Effects of Density on Survival, Development, and Fecundity of the Soft Scale, *Pulvinariella mesembryanthemi* (Homoptera: Coccidae), and Its Host Plant

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ABSTRACT We performed laboratory tests to examine effects of different densities of *Pulvinariella mesembryanthemi* (Vallot) on population growth, development, survivorship, and reproduction. We also measured survivorship and growth of its ice plant host, *Carpobrotus edulis* × *aqualateris* (Aizoaceae), supporting various scale densities. Scale body size and fecundity were inversely related to density, indicating intraspecific competition; both scale and host-plant survivorship were strongly density-dependent. Scale mortality at high densities was attributed to limited settling sites, honeydew fouling, physical crowding, and death of host plants and plant parts supporting scales. On dying plant tissues, scales reproduced prematurely and produced fewer offspring. Plant growth was negatively correlated with scale densities, and at high scale densities plants stopped production of new leaves and shoots, reducing the resource base for subsequent generations of scale.

HERBIVOROUS insects suffer from a variety of mortality factors, and a significant body of ecological literature has been devoted to assessing the relative influence of these factors on population dynamics. These studies are challenging to perform because the importance of individual regulatory factors varies in time and in space over a landscape of shifting population densities.

Intraspecific competition has been demonstrated for several sucking insect herbivores (e.g., Way and Banks 1967, Dixon 1970, Whitham 1978, 1980, McClure 1979a,b, 1980). Conspecifics are often temporally and spatially aggregated, which provides an ideal arena for competitive interactions. These interactions can produce density-dependent population regulation where the direction and magnitude of change depend upon population size. Documentation of density dependence requires more than simple correlation analysis; it requires both an accurate assessment of population levels (Smith 1961) and an understanding of the underlying regulatory processes and their direct effects on population dynamics (Eberhardt 1970). For many natural populations, these goals are hard to achieve, but some sessile insects are amenable to experimental manipulation, which in turn allows for measurement of a density-dependent response (e.g., Whitham 1978, 1980, McClure 1979a,b).

We expect intraspecific competition and resulting density-dependent regulation to be particularly severe in sessile forms because opportunities to reduce competitive interactions by movement (e.g., dispersal from areas of high density) are more restricted. Sedentary species are suitable subjects for examining population dynamics in detail because 1) they spend a major segment of their life attached to one site, 2) they often leave a record of mortality, and 3) it is frequently possible to assess fecundity of individuals (Mitchell 1983).

Our interest in density-dependent regulation and the mechanisms by which it is facilitated comes from observations on a plant-scale herbivore system in California where intraspecific competition may be a factor in regulating local insect abundance. *Pulvinariella mesembryanthemi* (Vallot) is an introduced pest of naturalized and ornamental ice plants (Aizoaceae), primarily of the genus *Carpobrotus*. This soft scale is native to southern Africa (Brain 1920, Quintana 1956, Gill 1979) and was first recorded in California in 1971. Since its introduction, it has spread throughout areas of the state where a Mediterranean climate prevails and ice plants are maintained (Washburn and Frankie 1981, 1985). At high densities, scale feeding causes decline and death of its host plants, and for this reason *P. mesembryanthemi* is considered an economic pest.

During several years (1978–1984) of monitoring scale infestations in the field, we observed that after several successive scale generations during which population levels increased, there was often a dramatic decline in scale numbers. These declines occurred even in the absence of intense pressure from natural enemies, and in many cases before significant impact (e.g., death or decline of plants or plant parts) on the host plants was evident. These observations suggested that density-dependent interactions among scales or between scales and their hosts may be operating to regulate field populations. We conducted two laboratory experiments to evaluate effects of different scale densities on the population dynamics of *P. mesembryanthemi* and on growth and survival of its host plant.

