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SANTA CRUZ ISLAND—REVISITED. SEQUENTIAL PHOTOGRAPHY RECORDS THE CAUSATION, RATES OF PROGRESS, AND LASTING BENEFITS OF SUCCESSFUL BIOLOGICAL WEED CONTROL

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ABSTRACT

Sequential photography once or twice-yearly has been used to record the results of biological control of the prickly pear cacti, *Opuntia littoralis* (Engelmann) Cockerell, *O. oricola* Philbrick, and their hybrids, by the cochineal insect, *Dactylopius opuntiae* Cockerell, on Santa Cruz Island off the coast of southern California. Photographic evidence of *D. opuntiae*-induced plant mortality, different degrees of host-plant susceptibility to cochineal insect injury and the long-term benefits of this program are presented. Progress has slowed in recent years as an ever greater proportion of the surviving prickly pear cacti is comprised of the less susceptible species, *D. oricola*, and as a result of added predation on *D. opuntiae* by the entomophagous moth, *Laetilia coccidivora* (Comstock), which first reached Santa Cruz Island during the early 1970s.

The use of photography to evaluate biological weed control programs is discussed, urging publication of multiple, mutually supportive, before-and-after photographic sequences from different locations, rather than sole reliance on a single, 'best', though reportedly representative, sequence of photographs.

INTRODUCTION

The biological control of prickly pear cacti on Santa Cruz Island, California, a project begun by the late Prof. H.S. Smith in 1939, is historically significant as the longest-standing biological weed control program in North America, as the only example to date of successful biological control of a native weed with purposely introduced insects, as well as one of the few examples of successful biological control of prickly pear cacti in North America (Goeden *et al.* 1967). In the mid-1960s, during the height of cactus destruction on Santa Cruz Island by the cochineal insect, *Dactylopius opuntiae* Cockerell (Hemiptera-Homoptera: Dactylopiidae), sequential photography was begun that now provides a unique, useful, qualitative record of the substantial degree of biological control that has been realized to date.

Certain before-and-after photographs have been used (and in some cases re-used, repeatedly) to illustrate the spectacular results that, fortunately, sometimes attend biological weed control efforts; e.g., prickly pear cacti (*Opuntia* spp.) in Australia (Dodd 1927, 1940, Sweetman 1936, Leach 1940, De Bach 1974, DeBach *et al.* 1976) and Klamath weed (St. John's wort, *Hypericum perforatum* L.) in California (Huffaker 1964, 1967, Huffaker and Kennett 1969, DeBach and Huffaker 1971, Van den Bosch and Messenger 1973, DeBach *et al.* 1976). We herein present mostly unpublished, photographic sequences depicting the biological control of prickly pear cacti on Santa Cruz Island, as well as brief commentary on the current status of this program.

MATERIALS AND METHODS

Beginning in 1963, selected individual plants and clumps of the prickly pear cacti, *Opuntia littoralis* (Engelmann) Cockerell, *O. oricola* Philbrick, and their hybrids, located at various points throughout Santa Cruz Island were photographed each spring (May or June) and/or fall (September or October). Fall

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photography was preferred because of the less foggy weather and the removal of grasses and other obscuring vegetation by grazing cattle during the spring and summer.

Plants initially were selected for photography, not on the presence or abundance of *D. opuntiae*, but rather for their accessibility via four-wheel drive vehicle, their location at some distance from other photographic sites, and by the visual composition of the photograph involved. Whenever possible, photographs included a recognizable background, landmark, or semi-permanent feature; e.g., a fenceline, post, or tree, that provided visual continuity during succeeding years. To further assure this continuity, 30-cm long, metal stakes fashioned of 2.3-cm wide, 3-mm thick, angle iron were driven firmly into the ground at the point from which each initial photograph was taken. A 4.7-cm diameter, metal washer was welded across the top of each stake to cover any sharp-angled edges. This construction, the low height, and bright orange colour of these stakes reduced their hazard to cattle, horses, and man, yet facilitated site relocation. The stakes were repainted *in situ* every two years. Each time a photograph was taken, its composition and that of the initial photograph was matched as closely as possible through the camera viewfinder. Notes on cactus condition and *D. opuntiae* abundance, illustrated by close-up photography, were taken on each sample date and later recorded in brief on the frames of the processed photographic slides. To date, 30 sites are monitored annually in this manner.

