Population Responses of *Pulvinariella mesembryanthemi* and *Pulvinaria delottoi* (Homoptera: Coccidae) to Nitrogen and Water Conditions of Their Host Plant

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ABSTRACT *Pulvinariella mesembryanthemi* (Vallot) and *Pulvinaria delottoi* Gill are closely related soft scales recently introduced to California, where they attack aizoaceous ground covers. Populations of both species were cultured on *Carpobrotus edulis* (L.) × *aequalateris* (Haw.) under greenhouse conditions to determine their responses to various fertilizer formulations and concentrations and five water regimes. We measured scale growth, survivorship, ovisac size, fecundity, and developmental time for each treatment population. There were no differences in population responses of *P. delottoi* to any water or fertilizer regime. Although all fertilizer treatments increased growth rate of *P. mesembryanthemi*, we found no significant correlation between amount or form of nitrogen addition and survivorship, ovisac size, or fecundity. Survivorship was similar among *P. mesembryanthemi* populations treated with different water regimes. However, as watering frequency increased, *P. mesembryanthemi* grew faster, ovisacs were larger, fecundity was greater, and developmental time was shorter.

KEY WORDS *Pulvinariella mesembryanthemi*, *Pulvinaria delottoi*, fertilizer, population dynamics, edaphic conditions

THE SUCCESS OF herbivorous insect populations is influenced by many chemical and physical attributes of their host plants. Although unifying theories relating plant characteristics to the success of herbivorous insects are rare, it is widely accepted that scarcity of usable nitrogenous compounds in the diet of many species is one of the major factors limiting their growth, development, and reproductive success (Rodriguez 1960, Southwood 1975, McNeill & Southwood 1978, White 1978). Supporting evidence for nitrogen limitation comes from two basic types of studies correlating the performance of herbivore populations with the nitrogen content of their foods. In the first type, levels of nitrogen in the host plant are augmented experimentally and changes in the developmental or reproductive rate, or both, of the herbivore population are observed (van Emden 1966, McClure 1977). Another group of studies compares insect populations feeding on several host individuals or different tissues within individuals having different amounts of available nitrogen. Typically, one or more population parameters are affected in such a way that the herbivore's intrinsic rate of increase is enhanced on tissues richer in usable nitrogenous compounds (Dixon 1970, McClure 1980a,b, Newberry 1980a, Port & Thompson 1980). Applied studies in this realm have direct corollaries in natural systems because they may elucidate fundamental mechanisms regulating herbivore populations with respect to the host plant.

Both ice plant scales and their aizoaceous host plants evolved in southern Africa (Brain 1920, DeLotto 1979, Gill 1979), and together they form a good model system for examining the effects of host-plant nutritional status on herbivore populations. Many of the host species are fast growing and easily rooted from small cuttings, making it possible to propagate virtually identical plants. They also tolerate a wide range of edaphic moisture and nutrient regimes that may have pronounced effects on the nutritional content of the host tissues. Responses of the scales are reasonably easy to observe because coccids are generally sessile after the first instar (crawler stage), and populations can be monitored accurately through the entire life cycle. Although male ice-plant scales are known, they are rare, and reproduction is parthenogenetic (Nur 1963, 1980, Gill 1979), thus eliminating the need to consider sexual differences in nutritional requirements and feeding effects.

In this study we examined how different fertilizer and water regimes affect the nutritional content of tissues of ice plants, *Carpobrotus* spp., and the population dynamics of two soft scales, *Pulvinariella mesembryanthemi* (Vallot) and *Pulvinaria delottoi* Gill, that feed on them. These imported scales were accidentally introduced into California, where they are significant pests of ornamental ground covers in the families Aizoaceae and Crassulaceae (Donaldson et al. 1978). Although the two species are now considered to be

in separate genera, they are very similar morphologically. The major life-history characteristic distinguishing the two scales is developmental time: under the same environmental conditions *P. mesembryanthemi* develops to maturity in about half the time required for *P. delottoi* (Gill 1979, Washburn & Frankie 1985).

Materials and Methods

First-instar *P. mesembryanthemi* and *P. delottoi* crawlers from greenhouse cultures were used for all fertilizer and watering experiments. We removed mature ovisacs from host plants and placed them in groups of 15–30 in glass petri dishes where crawlers could emerge. One hundred emerged crawlers <24 h old were collected from the dishes and transferred with a camel's-hair brush to each experimental plant. For each experiment the same ovisac source for crawlers was used for all plants in all treatments. Plants in all treatments in each experiment were infested on the same day when possible. For experiments where 2 d were required to infest all plants, identical numbers of plants (5–10 individuals) from each treatment were infested on each day.