Mature scales are small (averaging ca. 3.0–4.0 mm in length), and the life cycle includes an egg and four nymphal instars. Under field conditions in central California, the generation time of *P. mesembryanthemi* is 4–6 months, but under warm greenhouse conditions the generation time is approximately halved. Although males are known, almost all fourth-instar nymphs become adult females, and reproduction apparently occurs only by parthenogenesis (Nur 1972, 1980). No males were produced in the experiments reported here. Mature females form waxy ovisacs in which 400–2,000 eggs may be deposited, and die after oviposition. First-instar nymphs (crawlers) are the principal dispersal stage (Washburn and Frankie 1981, 1985) and search for feeding sites immediately after emergence from ovisacs. Crawlers disperse by walking and settle on leaves where acceptable feeding sites are located. If feeding sites are not available, crawlers can engage in active wind dispersal (Washburn and Washburn 1984). During settling, scales retract their legs under their bodies, adhere closely to the substrate, insert their stylet mouthparts into the plant tissues, and commence to feed. Scales feed by withdrawing fluids from phloem elements of leaves and stems, and as long as these feeding sites provide suitable nutrition, the insects show little tendency to move. Nymphs can successfully change feeding sites by moving to adjacent leaves, but attempted re-establishment often results in death of the scales.

Materials and Methods

Plant material was secured from terminal shoots of the ice plant cultivar, *Carpobrotus edulis* × *aqualateris*, the most commonly utilized host in California. All plant material was collected from a single uninfested ornamental planting on the campus of the University of California (UC), Berkeley. Shoots were labeled, weighed, and planted in plastic pots (60 by 60 by 70 mm deep) in a standard UC soil mixture of 50% peat and 50% sand. All plants were maintained under identical greenhouse conditions for 4 weeks before introduction of scale crawlers.

In the first experiment, 30 terminal shoots were infested with different numbers of crawlers. Individuals <24 h old were collected as they emerged from field-collected ovisacs and transferred to host plants with a fine camel's-hair brush. We infested 10 plants with 25 crawlers each and 10 plants with 150 crawlers each. Four additional plants were infested by placing a single ovisac (ca. 500 crawlers) at the base of each plant; three plants were infested with two ovisacs and three plants with three ovisacs. In each case, we infested plants with similarly sized ovisacs that were full of emerging crawlers. Ten additional plants without scales served as controls. Plants were randomly divided into groups of 10 in plastic trays, which were maintained in organdy-covered cages in a greenhouse where temperatures fluctuated between 20 and 30°C. Interplant movement of crawlers was prevented by separating the potted plants and by partially filling each tray with water. Under these conditions, subsequent infestation of plants without scales in the trays was a very rare event and never exceeded one or two scales per plant. At regular intervals (7–10 days), we added a measured volume of water (200 ml per plant) to each tray to ensure that all plants experienced similar edaphic conditions.

The development of scale populations was followed by measuring the lengths of 10 randomly selected immatures per plant to the nearest 0.5 mm every 10 days until they began to form ovisacs. When ca. 25% of the surviving scales on all plants had formed ovisacs, we counted living immatures and ovisacs and removed from each density category a random sample of fully developed ovisacs that had not yet released crawlers. These were secured individually to the centers of paper disks bordered by insect trapping adhesive (Tanglefoot). The adhesive barrier captured emerging crawlers and allowed a census of their total numbers. Additionally, we dissected these ovisacs and scored numbers of unemerged crawlers. Emerged and unemerged crawlers were summed to determine fecundity of each ovisac.

Two days before the final census, all plants were watered to repletion (standing water remained in the trays) to compensate for any differential water loss that may have occurred. Water loss from plant tissues results from scale feeding, and the magnitude of loss varies with scale density. Water addition before measurement of final wet weight was intended to replenish their water supply and help standardize the water content. After ovisacs were collected in the final census, plants were carefully removed from pots with roots intact. We rinsed soil from around the roots and blotted them dry with paper towels before recording a final wet weight for all surviving plants.

