LICHENS ON ROCK AND BIOLOGICAL CRUSTS ENHANCE RECRUITMENT SUCCESS OF RARE *DUDLEYA* SPECIES [CRASSULACEAE] IN SOUTHERN CALIFORNIA

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ABSTRACT: *Dudleya* (Crassulaceae), a genus of about 45 taxa restricted to the southwestern United States and Baja California, México, has a number of species with narrowly restricted geographic distributions, specific microhabitat requirements, and low population numbers that make them vulnerable to extinction. In southern California, these include the federally listed threatened *Dudleya cymosa* (Lemaire) Britton & Rose ssp. *agourensis* K. Nakai, *D. cymosa* ssp. *marcescens* Moran, *D. cymosa* ssp. *ovatifolia* (Britton) Moran, *D. parva* Rose & Davidson, *D. stolonifera* Moran, and *D. verityi* K. Nakai. Other rare species include *D. blochmaniae* (Eastw.) Moran ssp. *blochmaniae*, *D. multicaulis* (Rose) Moran, *D. variegata* (S. Watson) Moran, and *D. viscida* (S. Watson) Moran.

Rock-inhabiting lichens serve to trap seeds and to enhance seedling survival of the rare and/or threatened *Dudleya* species that are restricted to steep cliff and rock habitats. Fruticose lichens, especially *Niebla ceruchoides* Rundel & Bowler (the pincushion lichen), are richly branched, and thereby, effectively trap minute *Dudleya* seeds as they are dispersed by wind and rain across rock outcrops. These bush-like lichens collect airborne soil particles and absorb moisture from fog, thereby creating a microhabitat that facilitates the establishment of *Dudleya* seedlings in the otherwise inhospitable conditions found on sheer rock faces.

Biological crusts that grow as a thin mantle over rock or soil may also play an important role in the establishment and survival of many *Dudleya* species. In particular, members of the *D. cymosa* complex appear to be associated with moss-dominated crusts over rock. The biological association of these cryptogams with rare *Dudleya* species is important in designing habitat-specific conservation plans for these rare species. Habitat assessment programs must include monitoring of these lichens, bryophytes, and crust organisms not only for their own sake, but also to assure that these habitats persist in order to sustain viable populations of these rare *Dudleya* species.

KEYWORDS: biodiversity, biological crusts, bryophytes, conservation biology, Crassulaceae, cyanobacteria, *Dudleya*, lichens, liverworts, mosses, *Niebla*, southern California, threatened species.

INTRODUCTION

The conservation issues and problems associated with a rapidly expanding human population are particularly acute in southern California, where large-scale urban development is leading to a massive reduction in the state's unique and varied biota (Sala et al. 2000). This situation presents a difficult test for those interested in protecting the natural environment: can southern Californians develop effective programs to preserve the state's rich biotic diversity? One of the challenges is to identify "vital signs," including measurable attributes of biodiversity, and then to develop practicable approaches to monitor them. However, biodiversity has often been a minor consideration in environmental policy, because ecological relationships are often difficult to take into account (Noss 1990).

One example of the progress made in developing and implementing policy pertaining to biodiversity involves a recent California Environmental Quality Act (CEQA) court decision (Superior Court of California, County of Ventura, 1998). At issue was the significant potential adverse impact from vehicle emission pollution to the pincushion lichen, *Niebla ceruchoides* Rundel & Bowler, and its biological association with the federally listed threatened vascular plant species, *Dudleya verityi* K. Nakai (Riefner and Bowler 1995; Figure 1). In this case, the decision served both to protect the threatened *Dudleya,* and to strengthen the ability of CEQA to protect a lichen-dominated microhabitat that facilitates recruitment of a threatened vascular plant. Because of the awareness created by this decision, conservation biologists in southern California are now beginning to recognize that biodiversity encompasses a wide range of organisms, and is not limited to the old "laundry lists" of vascular plants, vertebrates, or vegetation types. Accordingly, the cryptogams, which have often been excluded entirely from study, and subsequently, overlooked in restoration and management programs are now considered for conservation and study. In this paper, we demonstrate the ecological importance of preserving cryptogamic organisms, and the need to recognize them in management, restoration, and monitoring programs.

THE *NIEBLA* – *DUDLEYA* BIOLOGICAL ASSOCIATION

The genus *Dudleya* Britton & Rose (Crassulaceae) is comprised of rosette-forming succulent perennial herbs adapted to arid environments, typically inhabiting ocean bluffs, sheer cliffs, and rock outcrops (Mulroy 1976; Dodero 1995). *Dudleya* (commonly known as "live-forever") attains its greatest diversity along the southern California coast, the Channel Islands, Baja California, México, and islands off Baja California's Pacific coast. Many species have restricted geographical distributions, and some are very narrow endemics with specific habitat requirements (Moran 1951; Mulroy 1976).

Dudleya species are particularly successful as colonizers, as few other vascular plants can endure the inhospitable conditions of rock outcrops, weathered soils, and other nutrient-poor habitats in arid southern California. Some *Dudleya* species grow in thin soils of rock fissures, and other species appear to form associations with lichens and bryophytes (Mulroy 1976). As described below, lichens and bryophytes may be important in the establishment of both groups of *Dudleya* species. In contrast, the small geophytes, such as *Dudleya blochmaniae* (Eastw.) Moran ssp. *blochmaniae*, *D. multicaulis* (Rose) Moran, and *D. variegata* (S. Wats.) Moran, are rarely found on vertical cliffs, but are most abundant about the base of outcrops, between shrubs in open patches of soil, or in grasslands (Dodero 1995; Marchant et al. 1998). Although a number of small vascular plants germinate in moss, we are not aware of another genus of vascular plants that grows in such an intimate relationship with the cliff-inhabiting lichens of the genus *Niebla* as species of *Dudleya* (Figure 2). These cryptogams act as nurse plants, providing an organic and microhabitat foot-hold on open, sheer rock that enables *Dudleya* to germinate, flower, and set seed in a microhabitat that otherwise would not be available for colonization (Figure 3).