Host-plant material consisted of terminal shoots (15–20 cm long) collected from a single, uninfested ornamental planting of *Carpobrotus edulis* (L.) × *aequalateris* (Haw.) (Aizoaceae) on the Berkeley campus, University of California. We planted shoots individually in a standard potting soil mix (50% sand/50% peat) in square plastic pots (70 by 70 mm, 60 mm deep). Plants were grouped by treatment and maintained in plastic trays in groups of 5–10 plants in the greenhouse for ≥3 wk before introduction of scale crawlers.

We conducted two basic types of experiments in which we altered the edaphic conditions of the host plants. For watering tests, we established five treatments that differed only in the frequency of watering (5-, 10-, 15-, 20-, and 25-d). All trays were watered weekly before introducing crawlers to allow root development, and all treatment trays were watered on the day crawlers were introduced. After infestation with crawlers, 200 ml of water were added to the trays containing the plants at intervals prescribed by the treatment. Plant trays were cultured in organdy cages in the greenhouse, where temperatures fluctuated between 22 and 38°C depending on the season. We conducted two water-regime experiments with *P. mesembryanthemi* and one experiment with *P. delottoi*.

For fertilizer experiments, we used two dosages (low and high) of each of three fertilizer formulations: ammonium sulfate (21-0-0; Occidental Chemical, Lathrop, Calif.), slow-release Nitroform (38-0-0; Boots Hercules Agrochemicals, Wilmington, Del.), and a complete fertilizer (14-14-7; Occidental Chemical, Lathrop, Calif.). The amount of fertilizer added in each treatment was adjusted so that each plant in the low-dosage treatment received the average equivalent of 0.12 g of nitrogen, and high-conc ntration plants received 0.36 g. Low-dosage treatments corresponded closely to rates recommended by the manufacturers. Weighed amounts of fertilizer were added to treatment trays in a 1,000-ml aqueous solution at the same time crawlers were added to the plants. Each fertilizer experiment also included a control population of plants that received no fertilizer. Two fertilizer experiments were performed with *P. mesembryanthemi* and one with *P. delottoi*.

We monitored scale growth for all experiments periodically by measuring randomly chosen scales to the nearest 0.5 mm on all surviving plants in all treatments. The sampling period for *P. mesembryanthemi* was 10 or 14 d, and that for the slower-growing *P. delottoi* was 21 d. For each sampling period, we also counted the number of scales in ovisac stage on each plant. When ≥25% of the surviving scale population in a treatment had formed ovisacs, we counted the surviving scales in that treatment and removed a random sample of ovisacs from each plant for fecundity counts. Because most scales that survive to the fourth instar reproduce successfully, survivorship counts taken at that time are a reasonably accurate assessment of the number of scales that will eventually reproduce (Washburn & Frankie 1985). For fecundity counts, we selected only expanded ovisacs that contained a full complement of eggs from which no crawlers had emerged. We recorded the length of each ovisac to the nearest 0.5 mm. Ovisacs were excised from their host plants on a thin slice of host tissue and secured in the center of a paper disk bordered by a Tangletrap (Tanglefoot, Grand Rapids, Mich.) barrier by placing a pin through the section of plant supporting the ovisac. Ovisacs were stored on racks in organdy-covered cabinets under greenhouse conditions. Fecundity was recorded by summing the number of crawlers that emerged and were entrapped on the Tangletrap and the number of dead crawlers that remained in the ovisac.

To assess levels of nitrogenous compounds in plant tissues, we measured concentrations of amino acids and soluble proteins in leaves and stems of *Carpobrotus* plants from the second *P. mesembryanthemi* water and fertilizer experiments. Assays were conducted when the experiments were terminated (i.e., at the end of one scale generation). These measures are preferable to those of total nitrogen content because free amino acids and amides are the main dietary source of nitrogen for aphids and scales (Auclair 1963). Samples were collected by making cross-sectional cuts through the tissues and pressing the cut plant surfaces onto filter paper strips (Whatman no. 1). Five spots from each plant were placed on a strip; we collected one spot sample from a cross section of the newest leaf pair, two samples from cross sections of the stem approximately one-third and two-thirds of the way up the stem from the soil surface

Table 1. Plant nitrogen levels, fertilizer regimes (experiment 2, *P. mesembryanthemi*)

Concn	Control	Complete (14-14-7)		Ammonium sulfate (21-0-0)		Slow release (38-0-0)	
		0.12[a]	0.36	0.12	0.36	0.12	0.36
Amino acid (μg/ml)[c] (n = 5)	295 ± 131a[b]	606 ± 157b	727 ± 140b	606 ± 161b	—	561 ± 115b	492 ± 168b
Soluble protein (mg/ml)[d] (n = 5)	0.65 ± 0.30a	2.86 ± 1.63bc	1.31 ± 1.26b	1.30 ± 0.96b	—	3.37 ± 0.42c	3.62 ± 0.52c

Means in the same row followed by the same letter are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test).