RESULTS AND DISCUSSION

Figures 1 to 6 depict host-plant destruction achieved by the addition of *D. opuntiae* to the rather small guild of specialized, phytophagous insects already associated with the prickly pear cacti native to Santa Cruz Island (Goeden *et al.* 1967). This cochineal insect, though native to southern California, was introduced to Santa Cruz Island from Hawaii, where it had been colonized with material supplied by Australians, who, in turn, first introduced it from Mexico in 1928 (Goeden *et al.* 1967, Goeden 1978). During these circuitous travels, *D. opuntiae* had escaped from its natural enemies, those predators that attack it in its natural range from southern cismontane California southward into Mexico: *Sympherobius barberi* (Banks) (Neuroptera:Hemerobiidae), *Leucopis* sp. (Diptera:Agromyzidae), *Laetilia coccidivora* (Comstock) (Lepidoptera:Pyralidae), and *Hyperaspis taeniata significanus* Casey (Coleoptera: Coccinellidae). In 1961, 10 years after the introduction of *D. opuntiae, S. barberi* and *Leucopis* sp. were found attacking the cochineal insects at several locations (Goeden *et al.* 1967). However, these predators apparently had little deleterious effect on *D. opuntiae* as a biological control agent, for as illustrated by Figures 1 to 6, cactus destruction by *D. opuntiae* continued unabated and frequently resulted in complete host-plant mortality. Furthermore, as also shown by Figures 1 and 4 to 6, biological control has lasted up to the present time, which illustrates another advantage of the method; i.e., the 'permanent' weed control that it may afford.

Different degrees of intraspecific, as well as interspecific, host-plant sensitivity of *D. opuntiae* attack, evidenced as differential rates of cactus destruction, were indicated by these photographic sequences. For example, *D. opuntiae* took eight years to kill completely the *O. oricola* pictured in Figure 1; whereas, the *O. oricola* illustrated in Figure 6 was destroyed in less than five years. The