Within the genus *Dudleya*, there are species that are consistently pulverulent or glaucous from a whitish waxy deposit on the leaves, other species whose leaves are always green, and a third group with either variable pulverulence or with both a green and a "white" morphology. Based on experiments upon the green and pulverulent morphs of *Dudleya brittonii* D.A. Johansen, and field observations of most other species in the genus, Mulroy (1976, 1979) proposed that glaucescence (a white or bluish-silver powdery wax) is genetically controlled, and that white or green morphologies are often habitat specific: i.e., non-glaucous plants tend to occupy deeper soils; and plants that produce glaucescence are able to survive on steep, nutrient-poor, sheer rock and cliff habitats. Ecologically significant characteristics attributed to glaucescence include high reflectance of ultraviolet light, increased protection against predation, reduced susceptibility to nutrient loss caused by leaching in fog zones, and conservation of nutrient capital and biomass that enable the rapid uptake and storage of water (Mulroy 1976, 1979). *Dudleya* species display genetically controlled adaptations that allow them to colonize habitats unavailable to most other plants.

Dudleya species also have the ability to rapidly absorb moisture when it is available by rapid production of roots. Mulroy (personal observation) found that *Dudleya* species produce roots in response to high humidity with no direct contact with water. The water is stored in the succulent leaves and spongy tissue of the caudex. Like many succulents, *Dudleya* species use Crassulacean Acid Metabolism (CAM); these plants are usually found in environments where water availability is restricted temporarily or seasonally, such as rock outcrops (Bartholomew 1973; Gibson 1982). This water-conserving adaptation is characterized by nocturnal opening of stomata for gas exchange and fixation of C02 into organic acids that subsequently is released during the daylight hours for use in photosynthetic carbon fixation. The closure of stomata reduces water loss due to transpiration, thereby saving water, and enabling *Dudleya* species to exploit exposed habitats where moisture is scarce.

Perhaps these evolutionary traits also allow *Dudleya* to exploit the micro-scale differences of moisture, soil, and nutrient availability provided by the cryptogams in barren habitats. Because of these ecological subtleties, knowledge of demographic characteristics, ecology, and natural history are important for the conservation of genetic diversity when assessing the biodiversity of *Dudleya* species.

The genus *Niebla* (Ramalinaceae) is comprised of fruticose (shrubby or bush-like) lichens that form a conspicuous component of the vegetation within the maritime fog zone from Washington to Baja California Sur, México, the Channel Islands, and islands off Baja California's Pacific coast (Bowler et al. 1994). Moisture availability and substrate type may be important selective factors in the distribution of *Niebla* species (Spjut 1996), which include saxicolous (growing on rock), terricolous (growing on soil), and corticolous (growing on wood, bark, or tree branches) taxa. In Baja California Norte, México, *Niebla josecuervoi* (Rundel & Bowler) Rundel & Bowler and allied species dominate the vegetation of open-habitat soils that rival the abundance of other lichen micro-bush (*Cladina* spp. and *Cladonia* spp.) dominated habitats of eastern North America (Rundel et al. 1972). Many *Niebla* species have open patterns of branching that resemble a naked winter shrub, such as *Niebla homalea* (Ach.) Rundel & Bowler, and others may be cushion-like (rounded) such as *Niebla ceruchoides,* or cespitose (clumped or tufted) like *N. combeoides* (Nyl.) Rundel & Bowler. Tufts of lichens may act like a comb for dew and fog condensation (Büdel & Scheidegger 1996). Apparently, a strong relationship exists between the cushion-like growth form and the functions performed by *N. ceruchoides* that benefit species of *Dudleya* growing on cliff and rock habitats.

Most *Niebla* species fall within two general groups: the "ceruchoid" group, taxa that are characterized by a predominately terpenoid chemistry and lack well-developed chondroid (fiber-like) strands in the thallus (body of the lichen); and the "homalea" group that is characterized by conspicuous chondroid strands and a more diverse chemistry that includes divaricatic, barbatic, and sekikaic acids (depsides), and hypoprotocetraric, protocetraric, and salazinic acids (depsidones) (Bowler 1981; Bowler et al. 1994). Spjut (1996) transferred species of the ceruchoid group into a new genus, *Vermilacinia* Spjut & Hale, which is beyond the scope of discussion for this paper. Species of the ceruchoid lineage most frequently associated with *Dudleya* species in southern California include *Niebla ceruchoides,* and occasionally, *N. combeoides*. *Niebla homalea* is the most important of the homalea group.

Riefner (1992) and Riefner and Bowler (1995) made autecological observations of *Niebla ceruchoides*. This saxicolous lichen forms an interesting association with the threatened cliff-dwelling *Dudleya stolonifera* and *D. verityi* on coastal bluff habitats in southern California. *Niebla ceruchoides* is intricately branched, and its cushion-like morphology facilitates capture of minute *Dudleya* seeds dispersing across rock outcrops. Seed capture by these lichens appears to enhance seedling establishment in otherwise unfavorable microhabitats such as bare rock, where conditions are not favorable to germinating plants. These small lichen bushes also collect soil particles and absorb moisture and nutrients from fog, thereby providing an organic seedbed that increases overall seedling establishment of *Dudleya* on these rock habitats. There may be a mutually reinforcing feedback loop whereby both the lichen and the *Dudleya* plants increase microhabitat soil, each providing the other with a greater opportunity for colonization.

