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## PRICKLE DISTRIBUTION IN *ARALIA SPINOSA* (ARALIACEAE)<sup>1</sup>

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### ABSTRACT

The density of *Aralia spinosa* prickles varied with the age and architectural position of annual increments. Prickles were most common on young (1-4 years old, 2-3 m tall), unbranched stems. Prickles were less common on branches and were absent on inflorescences. Ramets that grew as sprouts after injury had more and longer prickles than ramets that had not arisen in this way. Leaf prickles were also more common on the leaves of trunk annual increments than on the leaves of branch annual increments. As with stem prickles, leaf prickles were more common on the leaves of stems that had sprouted after cutting than on the leaves of ramets that had not been previously cut. As bark developed, stem prickles were lost at a rate of about 10% per year. While dense prickles characterized young individuals, older individuals (>15 years old) had very few prickles.

*ARALIA SPINOSA* L. is a small tree of disturbed patches in the deciduous forests of eastern North America. Among *Aralia*'s distinctive traits are large, bi-tripinnately compound leaves, large terminal inflorescences, and abundant prickles on stems and leaves. While engaged in a study of the shoot architecture of *Aralia spinosa* (White, 1984), I noted that young, unbranched individuals were often more densely prickly than older *Aralia* individuals in the same population. I therefore posed the question: is the change in armature related to architectural development in *Aralia*? The shoot architecture of *Aralia* is distinctive (White, 1984). During the first three to five years of growth (the "trunk-building" phase), the ramet grows upward at 75 cm per year and is sterile and unbranched. During this phase, the spread of leaf area is accomplished entirely by means of the large, compound leaves. On average the ramets flower in their third or fourth year. The year after flowering, branches develop and the ramet slows greatly in annual extension growth. This study characterizes the distribution of *Aralia* prickles in space (i.e., their distribution relative to stem height and architecture) and time (i.e., their production, persistence, and relation to ramet development and bark formation).

*Aralia* prickles are outgrowths of the epidermis and cortex (Davies, 1942). When lignified (by early summer of their first year), they are hollow, lack vascular tissue, and have ceased

expansion. The prickles are produced only during an annual increment's first year of growth, contrary to Davies's suggestion that they are produced during the first two years of growth.

**METHODS**—*Aralia spinosa* populations were sampled on three moist, disturbed sites (500-600 m elevation) in the Great Smoky Mountains, Tennessee. Two populations were on old fields, while the third was in a woodlot disturbed by a severe windstorm. The sampling of ramets was a stratified, random design in which 114 ramets, ranging from 1-15 yr in age, were selected (White, 1984). Because of persistent terminal bud scale scars, characteristics of each annual increment could be measured and the developmental history of each ramet could be reconstructed. The annual increments were numbered from the base of the plant to the most recent year's growth. In this way, prickle distribution could be analyzed as a function of both the age and position of annual increments in each ramet. Annual increments were separated into two classes: "trunk" (below the point of the first branches) and "branch." The mean age at flowering and branching (and thus the mean separation between trunk and branch annual increments) in these populations was 3.5 yr (White, 1984). The mean height of the stem at branching was 2.6 m.

Because leaf scars also persist, nodes and internodes could be recognized on all annual increments. A random numbers table was used to select one internode and node from each annual increment. All prickles were counted and measured. The length and circumference of the internode were recorded for computa-

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tion of prickle density per  $\text{cm}^2$  of stem surface. Because abscised prickles leave a scar on the stem surface, the persistence of prickles could be analyzed as a function of stem age and bark development. Prickles were also counted on randomly selected leaves from all phases of stem growth.

A subsample of the stems was harvested for determination of biomass. Prickles were cut from the stems, and the prickles and stems were dried at 90 C for 48 hr and weighed. For each annual increment of the harvested stems, prickle biomass was expressed as a percent of total woody biomass.

On one of the old field sites, a number of *Aralia* ramets had been cut down the year before sampling. First year stems that had sprouted as a result of this injury were among those selected for sampling. Because these stems had more and longer prickles than ramets that had not sprouted after cutting, I separated all sampled stems into two classes: uncut and sprout stems. In order to experimentally verify the greater density and length of prickles on stems that sprouted after cutting, prickles on 25 first year ramets were counted and measured. These stems were then cut. The year following cutting, prickle density and length were measured on the sprouts that grew from the root systems of these ramets.

For all statistical tests, *t* tests were used.