[a] Grams of nitrogen per plant added in an aqueous solution to the treatment tray.

[b] Mean ± SD.

[c] Amino-acid concentrations expressed as equivalents of histidine in an aqueous solution.

[d] Soluble protein concentrations expressed as equivalents to albumin protein in an aqueous solution.

to the apex of the plant, and two samples from cross sections of mature leaves. We made a second, identical spot strip immediately by making a second cross section within 1 mm of the initial cut and following the same procedures described above. One of the spot strips was used for amino acid analysis, and the second was used for analysis of soluble proteins. After the plant fluids on the filter paper strips had dried, they were stored in a freezer (−10°C) until chemical analysis.

Amino-acid concentrations of plant tissues were determined by placing ninhydrin reagent on each spot. Color changes in spots were complete after 24 h, at which time they were compared with a dilution series of histidine solutions spotted on filter paper and stained with ninhydrin. The second spot series for each plant was treated in a similar fashion with bromophenol blue to determine the concentration of soluble proteins (for methods see Baker & Baker [1973, 1975]). Levels of soluble proteins were determined by comparing the color of the stained spots after 24 h with a dilution series of bovine albumin protein. We calculated the level of soluble proteins and amino acids in *Carpobrotus* plants by converting the five values per plant to equivalents of albumin and histidine concentration, respectively, and computing individual means for each plant. We computed average values from the five measurements per plant because we found scales feeding on leaves of different ages. Individual mean values of amino-acid and soluble nitrogen concentrations for all plants in a treatment were averaged to obtain the treatment means reported here.

In statistical analyses, we employed standard analysis of variance (ANOVA) (Sokal & Rohlf 1969) techniques and Duncan's (1955) multiple range test.

Results

Nitrogen Content of Plant Tissues and Scale Feeding. The spot technique allowed us to evaluate the partitioning of amino acids and soluble proteins within leaves and stems. Spots dried quickly, leaving the nonvolatile tissue fluids in place, and phenolic compounds stained these spots brown, producing a clear outline of the tissues in cross section. Leaves of *Carpobrotus* are triangular in cross section, and both scale species feed predominantly on a network of vascular bundles underlying the epidermis and mesophyll tissues. Because scale feeding is restricted to the vascular network, we used only the amino-acid and soluble-protein measurements from that region to calculate nitrogen concentration for individual plants. A similar vascular network occurs beneath the epidermis of the green stems. Although both stems and leaves have major central vascular bundles, these are generally too deeply embedded to be reached by the scales' stylets, and we have not found scales feeding in that area (Washburn &

Table 2. Plant nitrogen levels, water regimes (experiment 2, *P. mesembryanthemi*)

Concn	Frequency of watering				
	5-d	10-d	15-d	20-d	25-d
Amino acid (μg/ml)[c] (n = 8)	485 ± 184a[a]	538 ± 105a	511 ± 126a[b]	572 ± 88a	550 ± 85a
Soluble protein (mg/ml)[d] (n = 8)	4.21 ± 0.83a	4.02 ± 0.73a	4.07 ± 0.74a	3.83 ± 0.67ab	3.03 ± 0.49b

Means in the same row followed by the same letter are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test).
[a] Mean ± SD.
[b] n = 7.
[c] Amino acid concentrations expressed as equivalents of histidine in an aqueous solution.
[d] Soluble protein concentrations expressed as equivalents of albumin protein in an aqueous solution.

Frankie 1985). The central core of the succulent leaves of *Carpobrotus* is devoted primarily to water storage, an adaptation to arid habitats. This region of the leaf contains extremely low levels of amino acids and soluble proteins but is rich in phenolic compounds and crystals of calcium oxalate (J.O.W., unpublished data).

Mean nitrogen levels for *Carpobrotus* plants grown under the various fertilizer and water regimes appear in Tables 1 and 2. Amino-acid concentrations did not differ significantly among the five fertilizer regimes for which data are available, but all were significantly higher than in the control plants, which received no fertilizer. Similarly, the concentration of soluble proteins in control plants was significantly lower than the levels in all the fertilizer treatments. Although soluble protein levels differed among the fertilizer treatments, plants in treatments that received an average of 0.36 g of nitrogen per plant did not exhibit consistently higher levels of soluble protein than plants receiving 0.12 g. Levels of soluble proteins in the slow-release treatments were equivalent to those in the low-dosage complete-formulation treatment and higher than those in both ammonium-sulfate treatments.