Another possible mechanism by which *Niebla* species may increase seedling survival of *Dudleya* is by providing protection from insect and slug herbivory. Lichens produce chemical compounds, such as usnic acid, which are unique in nature and have been documented as a deterrent to herbivory (Lawrey 1983; Emmerich et al. 1993). As the seedlings begin to grow among or inside the lichen bushes, the lichens also physically protect young *Dudleya* plants from snails and other herbivores (Figure 4). These *Dudleya* species may have developed a resistance to these lichen substances, which have been shown to inhibit seed germination and/or growth of certain vascular plants (Pyatt 1967; Rundel 1978; Hobbs 1985; Nishitoba et al. 1987; Frahm et al. 2000). Quantitative analysis has shown that depsides and orcinol derivatives such as barbatic acid are significant "allelochemicals," which exhibit strong growth-inhibitory properties against seedling development in the higher plants (Nishitoba et al. 1987). Although no experimental data are available, indirect evidence suggests that lichen acids may play an important role in excluding certain vascular plants from colonizing these lichen-dominated cliff microhabitats in southern California, and should be carefully considered in future research. Thus, these cliff-dwelling lichens appear to enhance seedling recruitment of these local *Dudleya* endemics in several ways.

Not only lichens, but mosses, liverworts, and cyanobacteria that form biological crusts on rock are an often-overlooked component of the biodiversity of cliff habitats. Crust organisms have low moisture requirements, and their ability to utilize fog and dew as water sources enables them to exist where moisture deficit limits vascular plant cover and productivity (Belnap et al. 2001). Our qualitative observations indicate that these rock-inhabiting biological crust organisms, in addition to *Niebla*, may contribute in an important way to the establishment and survival of local cliff-dwelling *Dudleya* species (Figure 5). This observation is in concurrence with Mulroy (1976) who noted the association of a cryptogamic community with *Dudleya* in such habitats (USFWS 1999). Dodero (1995) also provides similar observations, whereby moss growing on rock acts as a rooting medium for *D. cymosa* ssp. *marcescens* (Figure 6). These relationships point to the importance of lichens and bryophytes in sustaining the biodiversity of endemic vascular plants of these habitats, and the need for broad community-based monitoring that includes these much-neglected organisms.

HABITATS AND ASSOCIATED BIOTIC FUNCTIONS OF SOME RARE OR THREATENED *DUDLEYA* SPECIES

Toward the development of a monitoring program for the *Dudleya* – cryptogamic associations in southern California, we recognize three primary attributes of ecosystems described by Franklin et al. (1981): composition, structure, and function. In the sense of a whole ecosystem, these three integrated attributes encompass and define its biodiversity (Noss 1990). Composition is characterized as the identity and variety of elements in an area and is recorded in species lists, measurements of the diversity of species, and higher taxonomic levels. Structure is the physical organization or pattern of a system, including habitat complexity within a community, and micro-distributions or broad patterns at the landscape scale. Function involves ecological and evolutionary processes, including gene flow, disturbances, colonization and demographic processes, and nutrient cycling. Compositional diversity has been the traditional focus of study, and the structural simplification and disruption of functional ecological processes have not been adequately addressed (Noss 1990).

One of the most important functions that lichens and bryophytes perform for colonizing *Dudleya* on barren rock is enhanced seedling establishment (Mulroy 1976; Riefner and Wishner 2000). Clusters of lichens and crust organisms form safe sites or "seed nests" where *Dudleya* can germinate if pockets of soil are lacking. The foliose (leaf-like) lichens *Flavoparmelia caperata* (L.) Hale, *Flavopunctelia flaventior* (Stirton) Hale, and *Xanthoparmelia* spp., *Niebla* spp., and the small, tufted *Cladonia* species are often major components of seed nests on sheer rock. Mosses, similarly, can serve as seed traps (van Tooren 1988) and germination substrates (During and van Tooren 1990), and at some localities they are better seed traps for *Dudleya* species than lichens (Figures 7 & 8). Seedling establishment (positive or negative) of vascular plants in bryophyte mats has been correlated with characteristics of the "turf" structure of the carpet, moisture availability and other microclimate conditions, light intensity and quality, seasonal patterns of germination, and to allelopathic effects (During and van Tooren 1990; van Tooren 1990; Zamfir 2000). The frequency and duration of hydration or dehydration of the moss bed, and the rapidity of water loss and water uptake by individual moss species (Norris 2003), may also play an important role in the recruitment success of *Dudleya* in bryophyte mats.

Seeds of *Dudleya* species germinate readily in the wild, or in the laboratory. Germination studies conducted by the Rancho Santa Ana Botanic Garden (2000) document relatively high percentages of germination, even for rare species or narrow endemics, including: *D. parva* – 67%; *D. blochmaniae* ssp. *blochmaniae* – 78%; *D. greenei* Rose – 76%; *D. nesiotica* Moran – 83%; *D. stolonifera* – 88%; and *D. verityi* – 62% & 90%. These data suggest that seed viability is not a limiting factor in the population dynamics of local or threatened taxa. Rather, successful dispersal and establishment into suitable habitats with favorable microclimates, soils, moisture, and so forth, with low competition may be key to the long-term persistence of these species.