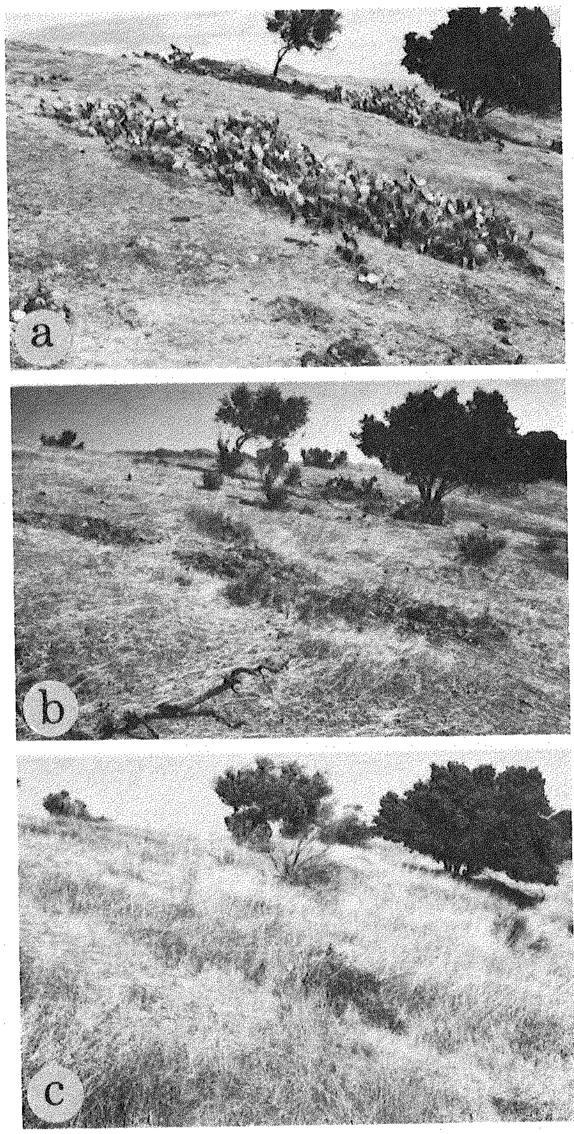

Figure 1. Destruction of *Opuntia oricola* by *Dactylopius opuntiae* on Santa Cruz Island, California. a. 1963, b. 1971 (all dead), c. 1978.

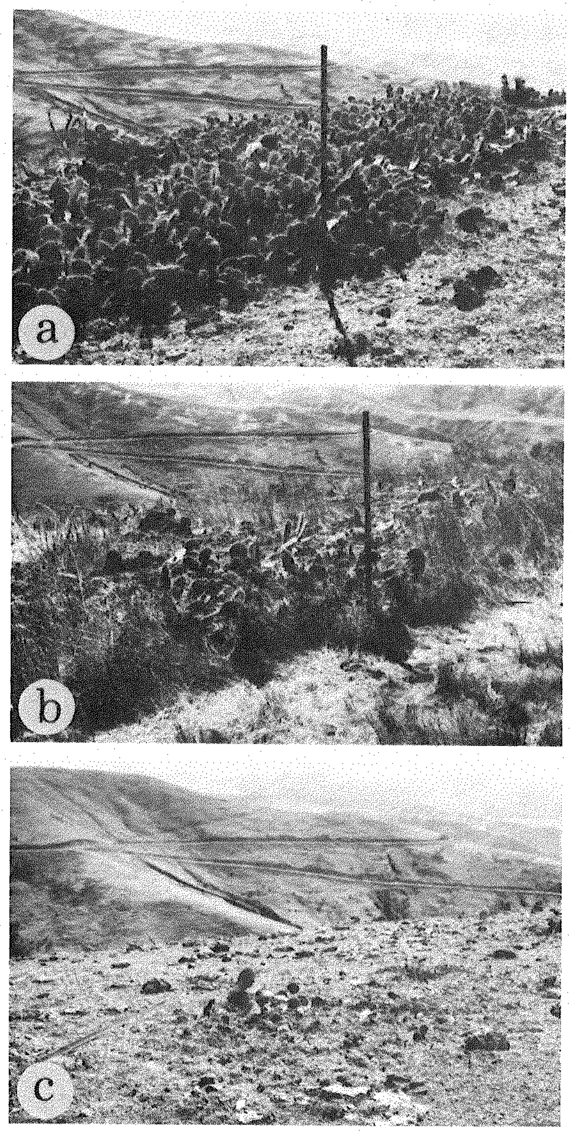

Figure 2. Destruction of *Opuntia oricola* by *Dactylopius opuntiae* on Santa Cruz Island, California. a. 1964, b. 1966, c. 1972.