In the second density experiment we used 90 plants that were collected, weighed, potted, and cultured in trays following the methods described above. Ten plants each were infested with 10, 25, 50, 100, 150, or 200 crawlers, and five plants each were infested with 300, 400, or 500 crawlers. The remaining 15 plants were not infested with scales and served as controls. Because 3 days were required to infest all plants with crawlers (a total of 11,250 insects), we infested the same proportion of plants from each density category on each day. After all infestations were completed, plants were maintained as described for the first experiment.

Host plants in the second experiment were left undisturbed except for watering until sufficient numbers of ovisacs were present on each plant to collect for fecundity counts. During this final census, total numbers of scales (immatures and ovisacs) surviving on each plant were determined, ovisacs were collected for fecundity determina-

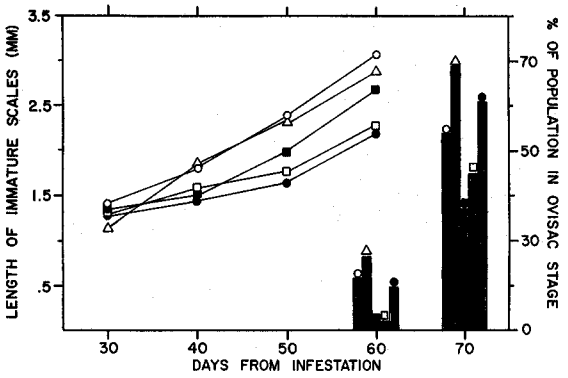

Fig. 1. Growth and development of *P. mesembryanthemi* populations at different densities in the first experiment. Plotted points are average lengths of immature scales (n = 30–100 scales). Scale density categories are represented by the following symbols: 25 crawlers, ○; 150 crawlers, △; one ovisac (ca. 500 crawlers), ■; two ovisacs (ca. 1,000 crawlers), □; and three ovisacs (ca. 1,500 crawlers), ●. Proportions of each density group in ovisac stage were determined 60 and 70 days after infestation. Mean scale lengths at 60 days at all densities are significantly different from each other (ANOVA of rank values, Tukey's studentized range test, $P < 0.05$).

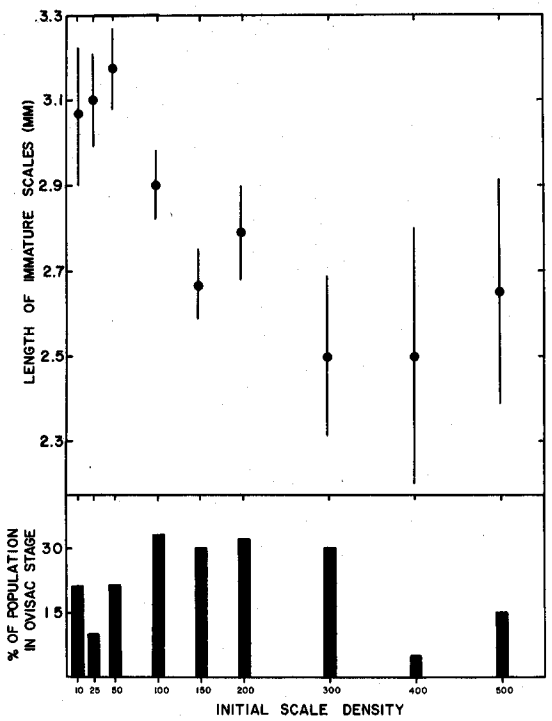

Fig. 2. Average length of immature scales (±95% confidence interval) and the proportion of surviving scales in ovisac stage during the final census in the second experiment. Each mean represents between 10 and 80 scales. Data were collected 85 days after infestation with crawlers.

tions, and the final wet weight of each plant was recorded. Additionally, dead scales on representative plants from each of the density categories were examined to determine numbers dying from various mortality factors (e.g., physical crowding, leaf death, honeydew fouling). In this experiment, we did not monitor scale growth and development at regular intervals.