Lichens and bryophytes are poikilohydric; poikilohydry is the rapid equilibration of internal water content to the external environment (Mishler 2003). The uptake of water by lichens from non-saturated atmospheres is well known, and represents essentially the reverse of evaporation (Nash 1996a). Similarly, most bryophytes take up water and nutrients through the whole plant and do not need a root system to draw them from the soil (Gignac 2001). As a result, bryophytes can survive on very hard surfaces, such as rocks, where higher plants cannot because their roots cannot penetrate the surface. Accordingly, absorption and retention of moisture by rock-inhabiting lichen and biological crust organisms may be vital to *Dudleya* species occupying steep rock surfaces, especially during drought, since these species can absorb moisture from dew or mist in the absence of rainfall (Figure 9). The successful recruitment of *Dudleya traskiae* (Rose) Moran on Santa Barbara Island depends on a narrow range of moisture conditions for germination and seedling establishment (Clark and Halvorson 1987). Knowledge of the functional attributes of cryptogams may play an important role in enhancement and restoration projects involving *Dudleya* species.

Rock-inhabiting cryptogams may also improve nutrient cycling, including nitrogen fixation, on cliff and rock substrates. We have observed several cyanolichens (cyanobacteria photobiont rather than green alga) that become gelatinous (jelly-like) when wet, and occasionally cyanobacteria (blue-green algae), growing in moss over rock. Cyanobacteria, and cyanolichens, such as the genus *Collema*, are important components of biological soil crusts that fix atmospheric nitrogen (Isichei 1990; Johansen 1993) and contribute to net sources of total nitrogen in soil environments that are otherwise nitrogen-poor (Evans and Belnap 1999). Nitrogen released from these organisms is readily utilized by vascular plants (Belnap et al. 2001). No experimental data is available, but these nitrogen-fixing organisms likely also benefit the small vascular plants surviving in cliff and rock habitats. Cliff and rock dwelling microorganisms are exceedingly important in nature, and they may mediate numerous processes in the geochemical landscape; see Dorn (1998) for a review.

Epiphytic lichens (growing on trees and shrubs) of the forest communities along the Pacific Coast fog belt trap nutrients from atmospheric aerosols and fog, which otherwise would not be intercepted and utilized by the ecosystem. Munger et al. (1983) report that fog contains greater concentrations of nutrients than precipitation, by orders of magnitude. Most nutrients captured by tree-canopy lichens represent new inputs, and cycling of these minerals may be of ecosystem-level importance (Knops et al. 1991). For example, the lace lichen (*Ramalina menziesii* Taylor) contributes substantially to mineral cycling and biomass turnover in the blue oak (*Quercus douglasii* Hook. & Arn.) savanna of California (Boucher and Nash 1990). Evidence is now mounting that lichens play important roles in rapid mineral cycling, such as the capture of allogenic nutrients that would otherwise not be retained in the ecosystem, which represent a highly significant input to nutrient-poor ecosystems (Nash 1996b). These critical ecosystem processes are unrecognized by many California biologists.

Epiphytic lichens and mosses have also been functionally linked to other critical ecosystem processes, including primary production (McCune 1993). Many mechanisms that facilitate these functions have been documented, but the rapid absorption of moisture and particulates associated with aerosols appears to be one of the most important. Lichens are known to rapidly absorb moisture equal to 150%-1200% of their dry weight (Hawksworth and Hill 1984). There is a lack of pertinent experimental data in southern California, but the importance of the biological functions of lichens documented in forest and woodland habitats in terms of nutrient and moisture capture and recycling may be transferable to cliff and rock communities (Figure 10), which are comparatively poorly studied.

Biological crusts on soil have only recently been recognized as important components of terrestrial ecosystems, playing a critical role in the functional ecology of arid lands (Eldridge 2000). These organisms likely improve the survival of several *Dudleya* species restricted to open-habitat soils, including species of the *D. abramsii* complex, *D. blochmaniae* ssp. *blochmaniae*, *D. multicaulis*, and *D. variegata*. Numerous studies suggest that biological soil crusts stabilize soil surfaces and reduce erosion, improve percolation and soil moisture storage, enhance vascular plant seedling establishment, and improve soil fertility by nitrogen fixation (Belnap et al. 2001). Biological soil crusts likely benefit these and other *Dudleya* species in similar ways (Figure 11).

HABITAT CATEGORIES

McCune (1993) identified functional groups comprised of epiphytes sharing similar ecological roles and morphology. Similarly, the distribution of saxicolous organisms is influenced by environmental characteristics: rock substrate type (volcanic, granite, sandstone), slope, aspect, and degree of shading (north-facing, shaded versus full sun), frequency of fire, associated vascular plant habitat (woodland versus scrub), and microclimate variables that include light, temperature, and moisture. The morphological groups that provide important functions to the saxicolous *Dudleya* - cryptogamic community habitats are the fruticose and foliose lichens, cyanolichens, cyanobacteria, the cushion or turf-forming (acrocarpous) and the highly branched mat-forming mosses (pleurocarpous), and non-seed-bearing vascular plants such as the ferns and spike-mosses. A strong relationship exists between the morphology of these organisms and the way in which they function. Accordingly, morphological groups have been proposed as surrogates for individual species in monitoring programs (Rosentreter et al. 2001). These morphological groups, and recognition of their observed and potential associated functions, could aid in a rapid assessment (Eldridge and Rosentreter 1999) of *Dudleya* habitats, especially on cliffs that are difficult to get to reach without disturbing sensitive *Dudleya* species. Table 1 provides a summary of these morphological groups, their associated functional attributes, and representative species, which are generally easy to identify that often occur in sensitive *Dudleya* habitats.