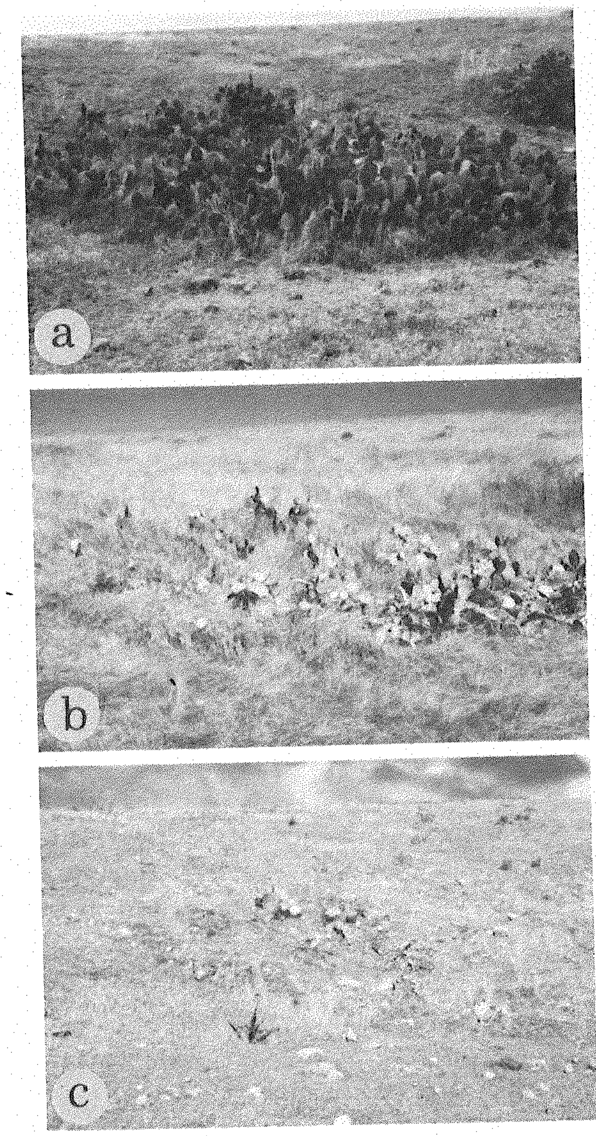

Figure 3. Destruction of *Opuntia oricola* by *Dactylopius opuntiae* on Santa Cruz Island, California. a. 1964, b. 1966, c. 1972.