Concentrations of amino acids in tissues of *Carpobrotus* plants grown under different water regimes were equivalent, but concentrations of soluble proteins differed significantly (Table 2). Overall, levels of amino-acid concentrations in plants from the different water regimes were comparable with levels from plants receiving fertilizer additions, but concentrations of soluble proteins from plants in the latter experiment were considerably higher. The concentration of soluble proteins increased with an increase in the frequency of watering up to 15–20 d (Table 2). Tensiometer measurements from soil surrounding plants in the 5-d regime indicated that the substrate was continuously 100% saturated with water.

Population Responses of *P. mesembryanthemi*. Population characteristics of *P. mesembryanthemi* reared on plants in the two fertilizer experiments are shown in Tables 3 and 4. In both experiments, survivorship, ovisac size (=adult size), and fecundity did not vary in any systematic way among fertilizer formulations or from the control. Scale-size data reported in these and later tables represent the average size of immature scales during the last sample period before ovisacs appeared in any of the treatment populations. In both experiments, scales growing in high-concentration fertilizer treatments tended to be smaller than corresponding scales in low-concentration treatments, but in only two cases (Table 3, ammonium sulfate; Table 4, slow-release) were these differences significant. Size differences may have resulted from stress conditions experienced by plants in the high-concentration regimes.

The average ovisac sizes and fecundities in the second fertilizer experiment were larger than those in the first experiment because of the difference in rearing temperatures. In general, developmental time, ovisac size, and fecundity of *P. mesembryanthemi* are increased at lower temperatures (Washburn & Frankie 1985). All populations within each experiment described in this report developed simultaneously, but different replicates were run in different seasons over a period of 2 yr. The first fertilizer experiment was conducted over 3 mo beginning in June; the second experiment was begun in January and continued through March. Because greenhouse temperatures fluctuated seasonally, averages cannot be compared between experiments.

Although ovisac size did not vary among treatments with respect to type or amount of nitrogen addition, the mean size of immature scales on control plants was significantly smaller than that of scales on all fertilizer treatments in experiment 1 (Table 3) and on low-fertilizer treatments in experiment 2 (Table 4). Differences in scale size among treatments in Tables 3 and 4 reflect differences in the developmental rates of the populations. This is further illustrated by the percentages of each fertilizer-treatment population in ovisac stage during the sample periods (Fig. 1 A and B). For both replicates, at any sample period when ovisacs were present, there was a greater percentage reproducing in the treated populations than in the control populations. The only exception to this trend was in the second experiment, where the percentages of reproducing scales in control and high-dosage slow-release treatments were similar (Fig. 1B). In summary, the principal effect of fer-

Table 3. Population response of *P. mesembryanthemi* to different fertilizer regimes (experiment 1)

Population variable	Control	Complete (14-14-7)		Ammonium sulfate (21-0-0)		Slow release (38-0-0)	
		0.12[a]	0.36	0.12	0.36	0.12	0.36
Scale survivorship (%) ($n = 5$)[c]	39.6 ± 10.2b[b]	63.0 ± 13.7a	61.3 ± 10.9a	60.7 ± 4.1a	48.0 ± 12.0ab	60.3 ± 21.8a	53.9 ± 15.8ab
Scale size (mm) ($n = 35$)[d]	1.24 ± 0.33a	2.57 ± 0.49b	2.41 ± 0.46bc	2.57 ± 0.54b	2.17 ± 0.50c	2.40 ± 0.36bc	2.27 ± 0.60c
Ovisac size (mm) ($n = 28$)	3.34 ± 0.36ab	3.09 ± 0.39c	3.34 ± 0.36ab	3.29 ± 0.40bc	3.46 ± 0.33ab	3.55 ± 0.39a	3.34 ± 0.45ab
Fecundity ($n = 28$)	538 ± 239ab[e]	477 ± 238b	628 ± 203a[f]	462 ± 221b	499 ± 245ab	578 ± 300ab	470 ± 264b

Means in the same row followed by the same letter are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test).
[a] Grams of nitrogen per plant added in an aqueous solution to the treatment tray.
[b] Mean ± SD.
[c] No. plants per treatment. In all other cases n refers to the number of scales measured for means.
[d] Scale size 45 d after infestation.
[e] $n = 30$.
[f] $n = 27$.