Table 1: Description of morphological groups and associated functional attributes of the cryptogams and lower vascular plants of *Dudleya* habitats.

MORPHOLOGICAL GROUPS	HYPOTHESIZED PRIMARY FUNCTIONAL ATTRIBUTES	REPRESENTATIVE SPECIES
Lichens		
Fruticose (bush-like)	Seed trapping, absorption and retention of moisture and nutrients, soil accumulation	*Cladonia fimbriata, C. furcata, Niebla ceruchoides, N. combeoides, N. homalea*
Foliose (leaf-like)	Absorption and retention of moisture and nutrients, seed trapping, soil accumulation	*Flavoparmelia caperata, Flavopunctelia flaventior, Physcia dubia, Xanthoparmelia coloradoensis, X. mexicana*
Crustose (granular) & Squamulose (scaly)	On Rock: Moisture absorption and retention	*Acarospora bullata, Caloplaca bolancia, Lecanora muralis, Lecidea atrobrunnea, Pertusaria flavicunda, Tephromela atra*
	OnSoil: Soil stabilization, moisture absorption and retention, seed trapping	*Acarospora scheicheri, Diploschistes scruposus, Placidium squamulosum, Psora californica, P. decipens*
Mosses		
Turf-forming (acrocarpous)	Soil accumulation, absorption and retention of moisture and nutrients, germination substrate	*Bryum argenteum, Didymodon vinealis, Grimmia laevigata, Tortula brevipes*

Mat-forming (pleurocarpous)	Soil accumulation, absorption and retention of moisture and nutrients, germination substrate	*Anacolia menziesii*, *Pterogonium gracile*, *Scleropodium cespitans*
Liverworts	Moisture absorption and retention, soil stabilization	*Asterella californica*, *Riccia nigrella*, *R. trichocarpa*
Cyanolichens (gelatinous)	On Rock: Nitrogen-fixation, moisture retention, soil accumulation	*Collema fuscovirens*, *Leptogium corniculatum*
	On Soil: Nitrogen-fixation, moisture retention, soil stabilization	*Collema tenax*, *Peltula patellata*
Cyanobacteria (blue-green algae)	Nitrogen-fixation, moisture retention, soil stabilization	*Microcoleus vaginatus*, *Nostoc* sp., *Oscillatoria* sp.
Non-Seed BearingVascular Plants		
Spike-Moss (mat-like, cushion-like or cespitose)	Soil accumulation and stabilization	*Selaginella bigelovii*, *S. cinerascens*
Ferns (erect to spreading habit with creeping underground rhizome)	Soil accumulation and stabilization	*Cheilanthes covillei*, *Pellaea andromedifolia* *Polypodium californicum*

It is useful to group the habitats of the rare and threatened *Dudleya* species of southern California's cismontane habitats into three broad categories, in order to provide a general characterization of the composition, structure, and functional biodiversity of their associated biological crusts and non-seed-bearing vascular plant components. These artificial categories are intended only to provide a preliminary profile of the composition and structure of *Dudleya* habitats, since the micro-distribution of these organisms can vary greatly with aspect, substrate, and elevation, and only a small fraction of these areas has been carefully studied. The categories are: fog-swept cliff and rock habitats; inland, lightly-shaded to exposed cliff and rock habitats; and undisturbed, open-habitat soils free of exotic weeds.

FOG-SWEPT CLIFF AND ROCK HABITATS

Fruticose lichens of the genus *Niebla* frequently dominate exposed, fog-swept cliff and rock outcrops. These lichens resemble "miniature forests" on cliff and rock outcrops along the coast of California and Baja California, México. Other important components include biological crusts of mosses, foliose lichens, and tufts of smaller fruticose lichens such as *Cladonia* species. Crustose lichens (those appearing to be "painted" on the rock surface or appearing granular) and squamulose forms (scaly) are almost always present. The prostrate, mat-forming pleurocarpous mosses and the short or tall turf-forming acrocarpous species are important germination substrates on locally shaded to exposed coastal cliff sites. Small ferns with long-creeping rhizomes, such as *Polypodium californicum* Kaulf., and the bushy spike-moss (*S. bigelovii* L. Underw.), contribute to soil-building processes in rock crevices and stabilize thin soil pockets on outcrops in these habitats.

Dudleya stolonifera and *D. verityi* are federally listed threatened species, and *D. greenei* is an uncommon species restricted to several of the Channel Islands. These species occupy cliff and rock habitats in the fog belt. We have not studied other rare *Dudleya* species that are restricted to the Channel Islands. Reference sites for these *Dudleya* species include mostly north-facing outcrops near Avalon on Santa Catalina Island, Los Angeles County; in Aliso Canyon and the mouth of Aliso Creek in Laguna Beach in Orange County; and Conejo Mountain, Point Mugu, and Long Grade Canyon in Ventura County. We have also examined the cliff and coastal bluff cryptogamic associations of more common but local *Dudleya* species at a variety of locations, including *D. caespitosa* (Haw.) Britton and Rose, at Abalone Point in Orange County; Morro Bay and Morro Rock Reserve in San Luis Obispo County; and *D. farinosa* (Lindley) Britton and Rose at Big Sur and Point Lobos in Monterey County.