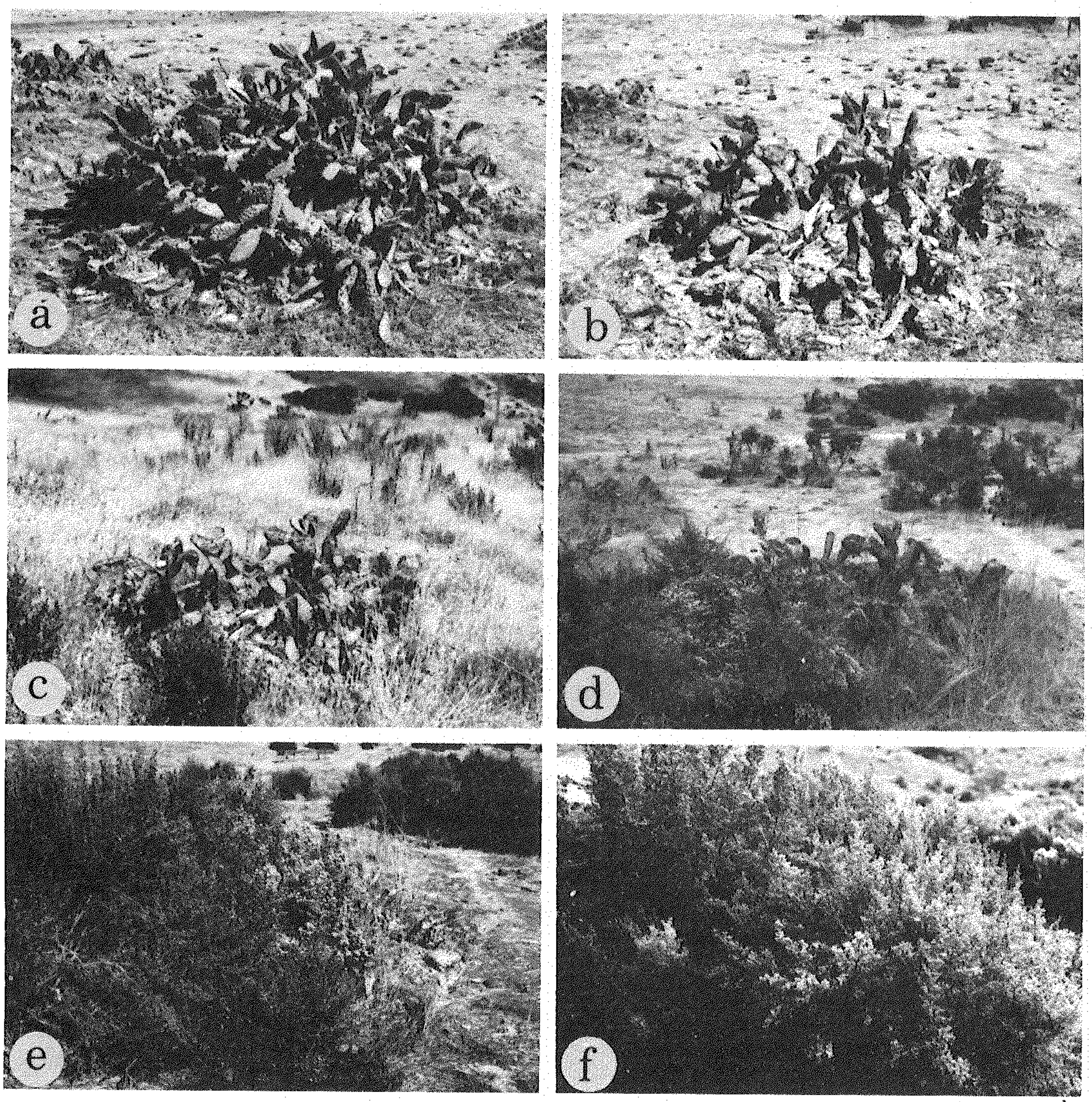

Figure 4. Destruction of *Opuntia littoralis* by *Dactylopius opuntiae* on Santa Cruz Island, California. a. 1964, b. 1965, c. 1966 (all dead), d. 1967, e. 1969, f. 1972.