Table 4. Population responses of *P. mesembryanthemi* to different fertilizer regimes (experiment 2)

Population variable	Control	Complete (14-14-7)		Ammonium sulfate (21-0-0)		Slow release (38-0-0)	
		0.12[a]	0.36	0.12	0.36	0.12	0.36
Scale survivorship (%) ($n = 5$)[c]	48.8 ± 12.8ab[b]	53.4 ± 15.4a	39.4 ± 3.9bc	58.6 ± 4.8a	61.6 ± 5.8a	51.6 ± 3.4ab	58.4 ± 11.9a
Scale size (mm) ($n = 50$)[d]	2.86 ± 0.60c	3.11 ± 0.44ab	3.07 ± 0.52abc	3.24 ± 0.54a	3.06 ± 0.54abc	3.29 ± 0.65a	2.88 ± 0.51bc
Ovisac size (mm) ($n = 30$)	3.93 ± 0.39a	3.40 ± 0.34b	3.38 ± 0.43b	3.62 ± 0.45bc	3.45 ± 0.30b	3.45 ± 0.24b	3.83 ± 0.48ac
Fecundity ($n = 30$)	1,260 ± 498a	801 ± 458b	518 ± 311c	805 ± 389b	765 ± 407b	975 ± 432b	1,360 ± 541a

Means in the same row followed by the same letter are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test).
[a] Grams of nitrogen per plant added in an aqueous solution to the treatment tray.
[b] Mean ± SD.
[c] No. plants per treatment. In all other cases n refers to the number of scales measured for means.
[d] Scale size 70 d after infestation.

Table 5. Population responses of *P. mesembryanthemi* to different water regimes (experiment 1)

Population variable	5-d	10-d	15-d	20-d	25-d
Scale survivorship (%) ($n = 5$)[b]	39.8 ± 10.1b[a]	58.6 ± 5.9a	—	44.0 ± 8.2b	53.4 ± 13.9ab
Scale size (mm)[c] ($n = 50$)	2.82 ± 0.55a	2.40 ± 0.38b	2.05 ± 0.44c	1.98 ± 0.55c	1.93 ± 0.31c
Ovisac size (mm) ($n = 30$)	3.17 ± 0.42a	2.98 ± 0.44ab	3.03 ± 0.35ab	2.88 ± 0.39b	2.68 ± 0.28c
Fecundity ($n = 30$)	507 ± 220a	453 ± 242a	420 ± 214a	282 ± 131b	223 ± 153b

Means in the same row followed by the same letter are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test).
[a] Mean ± SD.
[b] No. plants per treatment. In all other cases n refers to the number of scales measured for means.
[c] Scale size 45 d after infestation.

tilizer addition on *P. mesembryanthemi* populations was to shorten the development time by accelerating the growth rate.

Responses of *P. mesembryanthemi* populations reared on host plants experiencing different water regimes are shown in Tables 5 and 6. In the first experiment, there were significant differences in survivorship, but these differences did not correspond with watering frequency. Three of the plants in the 15-d regime from this experiment died, so scale survivorship was not evaluated. In the second experiment there were no significant differences in scale survivorship among the five water regimes, and, overall, this population variable appeared to be independent of the host plant's water regime.

Scale size, ovisac size, and fecundity of *P. mesembryanthemi* were positively related to frequency of watering in both experiments. Developmental time of scales was progressively longer as the interval between watering increased; this was reflected in lower percentages of reproducing scales (Fig. 1 C and D). In addition to reproducing earlier, scales reared on plants that were watered more frequently grew larger, formed larger ovisacs, and produced more crawlers (Tables 5 and 6). In both experiments the average fecundity of scales from 25-d treatments was about half the fecundity of scales from the 5-d treatments, but the sharpest decline in the fecundity trend occurred between the 15- and 20-d treatments.

Population Responses of *P. delottoi*. Populations of *P. delottoi* (Table 7) responded differently than those of *P. mesembryanthemi* to the fertilizer treatments (Tables 3 and 4). Scale survivorship was lowest on plants treated with low and high concentrations of the complete fertilizer, primarily because of declining host-plant quality. These treatment plants were somewhat withered and yellow. Some leaves on these plants died, and, in these situations, resident scales usually died, resulting in lower survivorship. All plants and scales in the high-dosage ammonium-sulfate treatment died, apparently from the combined stress of the fertilizer and scale feeding. Scale size did not differ significantly among any of the treatments at the last sample period before the first appearance of ovisacs (Table 7), and we did not observe a lower percentage of scales in the ovisac stage when comparing control and treatment populations (Fig. 2A). Finally, neither differences in ovisac size nor fecundity corresponded with nitrogen enrichment.

