ADAPTATIONS OF SCALE INSECTS TO HOST VARIABILITY

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Abstract: Scale insects survive by adapting to the phenotypic characteristics of a single host plant upon which they spend their entire life cycle. Coccoids must overcome host pheno-immunity and genetic immunity. Scales adapt to these defenses by being able to successfully reproduce in populations with low male frequencies and by forming demes on individual hosts. Polyphagous coccoids show host preferences, and may exhibit morphological forms peculiar to each host species. Varied forms may also occur on different organs of a host. Understanding interactions such as this between the Coccoidea, their hosts, and the environment, will facilitate our efforts to bring scale insects within the realm of integrated pest management.

Key Words: Coccoidea, scale insects, plant-herbivore interactions, pheno-immunity, genetic immunity, host forms.

Scale insects are noted for their extensive and sometimes bizarre adaptations to the plant parasitic regime. Their great variety of form, including sexual dimorphism, has enabled the Coccoidea to adapt to nearly all botanical habitats and feed on most plant organs.

One of the most important trends in coccoid phylogenesis is the increasingly sessile nature of females in the more advanced families. The female body form conforming most thoroughly to a sedentary lifestyle is found in the largest family, the armored scales (Diaspididae). Although many coccoids move from one site to another at various times during their developmental cycles, armored scales are incapable of wandering once they settle and commence feeding. Thus, scale survival requires thorough adaptation to the phenotypic differences of each individual host. Some of these adaptations, including responses to host defenses, are the subject of this paper.

Dispersal
The means by which scale insects disperse determines their probability of encountering potential hosts of different phenotypes or species. Because scales are notorious plant pests, many studies of scale dispersal have been conducted (McClure 1977a; Washburn and Washburn 1984; Moran et al. 1982). Scales spread principally by passive transport on infested plant material and as unsettled crawlers (first instars) (Beardsley and Gonzalez 1975). The wandering of crawlers generally serves to disperse young away from the mother onto new growth of the same host (Bennett and Brown 1958; Brown 1958) or between adjacent hosts if

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the plant crowns are in contact (Bodenheimer 1951). Wind, another important dispersal and mortality agent, permits short and/or long range transport. Crawlers of the ice plant scale, Pulvinariella mesembryanthemi (Vallot), exhibit active aerial dispersal behavior by standing on their hind legs and facing downwind until they are blown away (Washburn and Frankie 1981).

Scale Adaptations to Pheno-immunity

Even though scales can readily disperse to other hosts, many individuals remain on the same plant as their parents. An important factor in the success of the population when multiple generations occur on a plant is the continuing nutritional quality and vigor of the host. Scales must be able to tolerate changes in the chemical and physical composition of the host's sap due to environmental influences, plant maturation and senescence.

Environmental influences on host physiology can cause a phenomenon known as "pheno-immunity" (Thiem 1933), a "physiological resistance of a host plant to infestation by its indigenous coccid" (Flanders 1970). In some cases, this immunity is a permanent, local phenomenon, due to the host's physiological response to the prevailing climate (Compere 1935, 1940, 1961) and/or edaphic conditions (McClure 1977a). In other cases, the response is only temporary and induced by changing meteorological and edaphic conditions (Flanders 1970).

Pheno-immunity affects scale reproduction, causing high mortality and a temporary inability to reproduce (Thiem 1938), or a change in the population sex ratio. For example, male production by the black scale, Saissetia oleae (Bernard), under field conditions is normally rare. However, in 1909 Quayle and Rust (1911) reported that males were especially abundant on some host species in several locations between San Diego and Santa Barbara, CA. It has been suggested that the weak diaspidid genetic sex determination mechanism can be environmentally overridden (Hughes-Schraeder 1948; Beardsley and Gonzalez 1975).