<u>Species associated with these specialized environments include:</u>

Mosses: *Didymodon vinealis* (Brid.) Zander, *Grimmia laevigata* (Brid.) Brid., *Homalothecium nevadense* (Lesq.) Ren. & Card., and *Tortula brevipes* (Lesq.) Broth. **Liverwort**: *Asterella californica* (Hampe) Underw. **Lichens**: *Acarospora bullata* Anzi, *Buellia halonia* (Ach.) Tuck., *B. stellulata* (Taylor) Mudd, *Caloplaca bolancia* (Tuck.) Herre, *C. rosei* Hasse, *Cladonia furcata* (Hudson) Schrader, *Collema crispum* (Hudson) F.H. Wigg., *Flavoparmelia caperata*, *Flavopunctelia flaventior*, *Lecania dudleyi* Herre, *Lecanographa hypothallina* (Zahlbr.) Egea & Torrente, *Lecanora gangaleoides* Nyl., *L. rupicola* (L.) Zahlbr., *Lecidella carpathica* Körber, *Leprocaulon microscopicum* (Vill.) Gams *ex* D. Hawksw., *Neofuscelia verruculifera* (Nyl.) Essl., *Niebla ceruchoides*, *N. combeoides*, *N. homalea*, *Pertusaria flavicunda* Tuck., *Physcia dubia* (Hoffm.) Lettau, P. tribacia (Ach.) Nyl., *Physconnia* spp., *Rinodina bolanderi* H. Magn., *Tephromela atra* (Hudson) Hafellner, *Umbilicaria phaea* Tuck., and several species of *Xanthoparmelia*. **Spike-Moss**: *S. bigelovii*. **Fern:** *Polypodium californicum*.

Lichens proposed for rare status in southern California collected from fog-zone outcrops associated with sensitive *Dudleya* species include: *Gyalecta herrei* Vezda, *Phaeophyscia kairamoi* (Vainio) Moberg, *Punctelia punctilla* (Hale) Krog, and *Roccella fimbriata* Darbish (Magney 1999). Uncommon lichens of coastal sensitive *Dudleya* habitats include *Caloplaca stantonii* W.A. Weber ex Arup, *Dimelaena californica* (Magnusson) Sheard, *Lecanora xanthosora* B.D. Ryan & Poelt, *N. isidiascens* Bowler, Marsh, T. Nash, & Riefner, and *N. robusta* (R. H. Howe) Rundel & Bowler. Indeed, these habitats themselves are very limited, and there are relatively few sites with the complete community well represented. These sites should be protected.

As with the lichens, the conservation of bryophytes is long overdue. Continuing studies on the bryoflora of California may find that these south coast cliff and rock outcrop communities also support rare species of mosses and liverworts.

INLAND LIGHTLY-SHADED TO EXPOSED CLIFF AND ROCK HABITATS

Outside of the coastal fog belt, *Dudleya* species of cliff and rock habitats are most often found growing with biological crusts dominated by mat- and turf-forming mosses, liverworts, foliose lichens, and the black cyanolichens, such as species of *Leptogium*. Our general observations concur with those of Nash et al. (1979) who state that lichen abundance and species richness decrease with increasing distance from the Pacific Ocean; importantly, the saxicolous fruticose lichens are directly associated with the maritime microclimate influence, and disappear inland. As with the fog-belt association, the structural complexity within a community, its micro-distribution within a cliff system, or the broader pattern found at the regional scale vary greatly, and are beyond the scope of this paper. In addition to a rich bryoflora, these outcrops support several species of small ferns that are important soil consolidators. Also, the bushy spike-mosss is common in rock crevices and many open habitats on soil throughout cismontane southern California (Wilken 1993).

This inland habitat supports several local *Dudleya* species, including the federally listed threatened *D. stolonifera*, *D. cymosa* ssp. *agourensis*, *D. cymosa* ssp. *ovatifolia D. cymosa* ssp. *marcescens*, and the rare *D. viscida*. Reference sites for these habitats include north-facing or shaded outcrops: near Cotharin Road, Little Sycamore Canyon of the western Santa Monica Mountains in Los Angeles County; Agoura Hills area of the central Santa Monica Mountains in Los Angeles County; Laguna Canyon, Saddleback Peak, and San Juan Canyon in Orange County; San Marcos Creek in San Diego County. We have also examined the inland cliff and outcrop cryptogams associated with several broad-ranging *Dudleya* species, including *D. cymosa* ssp. *pumila* (Rose) K. Nakai, *D. edulis* (Nutt.) Moran, and *D. lanceolata* (Nutt.) Britton & Rose, in the upper Fremont Canyon region, Cleveland National Forest, Orange County; the San Jacinto Wilderness in Riverside County; at Colby Canyon in San Bernardino County; at Julian, the Cuyamaca Mountains, and on Palomar Mountain in San Diego County. *Xanthoparmelia mougeotii* (Schaerer) Hale is an uncommon lichen (Magney 1999) that co-occurs with *Dudleya viscida* on granitic outcrops at several inland sites.

Dudleya stolonifera is apparently unique since it grows along the immediate coast within the fog belt, and at somewhat inland sites beyond the maritime influence, mostly on north-facing outcrops. In north Laguna Canyon, which does not support large fruticose lichens or members of the obligate fog-zone cryptogamic community, mat- and turf-forming mosses support several hundred plants of this threatened live-forever. At other inland sites, such as Montclef Ridge in Ventura County, small ferns and spike-moss stabilize the soil of rock crevices that provides habitat for the threatened *D. parva*. We have not studied the cryptogams and lower vascular plants associated with other rare *Dudleya* species found in the central portion of the state.