Survivorship of *P. delottoi* differed significantly among the water regimes (Table 8), and these differences appeared to result from changes in host-plant quality. Highest scale survivorship occurred on 15- and 20-d plants; lower survivorship was recorded on plants receiving either more or less frequent waterings. Although we did not quantify individual mortality factors from each regime, several aspects of plant quality that relate to scale success were easily observed. Plants that were

Table 6. Population responses of *P. mesembryanthemi* to different water regimes (experiment 2)

Population variable	5-d	10-d	15-d	20-d	25-d
Scale survivorship (%) ($n = 8$)[b]	55.6 ± 8.7a[a]	47.6 ± 16.4a	57.6 ± 14.2a	60.6 ± 9.9a	60.7 ± 7.4a
Scale size (mm)[c] ($n = 40$)	3.32 ± 0.70a	3.27 ± 0.60a	2.79 ± 0.58b	2.44 ± 0.23c	2.57 ± 0.53bc
Ovisac size (mm) ($n = 30$)	3.77 ± 0.50a	3.52 ± 0.44bc	3.55 ± 0.44ab	3.30 ± 0.41cd	3.22 ± 0.49d
Fecundity ($n = 30$)	870 ± 322a	809 ± 345a[d]	855 ± 360a	510 ± 256b	499 ± 310b[e]

Means in the same row followed by the same letter are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test).
[a] Mean ± SD.
[b] No. plants per treatment. In all other cases n refers to the number of scales measured for means.
[c] Scale size 55 d after infestation.
[d] $n = 28$.

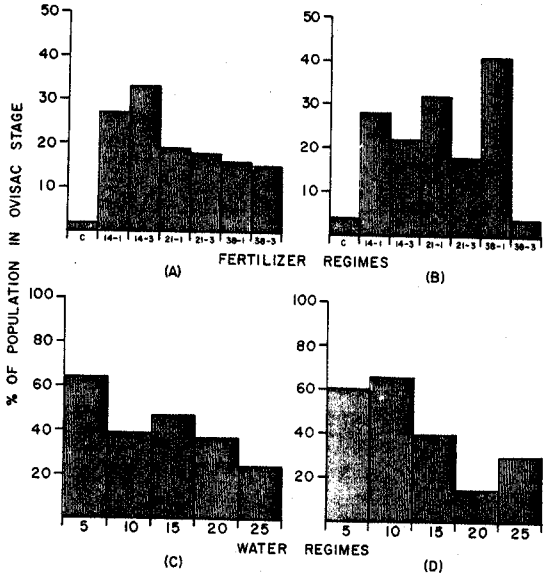

Fig. 1. Percentage of surviving *P. mesembryanthemi* populations in ovisac stage at the last sample period for the two fertilizer experiments (A, experiment 1; B, experiment 2) and two watering experiments (C, experiment 1; D, experiment 2). In A and B, 14-1, 21-1, and 38-1 are low-concentration treatments, and 14-3, 21-3, and 38-3 are high-concentration fertilizer treatments. Numbers for the water regimes indicate the number of days between waterings.

watered every 5 d were severely declining from water stress at the termination of the 167-d experiment. On most of these plants, <25% of the foliage was still green and healthy. Similarly, 25-d plants were stressed by low soil moisture, with many leaf surfaces shriveled and dying, and on these plant tissues scale mortality was very high. Host-plant decline was less of a factor in *P. mesembryanthemi* experiments because the generation time (=duration of the experiment) was shorter.

Surviving populations of *P. delottoi* were unresponsive to different water regimes experienced by their hosts (Table 8). Although average fecundities were not determined for these scale populations, both the average size of ovisacs and of immature scales did not differ significantly among the treatments. Throughout this experiment we found no correspondence between scale size and frequency of watering. This contrasts with *P. mesembryanthemi*, which grew faster, grew larger, and ultimately produced more crawlers as soil moisture was increased.

Discussion

The hypothesis that sap-feeding insects are generally favored by an increase in the soluble nitrogen component of their food is supported by our experimental data from populations of *P. mesembryanthemi* reared on fertilizer-enriched plants. Our manipulations with different fertilizer formulations clearly enhanced the availability of soluble proteins and amino acids in the feeding tissues, and *P. mesembryanthemi* responded by developing at a faster rate. Because amino acids are a main dietary source of nitrogen for aphids and scales, *P. mesembryanthemi* may have responded to the enhanced levels of these compounds in the fertilizer regimes. In similar studies, Dixon (1970) found that free amino-acid concentrations were the major limiting factor in the diet of the sycamore aphid, *Drepanosiphum platanoides*. Similarly, McClure (1977, 1980a) found higher survivorship, faster developmental rates, and greater fecundities in the elongate hemlock scale, *Fiorinia externa* Ferris, feeding on host plants receiving fertilizer additions.