As in the first experiment, we watered all plants to repletion 2 days before the final census and determination of plant wet weights. After recording plant wet weights, we removed a sample of three mature leaves from representative surviving plants from all density categories and measured their wet weights. These leaves were air-dried until their weights stabilized, and dry weights were recorded to assess water content.

Statistical procedures employed were least-squares regression (Sokal and Rohlf 1969) and analysis of variance (ANOVA) of ranked data values (SAS Institute 1982).

Results and Discussion

In both density experiments, growth and development of *P. mesembryanthemi* individuals were related to the initial density of crawlers infesting host plants. After 60 days, the average lengths of immature scales of each density group were found to be significantly different from each other (ANOVA of rank values, Tukey's studentized range test, $P < 0.05$) and showed an inverse relationship with initial scale densities (Fig. 1). Although scale lengths were not determined during development in the second experiment, mean lengths of immatures during the final census were found to be negatively associated with scale density (Fig. 2). Results of both experiments indicated that scale growth was inhibited as density increased.

Whereas scale size was negatively related to density, we found no consistent relationship between the onset of ovisac production and the number of scales per plant. Despite their faster growth, scales reared on plants with lower density levels did not consistently reproduce before scales from plants with higher density levels. Differences in the timing of reproduction can be measured by comparing the proportion of surviving insects in ovisac stage during a given sample period (Fig. 1 and 2). Sixty and 70 days after infestation in the first experiment, a greater proportion of surviving scales from plants initially infested with 25 crawlers, 150 crawlers, and three ovisacs (ca. 1,500 crawlers) was reproducing than were scales from plants initially infested with one or two ovisacs (Fig. 1). Similarly, in the second experiment ovisac frequencies in the surviving scale populations did not show any clear relationship with the initial density of insects per plant (Fig. 2).

Average scale fecundity in both experiments was significantly and negatively correlated with scale

Table 1. Mean fecundity of scales reared at different densities in the first experiment[a]

Initial scale density	Mean no. crawlers per ovisac ± 1 SD	*n*
25 Crawlers	531.9 ± 333.3a	49
150 Crawlers	384.4 ± 171.3a	50
One ovisac (ca. 500 crawlers)	232.0 ± 147.0b	50
Two ovisacs (ca. 1,000 crawlers)	246.1 ± 182.9b	55
Three ovisacs (ca. 1,500 crawlers)	91.1 ± 88.0c	48

[a] Initial scale densities are numbers of crawlers or ovisacs introduced onto host plants. Sample size (*n*) indicates the number of ovisacs used to calculate mean number of crawlers per ovisac. Means followed by the same letter are not significantly different (ANOVA of rank values, Tukey's studentized range test, $P < 0.05$).

density (Table 1). In the first experiment, the mean fecundity of ovisacs from plants infested with 25 crawlers was nearly 6-fold that of the three-ovisac group (Table 1). Similar results were recorded from the second experiment (Fig. 3) where there was more than a 10-fold difference in individual fecundity between the highest and lowest densities. In the second experiment there was a concomitant decline in the average length of ovisacs as scale density increased (Fig. 3). On plants supporting high densities of scales, ovisacs were typically very small and produced fewer offspring than corresponding ovisacs from plants with lower densities.

In addition to density-dependent growth and fecundity, scale survivorship and density were correlated in the second experiment (Fig. 4). Scale survivorship rates ranged from 2 to 48% and were negatively associated with initial scale densities. Plant survivorship was also negatively related to scale density (Fig. 4), and at higher densities plant mortality caused extensive scale mortality. At the highest initial density of 500 crawlers per plant, none of the plants was living at the final census, and only three females of the initial population of 2,500 insects on the five plants successfully reproduced. Results from plants infested with 300 crawlers each were similar.