**RESULTS**—The number of prickles produced per annual increment decreased from basal to distal increments (Fig. 1). If prickle abundance is represented by number of prickles per internode, the decrease is notable in the third year (Fig. 1). By contrast, if prickle abundance is represented by the number of prickles per unit area (prickles/ $\text{cm}^2$  of stem surface), the decrease occurs in the fourth year (Fig. 1). This is explained as follows. Both the surface area of internodes (White, 1984) and prickle abundance decrease from trunk to branch annual increments. From the second to the third annual increment, the number of prickles per internode decreases roughly in proportion to the decrease in internode surface area. Thus, absolute prickle density (prickles/ $\text{cm}^2$ ) has not yet decreased. After the third annual increment, however, the decrease in prickles per internode is steeper than the decrease in internode surface area and hence absolute prickle density shows a sharp decline (Fig. 1).

One year old trunk annual increments had over 30 times more prickles per internode and almost 20 times greater prickle density than one year old branch annual increments (means in both comparisons were different at the 0.001

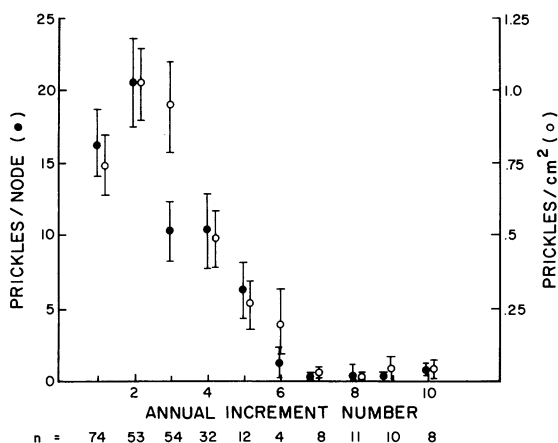


Fig. 1. Prickles per node (left) and per  $\text{cm}^2$  of stem surface (right) for first year stems as a function of position (annual increment number). One SE is shown on either side of the mean.

level) (Table 1). There was no difference between trunk and branch annual increments in prickle length (Table 1). No prickles were observed on inflorescence axes.

On trunk annual increments, prickle density decreased with age, from 1.3 prickles/ $\text{cm}^2$  the first year to very near zero at 15 years (Fig. 2). This decrease in prickle density paralleled an increase in bark thickness. As the stem aged, the epidermis and remnant prickles became isolated on bark ridges and were sloughed off (between age 6 and 10). The decrease in prickle density was about 10% per year.

Trunk annual increments that sprouted after cutting had three times more prickles per internode and about one and a half times greater prickle density than uninjured ramets (Table 1; means for both comparisons were significantly different at the 0.001 level). Prickles of ramets that sprouted after cutting were almost twice as long as those of uninjured ramets (Table 1; means different at the 0.001 level). Prickle biomass, expressed as a percent of total stem biomass, was three times higher in ramets that sprouted after cutting than in ramets that had not arisen in this way. A comparison using percent of total woody biomass was necessary because ramets that sprouted after cutting grew to greater dimensions of length, diameter, and biomass in their first year than uninjured ramets (White, 1984).

The distribution of prickles on leaves showed the same trends as those on stems (Table 1). Leaves on trunk annual increments had about nine times more prickles than branch leaves (means different at the 0.001 level). Leaves on ramets that sprouted after cutting had over two

TABLE 1. Prickle characteristics of first year annual increments in *Aralia spinosa*

Ramet position	Prickles per internode	Prickles per cm <sup>2</sup>	Length (mm)	% Woody biomass	Prickles per leaf
Trunk, uninjured ( <i>N</i> = 75)	17.2 <sup>a</sup> (20.4) <sup>b</sup>	1.2 (1.1)	3.9 (1.5)	0.05 (0.05)	19.6 (36.4)
Branch ( <i>N</i> = 50)	0.5 (1.2)	0.07 (0.17)	4.1 (1.1)	0.01 (0.05)	2.2 (4.4)
Trunk, injured ( <i>N</i> = 50)	56.8 (13.8)	1.9 (0.4)	7.7 (1.7)	0.16 (0.06)	43.6 (37.4)

<sup>a</sup> For each row, values on the first line are means.

<sup>b</sup> For each row, values on the second line (in parentheses) are SD.

times more prickles than leaves on uncut ramets (means different at the 0.01 level).

Genotype and site were uncontrolled in the observations reported above on differences between sprout and uncut stems. Therefore, an experiment was carried out in which prickles were counted on 25 first-year ramets. These stems were then cut and prickles were counted on the first year annual increments that sprouted the year after cutting.