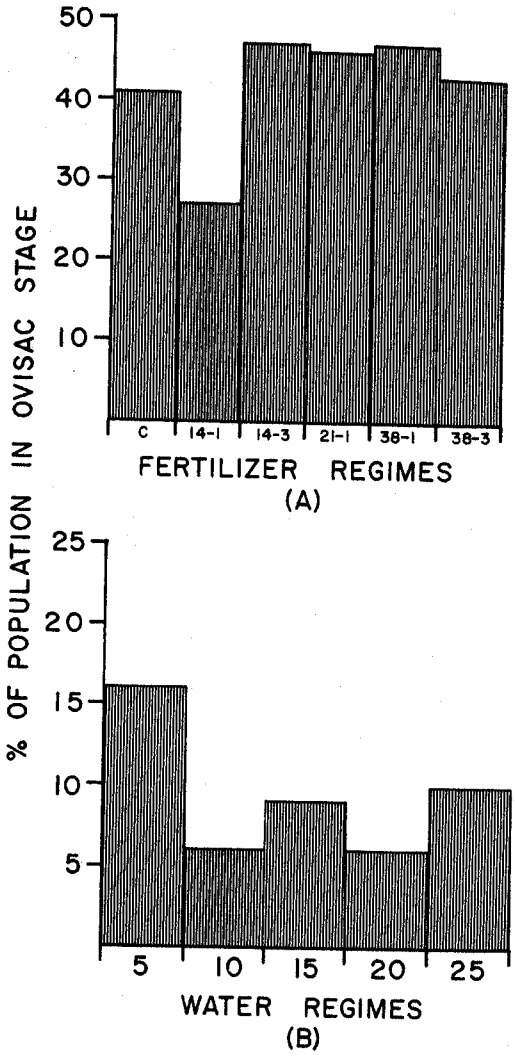

Fig. 2. Percentage of surviving *P. delottoi* in ovisac stage at the last sample period for the fertilizer (A) and watering experiments (B). See Fig. 1 for explanation of legends.

Our data from high-concentration fertilizer treatments suggest that excessive fertilization is deleterious to host plants, resulting in poorer population performance of *P. mesembryanthemi*. In some cases where fertilizer burn was observed on *Carpobrotus*, there was an obvious negative effect on scales residing on these declining tissues. A general trend of slower developmental rates in high-concentration treatments was evident in the second fertilizer experiment by the lower proportions of reproducing *P. mesembryanthemi* in high versus low concentrations for all three formulations (Fig. 1B). It has been suggested that phloem saps with high solute concentrations are detrimental to scale success, particularly in the early instars (Priesner 1938, Flanders 1970), and this can influence the distribution of herbivores among hosts. For example, Newberry (1980b) proposed that distribution of the coccid *Icerya seychellarum* (Westwood) among hosts may be governed by osmotic constraints of the phloem sap; host trees growing near sea water had lower water potentials and supported fewer scales than trees growing farther inland. Because high nitrogen would increase osmotic concentrations, our results are compatible with this hypothesis, but because we did not measure solute concentrations, we cannot sort out the effects of osmotic relations from those of general plant stress.

Population responses of *P. mesembryanthemi* to different water regimes were more striking than responses to fertilizer addition. Scales responded to more frequent watering of their host plants by growing at faster rates and ultimately producing larger ovisacs containing more crawlers. More frequent watering altered the nutritional status of the host plant by increasing concentrations of soluble protein but not of free amino acids. If amino acids are the principal nitrogenous compounds essential for coccid development, we cannot explain the performance of *P. mesembryanthemi* populations based on total levels of these compounds in the tissues.

More likely, the direct effects of the water regimes, mediated through turgor pressures in the phloem, produced the changes in scale performance. Although sap feeders possess cibarial pumps for withdrawing plant fluids through their stylets, much of the liquid entering the insect is a result of the turgor pressure exerted in the vascular bundles. This has been demonstrated empirically for aphids in which the mouthparts have been severed at the junction with the body. Phloem sap continues to flow from the cut stylets that maintain contact with the vascular elements, and this technique can be used to assess contents of phloem elements (Mittler 1953, 1957). For honeydew-secreting aphids and scales, feeding rates can be estimated from the amount of honeydew produced, because these anal secretions are a direct measure of the volume of liquid food passing through the gut. In our experiments with *P. mesembryanthemi*, we