Species associated with these specialized environments include:

Mosses: *Anacolia menziesii* (Turn.) Par., *Brachythecium* sp., *Bryum capillare* Hedw., *Didymodon vinealis*, *Homalothecium nevadense*, *Pterogonium gracile* (Hedw.) Sm., *Scleropodium cespitans* (C. Muell.) L. Koch, and *Syntrichia princeps* (DeNot.) Mitt. **Liverwort**: *Asterella californica*. **Lichens**: *Acarospora socialis* H. Magn., *Aspicilia cinerea* (L.) Körber, *Caloplaca modesta* (Zahlbr.) Fink, *Cladonia fimbriata* (L.) Fr., *C. pyxidata* (L.) Hoffm., *Collema fuscovirens* (With.) J.R. Laundon, *Dermatocarpon reticulatum* H. Magn., *Dimelaena radiata* (Tuck.) Hale & Culb., *Flavoparmelia caperata*, *Lecanora muralis* (Schreber) Rabenh., *Lecidea atrobrunnea* (Lam. & DC.) Schaerer, *Leptogium corniculatum* (Hoffm.) Minks, *Phaeophyscia* spp., *Physcia clementei* (Sm.) Lynge, *Thelomma mammosum* (Hepp) A. Massal., *Umbilicaria phaea* Tuck., and several species of *Xanthoparmelia*, including *X. coloradoensis* (Gyelnik) Hale, *X. cumberlandia* (Gyelnik) Hale, and *X. mexicana* (Gyelnik) Hale. On shaded or north-facing cliff and rock outcrops with recurrent saturation or seepage, **Cyanobacteria** such as *Microcoleus vaginatus* (Vauch) Gom., and green algae may be present. **Spike-Moss**: *Selaginella bigelovii*. **Ferns**: *Cheilanthes covillei* Maxon, *Notholaena californica* D. Eaton, *Pellaea andromedifolia* (Kaulf.) Fée, and *Polypodium californicum*.

Uncommon lichens co-occur with sensitive *Dudleya* species (*D. viscida*) on granitic outcrops at inland sites, including *Lecanora mellea* W.A. Weber.

OPEN-HABITAT SOILS

Undisturbed stabilized open-habitat soils are the bare, to sparsely vegetated microhabitats generally associated with nutrient-poor substrates. They occur in many plant communities, and over a wide range of geomorphic surfaces in southern California. Characteristically, these soils support a conspicuous and diverse biological soil crust comprised commonly of turf-forming mosses, squamulose and crustose lichens, fruticose lichen species (*Cladonia*), cyanolichens of the genus *Collema*, and cyanobacteria, which mostly grow within a few millimeters of the soil surface, and occasionally, the leaf-like *Xanthoparmelia* lichens. The bushy spike-moss is common, and the mesa spike-moss, *Selaginella cinerascens* Maxon, is often intimately associated with rare *Dudleya* species on mesas in San Diego County and Baja California, México. The most notable feature of encrusted open-habitat soils is the near absence of exotic weeds, regardless of soil type or plant community (Riefner and St. John 2000).

Species associated with this specialized environment include:

Mosses: *Bryum argenteum* Hedw., *B. capillare*, *Desmatodon convolutus* (Brid.) Grout, *Didymodon vinealis*, *Homalothecium nevadense*, *Scleropodium cespitans*, *Timmiella crassinervis* (Hampe) L. Koch, and *Tortula brevipes*. **Liverworts**: *Asterella californica*, *Riccia nigrella* DC., *R. sorocarpa*

Bisch., and *R. trichocarpa* M.A. Howe. **Lichens**: *Acarospora schleicheri* (Ach.) A. Massal., *Amandinea punctata* (Hoffm.) Coppins & Scheid., *Candelariella vitellina* (Hoffm.) Müll. Arg., *Cladonia pyxidata*, *Collema tenax* (Sw.) Ach., *Diploschistes scruposus* (Schreber) Norman, *Peltula patellata* (Bagl.) Swinscow and Krog, *Placidium lacinulatum* (Ach.) Breuss, *P. squamulosum* (Ach.) Breuss, *Psora californica* Timdal, *P. decipiens* (Hedwig) Hoffm., *Psora nipponica* (Zahlbr.) Gotth. Schneider, *Toninia* spp., *Trapeliopsis californica* McCune & Camacho, and occasionally *Xanthoparmelia coloradoensis* and *X. cumberlandia*. **Cyanobacteria**: species of *Microcoleus*, *Nostoc*, and *Oscillatoria*. **Spike-Mosses**: *Selaginella bigelovii*, *S. cinerascens*.

Open soil habitat supports several local *Dudleya* species: *D. blochmaniae, D. multicaulis, D. variegata*, and members of the *D. abramsii* complex. Reference sites for these species include many localities in the foothills of the Santa Ana Mountains, and San Clemente State Beach in Orange County; the Cuyamaca Mountains, Del Mar, La Jolla Canyon, Mission Trail Park, Otay Mountain, San Onofre State Beach, and Torrey Pines Reserve in San Diego County; the "pebble plains" in San Bernardino County; and Long Grade Canyon and Conejo Mountain in Ventura County. *Dudleya brevifolia* (Moran) Moran, which is endemic to the concretionary soils of the Lindavista Formation in San Diego County (Cochrane 1985), is one of the species that almost always does not grow in close association with well-developed biological soil crusts.