As scale density on plants increased, several kinds of intraspecific interactions became important mortality factors. Nymphs of *P. mesembryanthemi* secrete copious quantities of honeydew that can be ejected several millimeters from the insect. If a honeydew droplet lands on a neighboring scale, the insect usually dies from either suffocation or the subsequent growth of sooty mold. If the droplet falls on an ovisac, young crawlers cannot escape and they die within the ovisac. In the second replicate, mortality to immatures and ovisacs by honeydew fouling generally increased at higher densities (Table 2). At high scale densities this interference competition was even more important because total honeydew production was greater, interscale distances were shorter, and the resulting probability of honeydew fouling increased. A second type of mortality from competition at

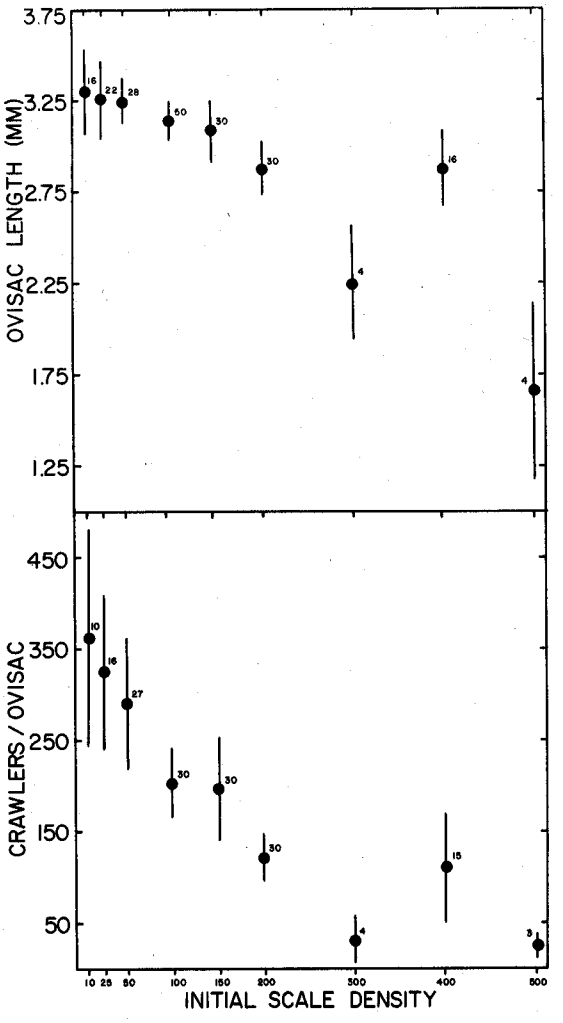

Fig. 3. Average ovisac length and fecundity (±95% confidence interval) of *P. mesembryanthemi* reared at different densities in the second experiment. Sample sizes are indicated.

feeding sites also occurred more frequently at the higher scale densities (Table 2). Under crowded conditions, scales often smothered one another as they grew larger, and in many situations this led to scale death.

Other mortality factors (Table 2) included crawler settling failure and mortality due to decline and death of leaves and shoots supporting the insects. Failure to settle successfully is probably the single greatest contributor to total scale mortality independent of density (Washburn and Frankie 1985). Scale death due to decline of plant parts is more important at higher densities, since these plants are less healthy. In both experiments we found a significant negative correlation ($P < 0.01$) between the final density of surviving scales and the change in wet weight of the plants over the course of one scale generation, the duration of