Table 7. Population responses of *P. delottoi* to different fertilizer regimes

Population variable	Control	Complete (14-14-7)		Ammonium sulfate (21-0-0)		Slow release (38-0-0)	
		0.12[a]	0.36	0.12	0.36	0.12	0.36
Scale survivorship (%) ($n = 5$)[c]	26.4 ± 15.0a[b]	12.2 ± 17.0b	8.4 ± 12.3b	20.0 ± 19.3ab	—	22.2 ± 11.9a	34.2 ± 21.7a
Scale size (mm) ($n = 30$)[d]	2.45 ± 0.40a	2.43 ± 0.37a	2.59 ± 0.33a	2.54 ± 0.30a	—	2.53 ± 0.31a	2.45 ± 0.27a
Ovisac size (mm)	3.45 ± 0.31a ($n = 29$)	3.45 ± 0.16a ($n = 10$)	3.42 ± 0.30a ($n = 30$)	3.25 ± 0.26b ($n = 20$)	—	3.28 ± 0.35b ($n = 26$)	3.57 ± 0.19a ($n = 7$)
Fecundity	359 ± 130a ($n = 29$)	359 ± 190a ($n = 9$)	320 ± 138a ($n = 30$)	248 ± 126b ($n = 17$)	—	262 ± 120ab ($n = 26$)	326 ± 96a ($n = 7$)

Means in the same row followed by the same letter are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test).
[a] Grams of nitrogen per plant added in an aqueous solution to the treatment tray.
[b] Mean ± SD.
[c] No. plants per treatment. In all other cases n refers to the number of scales measured for means.
[d] Scale size 122 d after infestation.

Table 8. Population responses of *P. delottoi* to different water regimes

Population variable	5-d	10-d	15-d	20-d	25-d
Scale survivorship (%) (n = 10)[b]	5.7 ± 6.9b[a]	8.1 ± 7.1b	16.0 ± 11.3a	12.9 ± 6.0ab	6.9 ± 7.4b
Scale size (mm)[c] (n = 30)	2.27 ± 0.52a	2.18 ± 0.40a	2.21 ± 0.28a	2.23 ± 0.34a	2.21 ± 0.39a
Ovisac size (mm)	2.89 ± 0.33a (n = 9)	2.80 ± 0.58a (n = 32)	3.07 ± 0.47a (n = 27)	2.82 ± 0.34a (n = 39)	3.85 ± 0.35a (n = 31)

Means in the same row followed by the same letter are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test).
[a] Mean ± SD.
[b] No. plants per treatment. In all other cases n refers to the number of scales measured for means.
[c] Scale size 145 d after infestation.

observed greater honeydew production from scales growing on plants watered more frequently. Increasing the turgor pressure has the effect of passing more liquid food through the gut of the sap-feeding insect. Thus, potentially limiting compounds may be provided in greater amounts, allowing for faster growth rates, enhanced fecundity, etc. Because we measured overall levels of soluble proteins and amino acids, we cannot identify either the specific compounds responsible for superior performance or the relative importance of turgor pressure versus the physiological consequences of changing water regimes on the nutritional status of host-plant tissues. The influences of these independent factors could be identified using artificial membranes and media (Mittler & Dadd 1962). Unfortunately, attempts to rear scale insects on artificial diets have not been successful (Auclair 1963; T. Mittler, personal communication).

Despite changes in levels of nitrogenous compounds in host-plant tissues with different water and fertilizer treatments, populations of *P. delottoi* failed to respond in any of the population parameters we measured. Population performance of the scales was similar on plants under all soil-moisture conditions and all fertilizer treatments. Because this species grows more slowly than *P. mesembryanthemi*, host plants must persist for longer times in all treatments. By the end of the water-regime experiment, plants at both extremes of the treatment spectrum (5- and 25-d) were declining and ultimately died. Thus, our water-stress range spanned the survival limits of the host plants, and within that range *P. delottoi* was unresponsive.

What accounts for the differential responses of these two closely related species to the nutritional environment of the host? Our results suggest that *P. mesembryanthemi* and *P. delottoi* differ physiologically in their utilization of ingested food. Further evidence is provided by significant differences between the two scale species in settling preferences and abilities on leaves of different ages (Washburn & Frankie 1985). Although we were able to trace feeding stylets of both *P. delottoi* and *P. mesembryanthemi* to the vascular bundle network beneath the epidermis, we did not examine individual cells in which stylets terminated. It is unlikely, however, that there is feeding segregation between the two species because analyses of their honeydews have shown similar total concentrations of amino acids dominated by glutamine and proline (J.O.W.; unpublished data).

One hypothesis is that *P. delottoi* and *P. mesembryanthemi* may possess distinct endosymbiotic assemblages that determine their ability to utilize host-plant constituents. Endosymbiotic microorganisms are common associates of sap-feeding insects (Auclari 1963, Miller & Kosztarab 1979), and Nur (1972) reported that races of some morphologically identical soft scales of the genus *Lecanium* harbor different endosymbionts. However, it remains to be seen whether this could account for the different population responses of ice-plant scales.

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