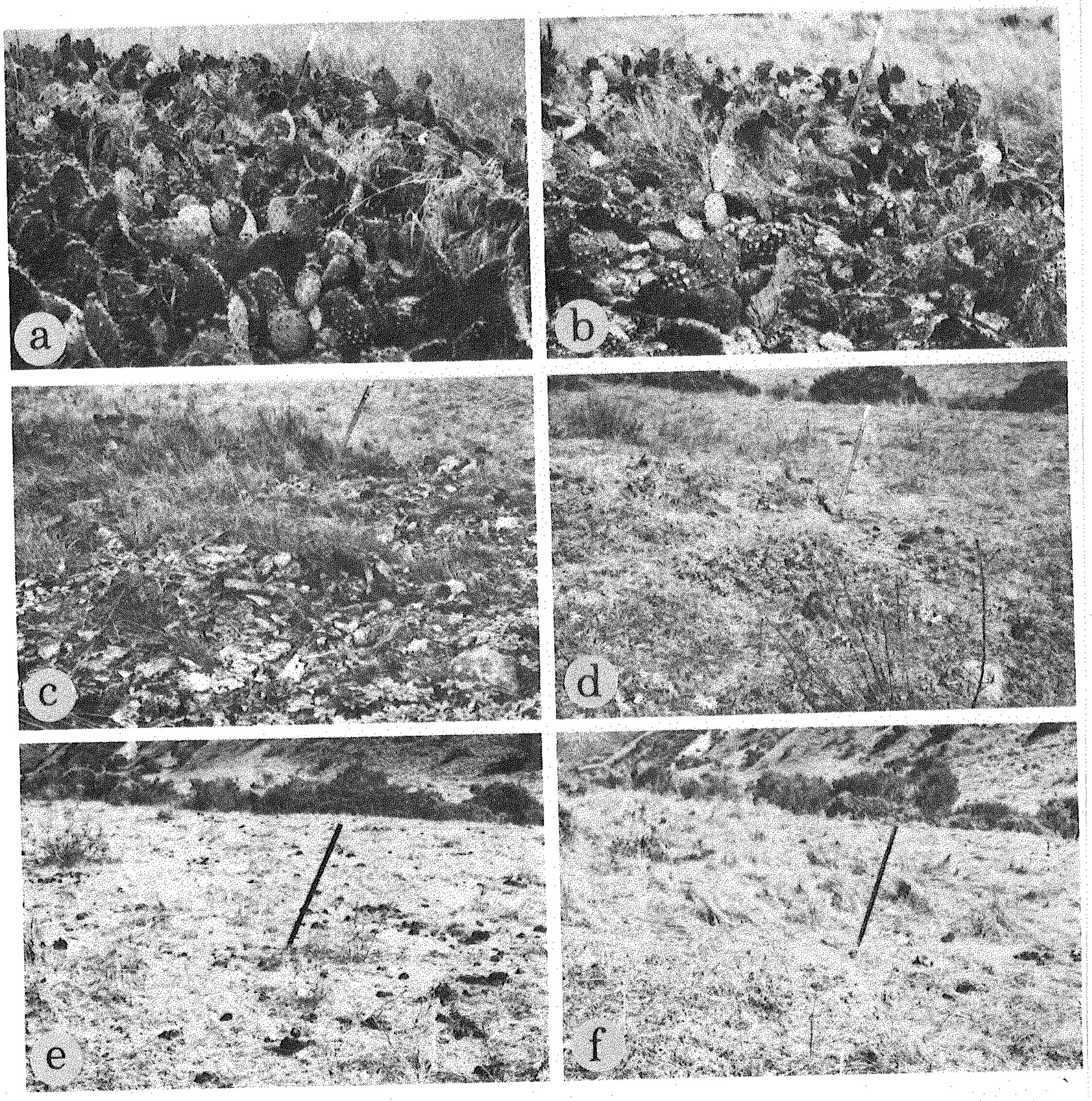

Figure 5. Destruction of *Opuntia littoralis* by *Dactylopius opuntiae* on Santa Cruz Island, California. a. May 1965, b. late-September 1965, c. 1967, d. 1969, e. 1975, f. 1978.