In 24 of the 25 sprout ramets there was an increase in prickle density and length compared to the uninjured phenotype of the same ramet (on the twenty-fifth stem prickle density decreased by 10 percent and length was unchanged). On these 24 ramets, prickle density increased from 3–800 percent, with a mean increase of 140 percent, and prickle length increased 20 percent. However, when the data were pooled (i.e., when ramets were not treated individually), there was broad overlap between stems that sprouted after cutting and stems that were measured before cutting. Sprout stems had from 0.2–3.7 prickles/cm<sup>2</sup> and uncut stems had from 0.1–1.7 prickles/cm<sup>2</sup> (means not significantly different at the 0.05 level). Similarly, mean prickle length on stems that sprouted after cutting ranged from 3.0–10.4 mm, while mean prickle length on uninjured stems ranged from 2.4–8.0 mm (means not significantly different at the 0.05 level). Casual observation suggested that the more vigorous the original shoot, the more vigorous the response to cutting. For example, the ramets used in the experiment may have differed in supply of stored carbohydrates and in competitive environment.

**DISCUSSION**—If prickle distribution reflects the vulnerability of *Aralia* to browsers, then *Aralia* stems are most vulnerable when young and within 3 m of the ground. Several lines of reasoning support this temporal (young tissues) and spatial (near the ground) vulnerability. *Aralia* is a clonal plant of full-sunlight habitats produced by disturbance. Mammals are often attracted to disturbed patches and prefer young

ger tissues (Peek, 1974). Resources are initially abundant to plants in early successional situations and productivity is high. With time since disturbance, competition intensifies. Thus, the early phases of stem establishment are critical (Grime and Hunt, 1975).

Adding to the potential vulnerability of establishing *Aralia* stems is their morphological simplicity. During the unbranched phase of growth, survival of an individual *Aralia* ramet depends on a single terminal meristem. In addition, each leaf bears about 10 percent of the total leaf area of the entire ramet. Thus, the success of the individual stem in this competitive environment depends heavily on a few morphological units.

Evidence to support the argument that prickle distribution reflects vulnerability is absent. White-tailed deer (*Odocoileus virginianus*) and eastern cottontail (*Sylvilagus floridanus*) were present in the study area, but were not observed to use *Aralia*. (There is a brief reference to deer use of *Aralia* in van Dersal, 1938.) Some damage to stems was found on about 5 percent of the ramets studied. This consisted of removal of bark patches in strips from lower stems and resulted from antler rubbing (Michael Pelton, personal communication). *Aralia* prickles may represent an adaptation to an extinct fauna: elk (*Cervus canadensis*) and bison (*Bison bison*) were important in the range of *Aralia spinosa* until ca. 1750–1850 and there was a much richer mammalian fauna in eastern North America before the Pleistocene (Kurtén and Anderson, 1980; Janzen and Martin, 1982).

The response of *Aralia* to injury parallels recently reported changes in chemical defenses after grazing. Plants subjected to damage have been shown to increase the concentration of secondary compounds in new leaves (Schultz and Baldwin, 1982; Fowler and Lawton, 1985), although it is unclear if this change in tissue quality affects herbivore populations in the field (Fowler and Lawton, 1985). The injury response also recalls the tendency for woody plants to express juvenile traits, including prickles and thorns, after injury (Goebel, 1900;

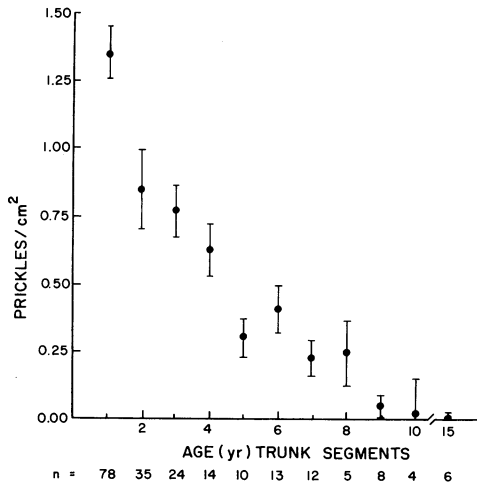


Fig. 2. Prickle density on trunk annual increments, as a function of age. One SE is shown on either side of the mean.

Arber, 1950; Sinnott, 1960). Sprout stems, which have a well-developed root system and which may have a ready supply of carbohydrates, are often robust compared to individuals that have recently established from seeds (e.g., Johnson, 1975). This would facilitate quick reestablishment after injury. Greater allocation to protection from further injury would be advantageous in the early successional habitats in which *Aralia* is found.

Prickle distribution in *Aralia spinosa* provides an illustration of the potential ties between the architectural development of a woody plant (i.e., its gross morphology) and the expression of other morphological traits. In the particular case presented here, the amount of investment in the trait examined (i.e., when prickle biomass was expressed as percent of

total woody biomass) was quite low. While the nonrandom distribution of prickles is interpretable with regard to the life history of *Aralia spinosa*, proof that this distribution has adaptive significance has not been sought and would be difficult to obtain. (See discussion in Fowler and Lawton, 1985.)

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