Scale Adaptations to Genetic Immunity

Differential resistance to scale attack within a plant species may be genetic in origin. From observations over 5 yr of the reproductive success of black pineleaf scale, Nuculaspis californica (Coleman), on ponderosa pine, Pinus ponderosa (Laws), Edmunds and Alstad (1978) concluded that the trees show a complex intraspecific variation in their defensive phenotype. Resistance to coccoid attack was not environmentally induced because adjacent trees had great variation in scale population density. The immunity was also not permanent. In severe outbreaks, scale-free trees eventually became infested.

By transferring black pineleaf scales from infested to uninfested trees, Edmunds and Alstad (1978) showed that "selection over many generations results in scale insect populations which are increasingly adapted to the defensive character of their host tree." Edmunds and Alstad called these populations "demes." When black pineleaf scale demes were followed on several ponderosa pines, a relationship was found between sex ratio, male behavior, and the degree of adaptation to the host. Sex ratios were female-biased as predicted by theoretical models of the evolution of the sex ratio in deme-structured populations (Hamilton 1967). However, the data showed a female bias stronger than any model predictions (Alstad et al. 1980). Alstad et al. hypothesized that the female-biased ratios did not result from a variation between production of the sexes, but were caused by
survivorship differences. *Nuculaspis californica* females are diploid and thus heterozygous for some traits. This may enable them to survive better than the haploid males during the early stages of population adaptation to a host. “As selection reduces genetic variance and the deme becomes better host fitted, male and female adaptations are more nearly equal.” (Alstad et al., 1980) Thus, male frequency should increase with time. This hypothesis was supported by data showing a higher percentage of males on trees with greater scale density, and presumably better insect adaptation (Spearman rank correlations, 1979: n = 11, P < 0.10; 1980: n = 18, P < 0.05). In addition, every tree sampled in both years showed a higher 1980 male frequency (sign test, n = 11, random probability < 0.01).

Based on black pineleaf scale male capture data and other observations, Alstad et al. (1980) concluded that male mating behavior also was consistent with increasing adaptation to a host. Most scale mating was very localized, and thus reduced gene flow between trees. This contributed to the differentiation of scale populations. Populations poorly fitted to their host had high male mortality which prompted more between-tree matings. This provided for new genetic combinations which might improve fitness.

The tannin-like compounds of ponderosa pines (Edmunds and Alstad 1978), and the resinosis of red pine, *Pinus resinosa* Ait. (McClure 1977b) are examples of plant chemical defenses to which scales must adapt. Morphological features, such as epidermal characters, may also counter scale attack. Agarwal and Sharma (1961) studied the occurrence and abundance of sugarcane scale, *Melanaspis glomerata* (Green), on different varieties and ecotypes of sugar cane, *Saccharum spontaneum* L., and found a direct relationship between heavy attacks and a high stomatal density on the stem.

**Adaptations Related to Polyphagy**

Even greater host adaptability than previously discussed is necessary when polyphagy is considered. Many coccoids are polyphagous and have adapted to interspecific phytochemical, morphological, and habitat differences. Preferences between host species occur, and may be evident in differences in fecundity (McClure 1983) or sex ratio (Voukassovitch 1933; Priesner 1938). An interspecific host preference is sometimes a local phenomenon mediated by climate. For example, black scale has a wide host range including citrus, but citrus is normally not a preferred host. However, in regions like parts of California, Chile, and Spain, black scale infestations of citrus can be severe. In these areas, Flanders (1970) believed citrus resistance to infestation was counteracted by especially favorable environmental factors. The climate was apparently unfavorable for citrus infestation in South Africa as Compere (1940) found citrus trees entirely free of black scale growing adjacent to oleanders (*Nerium* spp.) which were heavily infested. Smith and Compere (1928) reported that black scale on citrus seemed to be unusually responsive to slight weather variations.

Different hosts can also cause life history variations for scales. Stoetzel and Davidson (1973) compared the life history of the obscure scale, *Melanaspis obscura* (Comstock), on white oak, *Quercus alba* L., and pin oak, *Q. palustris* Muenchhausen, and found an ca. 1 month lag in development of most stages on white oak as compared with development on pin oak. On white oak, settled crawlers were the overwintering stage, while on pin oak second instars overwinter. Stoetzel and Davidson concluded that the two populations were reproductively
isolated. Although morphological differences between the populations could not be found, it appeared that two species were present, one of which was new.