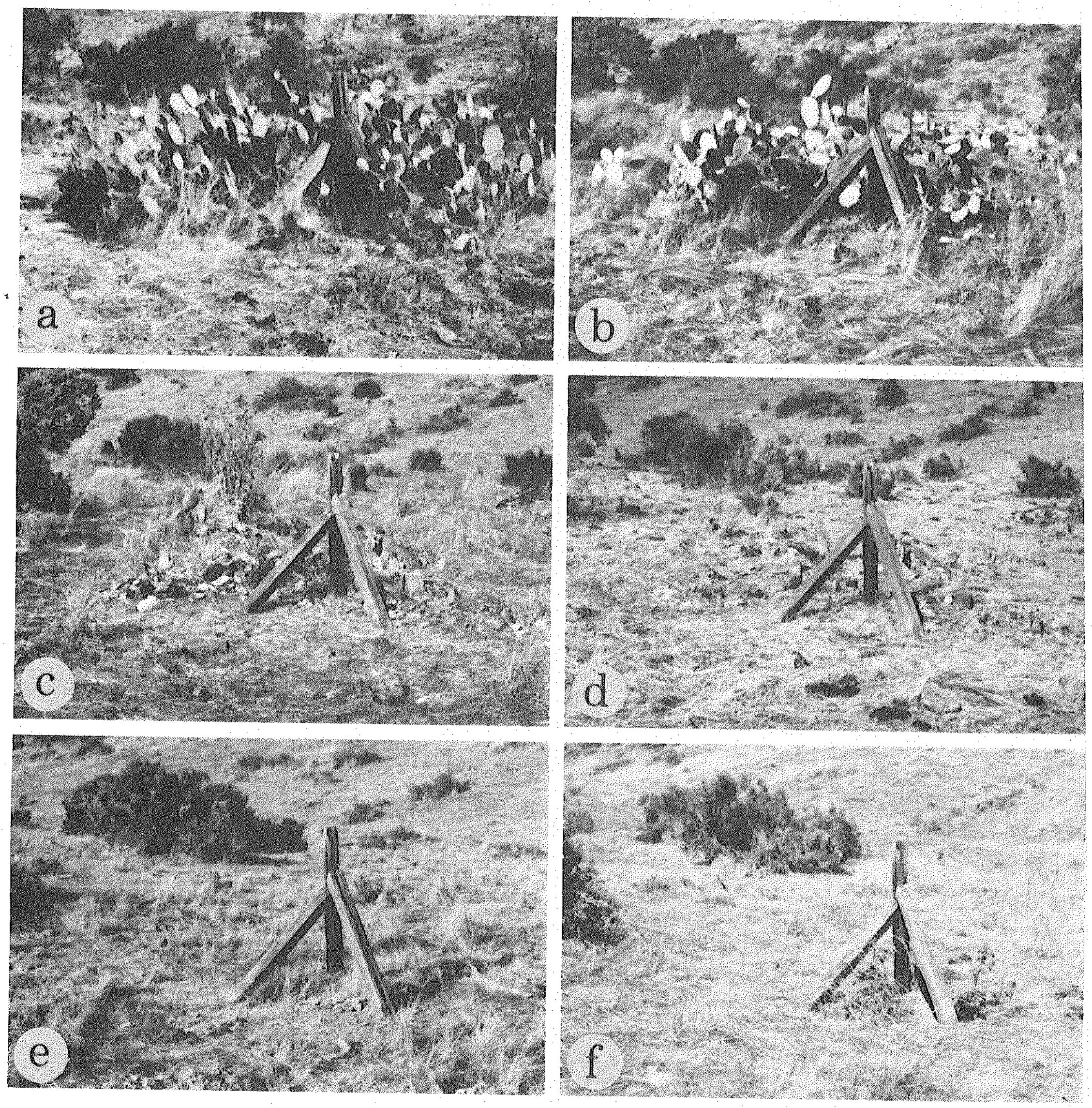

Figure 6. Destruction of *Opuntia oricola* by *Dactylopius opuntiae* on Santa Cruz Island, California. a. 1965, b. 1967, c. 1969, d. 1970 (all dead), e. 1975, f. 1978.

greater susceptibility of *O. littoralis* than *O. oricola* to *D. opuntiae*-induced mortality, noted by Goeden *et al.* (1967), is illustrated in Figures 4 and 5 *vs.* Figures 1 to 3 and 6.

Although cactus destruction by *D. opuntiae* has continued into the 1970s, the general rate of destruction has definitely slowed in recent years. This is because most of the more susceptible prickly pears, i.e., *O. littoralis*, has been killed during the 1950s and '60s. Current activity by *D. opuntiae* largely involves the less susceptible *O. oricola* and its hybrids with *O. littoralis* that favour the former species phenotypically.

Another reason that biological control currently proceeds at a much slower pace is that the entomophagous moth, *Laetilia coccidivora*, reached Santa Cruz Island presumably during the early 1970s. By 1974, this key mainland predator of *D opuntiae* had spread island-wide. Currently, few colonies of *D. opuntiae* remain free of attack by this natural enemy. Thus, a new lower, equilibrium density will be struck by *D. opuntiae* as a result of this added predation. Hopefully, this will not preclude the continued usefulness of this cochineal insect in regulating prickly pear population densities on the island. Luckly, biological control had already been achieved over much of the island's prime grazing lands before *L. coccidivora* arrived. We currently estimate that from two-thirds to three-fourths of the prickly pear cacti that once infested Santa Cruz Island have been destroyed by *D. opuntiae*. Furthermore, range management practices to reduce over-grazing and promote competing vegetation established concurrently with the biological control programs, i.e., restricted cattle grazing and feral sheep eradication (Goeden *et al.* 1967), promise to prevent the resurgence of the prickly pears as rangeland weeds on the island.

The replacement of the dead prickly pears by forage grasses is illustrated by Figures 1, 5, and 6. Again, range management practices have facilitated this revegetation, aided by ample winter rainfall in recent years after several years of drought experienced throughout California. Also, the return of native shrubs, e.g., *Baccharis pilularis* Decandolle, in once heavily overgrazed and prickly pear infested areas is illustrated in Figure 4.

