = 0.43\ \ln X - 1.69$	25	0.24	<0.05
Rantakyla	Age	$Y = 3.37 - 1.10\ \ln X$	25	0.60	<0.01
	Shoot Length	$Y = 0.01X - 0.39$	25	0.71	<0.01
Ylämylly	Age	$Y = 0.97e^{-0.06X}$	25	0.04	NS
	Shoot Length	$Y = 1.31\ \ln X - 5.03$	25	0.29	<0.01

with long 1986 shoots with large diameters and many leaves tending to grow at the distal locations on 1985 stems (Table 3), as well as the longest shoots growing at the highest location on the clone (Table 2).

These relationships show that the architecture of *S. cinerea* plants is highly predictable for searching sawflies, and many traits, including chemical ones, could provide information stimulating oviposition. The growth of a clone is much more regulated and predictable than a casual inspection would reveal.

Response of herbivore

In the three forest sites there was a significant positive correlation between mean shoot length and mean number of galls (Table 4). In all three sites a negative relationship between ramet age and numbers of galls was evident, and in two of the sites the relationship was signficant. The more even and extensive distribution of age classes in the Rantakyla sample permitted the better detection of pattern than in the other two forest sites (Fig. 3), with ramet age and shoot length accounting for 60 and 71 percent of the variance in galls per shoot respectively. Also, there was a significant negative correlation between ramet age and proportion of buds attacked by *E. mucronata* (Fig. 4).

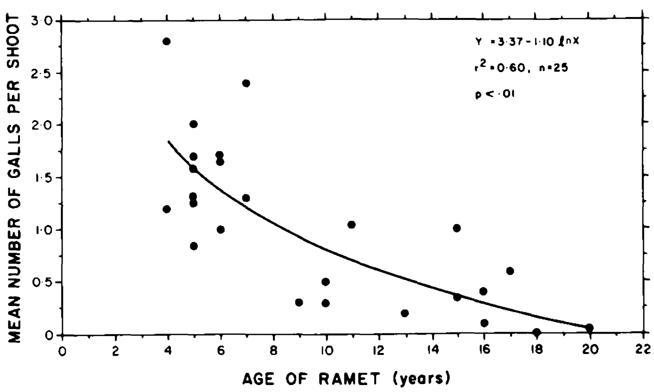

Fig. 3. Relationship between age of ramet and mean number of *Euura mucronata* galls per shoot, for 25 ramets in Rantakyla forest

These relationships were not detected in open sites probably because populations of willow clones were more even

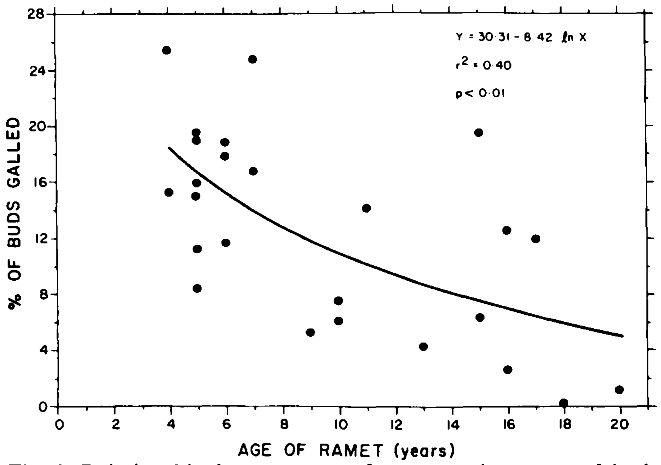

Fig. 4. Relationship between age of ramet and percent of buds galled by *Euura mucronata*, for 25 ramets in Rantakyla forest. Number of buds was calculated from the equation $Y = 0.045X + 2.01$, which was based on the relationship between total number of buds (Y) and shoot length (X) in samples from Linnunlahti forest ($r^2 = 0.86$, $P < 0.00001$)

aged, providing an inadequate range of conditions to observe (cf. Fig. 3 and Ukonnummi age range 8–17 years plus one at 26, Raivo Bog 9–18 years, plus one at 3), and the Mammin Island population was heavily browsed by mountain hare and cut by humans (8 of 25 clones), making the site less stable for pattern development.

Discussion

The pattern of growth in *Salix cinerea*, with decreasing shoot length as ramets age was seen in all six sites studied. The correlates of shoot length suggest that many plant traits change with ramet age in a predictable way. In the forest sites the herbivore, *Euura mucronata*, responded to this pattern of growth with high populations in young ramets declining monotonically to more or less zero on senescing clones at 18 years and above (Fig. 3). The fact that the percentage of galled buds is higher on younger ramets shows that the sawfly exhibits real preference for either the more juvenile shoots, or for the buds on them (Fig. 4). This pattern of growth and attack is very similar to the one documented for the stem galling sawfly, *Euura lasiolepis* (Smith), attacking *Salix lasiolepis* (Bentham), in Arizona (Craig et al. 1986) although ramets of *S. lasiolepis* die at a younger age than those of *S. cinerea*, and ramet ages of 10 years are hardly attacked by sawflies.

The response by sawflies to younger ramets with longer shoots is actually stronger than the analyses in this paper reveal. Younger plants are smaller, with fewer shoots, than older plants, so the older members of a plant population provide the largest physical targets for attack.

It is remarkable that the pattern of attack in response to ramet age and shoot length is so pronounced in forest sites when no other variables have been accounted for. Shading, soil type, drainage, and other herbivores could all increase variation in plant growth within sites and reduce the chances of detecting pattern. We conclude that the effects of plant growth, probably mediated by physical and chemical stimulae associated with the juvenility of willows, on *E. mucronata* are so strong that they are detectable through this background of other variation in the fairly stable and uniform forest sites. Such variables may well become more important in open sites and obscure the pattern.

The pattern of herbivore attack shows that, for a *E. mucronata* population to persist in one site, disturbance must occur at least every decade, which enables establishment of new willow genets and the maintenance of young classes of willows in the population. In genets with older ramets the production of new rapidly growing ramets appeared to be insufficient to replace the aging members of the ramet population.

There are many cases in the forest literature of young and vigorous plants being more susceptible to attack by some herbivores than older plants. Some examples in eastern North America include the weevils, *Pissodes strobi* (Peck) and *Hylobius pales* (Herbst), and the moths, *Eucosma gloriola* (Heinrich), *E. sonomana*, (Kft.), *Gypsonoma haimbachiana* (Kft.), *Petrova albicapitana* (Busck), *Rhyacionia buoliana* (Schiff) and *R. frustrana* (Comst.) (Baker 1972). Other cases are cited by Craig et al., (1986). *Euura mucronata* is another case of this general class of herbivores which attacks vigorous plants and plant parts. They need to be recognized more widely as a group apart from those that respond to plants with reduced vigor which are more commonly considered when "general" plant-herbivore relationships are developed (e.g., White 1974; Rhoades 1983).

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