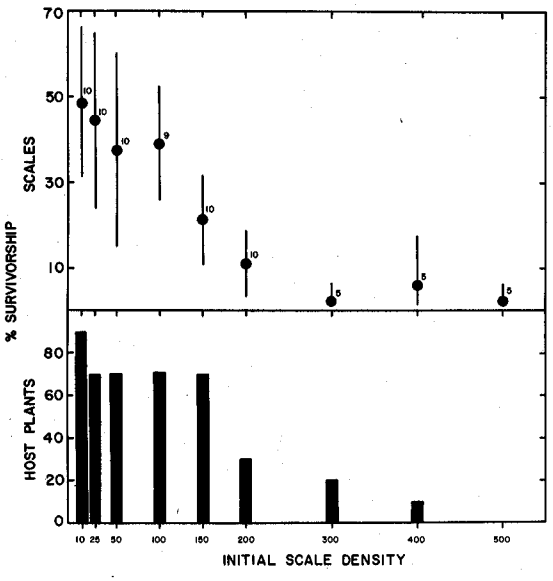

Fig. 4. Survivorship of scales (mean per plant ±95% confidence interval) and host plants in the second density experiment. No plants initially infested with 500 scales survived the experiment. Plant sizes are indicated.

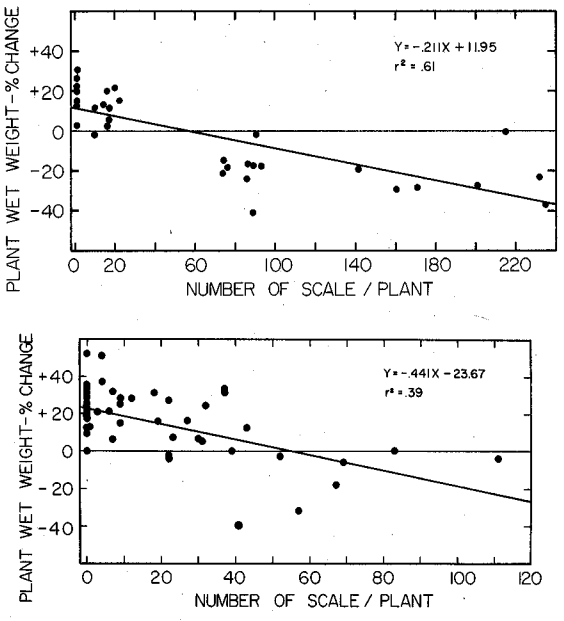

Fig. 5. Changes in wet weights of host plants supporting different densities of scales in the first (top) and second (bottom) experiments. Number of scale refers to the number of surviving scales on host plants during the final censuses. Lines calculated by least-squares regression ($P < 0.01$).

the experiments (Fig. 5). Wet weight changes could reflect growth or decline of plant parts, or they could reflect changes in the water content of tissues, which can be influenced by a variety of factors. For succulents like *Carpobrotus*, water content is particularly variable because the majority of the leaf volume is devoted to water storage, and under xeric conditions these stores can be recruited. By watering plants to repletion before the final censuses, we provided an excess of soil water to replace water that may have been depleted by heavy scale feeding. In a comparison of wet and dry leaf weights from surviving plants in the second experiment, we found no differences in the water content of tissues from plants supporting a wide range of scale densities (Table 3). This indicates that plant wet weight changes were not simply a result of dehydration. Rather, some plants lost weight because leaves and shoots died over the course of the experiment, and many plants failed to produce new tissues. These characteristics were typical of plants with high scale densities, and this retardant effect of *P. mesembryanthemi* on its host has been reported by Collins and Scott (1982). In our experiments, when leaves or shoots supporting scales died, the insects experienced one of three fates: 1) some scales prematurely reproduced provided they were sufficiently mature, 2) some scales secured new feeding sites on nearby healthy leaves, 3) some scales died. As in cases where whole hosts died, premature reproduction invariably resulted in smaller broods.