The biological weed control literature is not known to harbour a great deal of conflicting scientific opinion. Indeed, near unanimity characterizes contemporary writings relating to policies and procedures and the theoretical bases for each. At the risk of iconoclasm, we offer some critical comments relating to the use of photography in evaluating biological weed control programs.

Huffaker and Kennett (1969) remarked, 'Photogragphy and observations are powerful and legitimate scientific tools if used with discernment. . . There is truth in the cliche that a good photograph is worth more than a thousand words —perhaps at times more than a thousand statistical items.' The preceding report on the biological control of prickly pear cacti on Santa Cruz Island certainly could not have been presented as succinctly without recourse to Figures 1 to 6. However, to paraphrase another cliche, 'too much use can be made of a good thing.' For example, before-and-after photography reportedly was one of several means by which the biological control of Klamath weed in California by *Chrysolina quadrigemina* (Rossi) (Coleoptera:Chrysomelidae) was evaluated by C.B. Huffaker and co-workers (Huffaker and Kennett 1969). Yet, only a single photographic sequence involving the same three photographs has been used repeatedly in journal articles and textbooks to illustrate the spectacular results obtained with this program, in several instances accompanied by the statement that '. . . This story was repeated all over California' (Huffaker 1964, p.657; 1967, p.53; Huffaker and Kennett 1969, p.430; DeBach and Huffaker 1971, p.119; Van den Bosch and Messenger 1973, p.113; DeBach *et al.* 1976, p.271). Consequently, the question legitimately arises as to whether this overworked photographic sequence truly was representative of events that occurred 'all over California'. (Klamath weed probably never occurred over most of the southern third of the State, then, as now.) This criticism is not meant to detract from the accomplishment that the biological control of Klamath weed represented, but to caution that the repeated use of a single photographic sequence, unsupported by additional series of contemporary photographs taken at different locations, renders suspect the representative nature of the sole sequence used. This criticism cannot be applied to the diversity of sequential photographs used to effectively record the biological control of prickly pear cacti in Australia (Dodd 1927, 1940, Sweetman 1936, Leach 1940, DeBach 1974, DeBach *et al.* 1976). Nor does it apply to the variety of photographic sequences that we have used to record the biological control of prickly pear cacti on Santa Cruz Island (Goeden *et al.* 1967, Goeden and Ricker 1968, Andres and Goeden 1971, Figures 1 to 6).

Photography also has been used to record the biological control of annual and biennial weeds, e.g., *Emex* sp. in Hawaii (Holloway 1964) and musk thistle (*Carduus nutans* L.) in Virginia (Kok and Surles 1975) and Montana (Rees 1978). The former example involved two undated photographs erroneously published in reverse order (and thus mislabelled) of different groups of plants—characteristics that certainly reduced the visual impact and biological significance of the event that purportedly was illustrated.

Our field experience with puncturevine (*Tribulus terrestris* L.), Russian thistle (*Salsola iberica* Sennen and Pau), and milk thistle (*Silybum marianum* (L.) Gaertner) also suggests that sequential photography must be used with caution and discretion in recording density reductions in annual weeds during successive years and ascribing these reductions to direct and indirect seed destruction by natural enemies. As primary colonizers of disturbed lands, these annual weeds may 'disappear' from one year to another at specific locations when environmental conditions are unfavourable to weed seed germination (i.e., inadequate moisture, unfavourable temperatures, allelopathy, lack of soil disturbance), only to reappear, perhaps in even greater abundance, during subsequent favourable years. Timing of sequential photographs of stands of annual weeds within and between years also may considerably alter the appearance of events reportedly portrayed. Sequential photography of shoots poorly registers yearly fluctuations in the size of the soil reservoirs of seeds of annual weeds, especially those species having seeds that remain viable for many years under field conditions. We therefore, suggest that sequential photography intrinsically is less useful in assessing the degree of success of programs involving annual or biennial weeds.

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