Many examples illustrating the alteration of coccoid morphology by host species are reported in the literature. Taxonomists confused by host forms have mistakenly named a new scale species or genus (Knipscher et al. 1976). Ebeling (1938) divided the effects of host species on coccoid phenotype into two categories: (1) physical, when a scale changes shape to correspond to certain structural peculiarities of the host, and (2) physiological, when, consumed as food, the host affects certain physiological and morphological characteristics of the scale. He cited the conspicuous variety of forms of the European fruit lecanium scale, *Lecanium corni* Bouche, as a prime example of the latter category.

*Lecanium corni* has a wide host range which includes *Prunus* spp. This scale, occurring on black locust, *Robinia pseudoacacia* L., was believed to be a different species, *L. robiniarum* Douglas. By transferring scales between host species, Marchal (1908) and Voukassovitch (1930) showed that *L. robiniarum* was rarely a host-induced form of *L. corni*. The very marked differences in external appearances of the scales (i.e., the gradation of convexity from a lateral view) on different hosts are shown in Fig. 1. The greatest similarity exists between individuals from hosts which are most closely related, such as the *Prunus* spp. (plum, apricot, and peach) of Fig. 1. Ebeling (1938) transferred *L. corni* from apricot, *Prunus armeniaca* L., to Christmasberry, *Schinus terebinthifolius* Raddi, and from alder, *Alnus* spp., to apricot. He observed that these scales developed the host-form found on their new host rather than the form of their progenitors.

![Fig. 1.](image)

Fig. 1. Cross sections of dried specimens of *Lecanium corni* Bouche showing differences in form on various host species. (With permission from Ebeling 1938).
The Influence of Feeding Location on Eurymerous Coccoids

Many coccoids are eurymerous (i.e., they may feed successfully on more than one organ of their host) (Balachowsky 1932; Vayssiere 1926). In some eurymerous species, the location of the insect on the host plant may affect its morphological characteristics (Lupo 1943; Stafford and Barnes 1948; Takahashi 1953; Takagi and Kawai 1967; Tippins and Beshear 1970). Dimorphism is frequently the case, and also may be associated with the seasons. For example, females of Putnam’s scale, *Aspidiotus ancylus* (Putnam), overwinter on twigs, and are distinctively different from the summer leaf form (Fig. 2) (Stannard 1965). The factors affecting such changes have not been investigated, but the appearance of stem forms on senescing leaves and intermediate forms on petioles (Knipscher et al. 1976) suggests that the cause may be variations in the chemical nature of physiology of parts of the host plant (Miller and Kosztarab 1979). Danzig (1970) believed that nutritional differences in the sap of leaves and stems caused dimorphism.

Fig. 2. *Aspidiotus ancylus* (Putnam) showing pygidial lobes of (a) twig form and (b) leaf form; pygidial plates of (c) twig form and (d) leaf form. (With permission from Stannard 1965).
CONCLUSION

The Coccoidea have developed an array of chromosome systems reflecting the diversity of their specializations and allowing for new host adaptations as required for survival (Brown 1977). Continued study of these adaptations and host defenses will assist plant breeders in developing scale-resistant varieties. Pheno-immunity, which sometimes may be as complete as genetic immunity (Thiem 1938), must also be considered in scale resistance. Environmental factors responsible for pheno-immunity and host quality might be manipulated to promote this resistance. For example, McClure (1980) demonstrated how nitrogen fertilization affected host suitability of Eastern hemlock, Tsuga canadensis Carriere, for elongate hemlock scale, F. ex.tern.a Ferris. Understanding interactions such as this between the Coccoidea, their hosts, and the environment, will facilitate our efforts to bring scale insects within the realm of integrated pest management.

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