Experimental scale densities produced in these experiments were comparable to those encoun-

Table 2. Mortality of scales from plants infested with different numbers of crawlers (experiment 2)[a]

Initial scale density	No. plants examined	Types of mortality			
		Honeydew fouling	Smothering by other scales	Other mortality	Totals
10	3	0 (0)	0 (0)	10 (100)	10 (100)
25	3	2 (5.1)	1 (2.5)	36 (92.3)	39 (100)
50	3	4 (6.0)	1 (1.5)	61 (92.4)	66 (100)
100	3	31 (17.4)	12 (6.7)	135 (75.8)	178 (100)
150	3	51 (14.8)	23 (6.7)	270 (78.5)	344 (100)
200	1	34 (23.0)	16 (10.8)	98 (66.2)	148 (100)
300	1	31 (11.3)	22 (8.1)	220 (80.6)	273 (100)

[a] Numbers outside parentheses are absolute numbers of dead scales; numbers inside are percentages of total mortality in that density category. Other mortality includes crawler settling failure and mortality caused by decline and death of leaves and shoots.

Table 3. Average water content of *Carpobrotus* leaves from plants infested with different densities of scales[a]

Initial scale density	Mean % water content ± 1 SD	*n*
0	91.9 ± 3.5	14
10	92.9 ± 2.4	7
25	92.9 ± 1.3	7
50	93.2 ± 2.0	8
100	93.0 ± 0.8	8
150	90.4 ± 3.6	5
200	92.0 ± 1.6	3
300	—	—
400	—	—
500	—	—

[a] Sample sizes (*n*) are numbers of plants used to calculate means. Three leaves per plant were used to determine water content.

tered at field sites in California, and all the mortality factors we have recorded have been noted in field populations. Data from both density experiments indicate that *P. mesembryanthemi* populations can exhibit density-dependent population regulation, in part mediated by intraspecific competition and concomitant host decline. The effects of high scale densities are expressed by individual scales in smaller body size, lower survival, and production of smaller ovisacs with reduced brood sizes. Lower survival and growth rates are, in part, caused by interference competition for food, honeydew fouling, and suffocation, and in part by factors relating to host plant condition. These results are consistent with findings on other scale species. Moran and Cobby (1979) established that fecundity of the cochineal scale, *Dactylopius austrinus* DeLotto, was a function of the number of females feeding on cladodes of the host, *Opuntia aurantiaca* Lindl. Additionally, adult female size and fecundity were related to the condition of the cladode. Similarly, McClure (1979a,b) found that populations of the elongate hemlock scale, *Fiorinia externa* Ferris, were numerically self-limiting to some extent. Development rate, fecundity, and survival of nymphs of *F. externa* were all negatively correlated with scale densities on host trees.

The relative importance of interference interactions such as honeydew fouling and suffocation in a scale population is determined by conditions experienced by individual host plants. Some conditions are more or less stochastic, and may cause a mosaic of mortality patterns reflecting local conditions. For example, *P. mesembryanthemi* nymphs are commonly tended by ants that harvest honeydew droplets (Collins and Scott 1982). If ants are common and efficient at harvesting these exudates, mortality from honeydew fouling may be relatively unimportant in local population dynamics. If ants are absent, however, death by honeydew fouling may be very important. Similarly, host plant-induced scale mortality will be dictated to some extent by the initial health status of the host. A healthy and otherwise unstressed host plant may be able to withstand higher levels of herbivory before ceasing to grow or before plant parts begin dying. This aspect of resistance is influenced by edaphic components such as soil moisture and available nitrogen, and again these conditions vary on small spatial levels even within single host patches (unpublished data). If host plants are particularly susceptible to scale attack, we would expect host influences on scale population dynamics to be stronger.

In addition to direct effects on resident scales, host-plant responses to herbivory may influence the success of subsequent scale generations. Because high densities of scales cause plants to cease production of new leaves and stems, the quality and quantity of feeding sites for the subsequent generation can be altered in a density-dependent fashion. In previous studies we have found that *P. mesembryanthemi* crawlers have differential settling success on new leaves, mature leaves, and stems. Settling success of *P. mesembryanthemi* is highest on young leaves, moderate on mature leaves, and negligible on stems (Washburn and Frankie 1985). Since production of new leaves is curtailed at high scale densities, scale offspring may have difficulty finding a suitable settling site and may be forced to disperse to new plant patches.

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