Uncommon or rare lichens associated with *Dudleya* species and open-habitat soils in southern California include *Caloplaca* cf. *subpyraceella* (Nyl. in Hasse) Zahlbr., *Cladonia thiersii* S. Hammer, *Solenopsora "cladonioides"* B.D. Ryan & Timdal (in prep., see Nash et al. 2002), *Texosporium sancti-jacobi* (Tuck.) Nádv., and *Trapeliopsis steppica* McCune & Camacho (Riefner et al. 1995a; Magney 1999; Nash et al. 2002; McCune et al. 2002). Two special-status liverworts, *Geothallus tuberosus* Campb. and *Sphaerocarpos drewei* Wigglesw. (Tibor 2001) share similar habitat requirements with rare geophytes in San Diego County, and may co-occur with *D. variegata*.

FUNCTIONAL ATTRIBUTES OF CRYPTOGAMS AND MONITORING OF *DUDLEYA* HABITATS

Monitoring for sustained biodiversity is practical when causes and effects, probabilities, interactions, and alternative hypotheses are taken into account by a program that addresses current management programs and policies (Noss 1990). A monitoring program should document trends in seedling establishment and population dynamics of rare and threatened *Dudleya* species. To do this we propose selecting several species from each morphological-functional group as indicators of ecosystem health. Such a program could examine the following: (1) air pollution and fire impacts to lichens and other organisms that function as germination substrates or "seed nests;" (2) species which enhance nutrient inputs to the ecosystem such as nitrogen fixing cyanobacteria and cyanolichens; and (3) the "guild" of species that promote moisture retention and soil-building processes. Brief discussion of a few examples that could be included in a monitoring program, which may also be important in habitat enhancement efforts follow:

long-term information regarding trends in population dynamics. Ozone is formed from the interaction, mediated by sunlight, between nitrogen oxides and unburned hydrocarbons produced by vehicle exhaust (Richardson 1992), and has become an important atmospheric pollutant in southern California and elsewhere as vehicular traffic increased dramatically following World War II. For lichens, oxides of nitrogen are one of the most harmful components of air pollution in the Los Angeles basin

Figure 1. The pincushion lichen, *Niebla ceruchoides*, is intricately branched and its cushion-like morphology facilitates capture of minute *Dudleya verityi* seeds dispersing across rock outcrops in the western Santa Monica Mountains, Ventura County. These small lichen bushes also collect soil particles and absorb moisture and nutrients from fog, which provides an organic seedbed that increases overall seedling establishment of this federally-listed threatened plant species in otherwise unfavorable microhabitats such as bare rock.

Figure 2. *Dudleya caespitosa* often grows among the densely branched mats *Niebla homalea* on high sea cliffs at Abalone Point in Orange County and in the central coast, including Morro Rock in San Luis Obispo County, which is shown in this photograph. The miniature forest of lichens provides an organic and microhabitat foothold on open, sheer rock that enables *Dudleya* to germinate, flower, and set seed where other annual or perennial vascular plants cannot survive.

Figure 3. *Niebla ceruchoides* also forms associations with the threatened cliff-dwelling *Dudleya stolonifera* on coastal bluff habitats in Aliso Canyon, Orange County. Seed capture by these lichen cushions enhances seedling recruitment across expanses of barren rock, where conditions are not favorable to germinating plants. There may be a mutually reinforcing feedback loop whereby both the lichen and the *Dudleya* plants increase microhabitat soil and moisture, each providing the other with a greater opportunity for establishment in a microhabitat that otherwise would not be available for colonization.

Figure 4. Native landsnails, *Helminthoglypta tudiculata*, often congregate among outcrops for shelter during the daylight hours. *Niebla* and other lichens may increase seedling survival of *Dudleya* by providing protection from herbivory, including *Dudleya verityi* shown here at Long Grade Canyon, Ventura County. Lichens produce chemical compounds, such as usnic acid, which act as a deterrent to grazing by snails and slugs. Lichen chemicals are also significant alleochemicals, which exhibit strong growth-inhibitory properties against seedling development in many higher plants.

Figure 5. Lichens, mosses, liverworts, and cyanobacteria form biological crusts on rock that are an often-overlooked component of the biodiversity of cliff habitats. Crust organisms have low moisture requirements, and their ability to utilize fog and dew as water sources enables them to exist where moisture deficit limits most vascular plants from establishment. Our qualitative observations indicate that these rock-inhabiting biological crust organisms, in addition to the larger fruticose *Niebla*, may contribute to the establishment and survival of local cliff-dwelling *Dudleya* species, including *Dudleya stolonifera* shown here in north Laguna Canyon, Orange County.

Figure 6. Mat-forming species of moss (*Pterogonium gracile*) growing on rock act as a rooting medium for *D. cymosa* spp. *marcescens* on steep cliffs in the western Santa Monica Mountains, Los Angeles County. These relationships point to the importance of both lichens and bryophytes in sustaining the biodiversity of endemic vascular plants of cliff and rock outcrop habitats.

Figure 7. Members of the *Dudleya cymosa* complex appear to be associated with moss-dominated crusts over rock. The Agoura Live-Forever, shown here, is established in moss (*Anacolia menziesii*), which traps seeds that fall from above, on breccia outcrop crevices in the Agoura Hills, Los Angeles County.

Figure 8. Bryophyte crusts that grow as a thin mantle over sheer rock play an important role in the establishment and survival of many *Dudleya* species on vertical rock faces. Poikilohydry and desiccation tolerance (the ability to recover after being air-dry at the cellular level) defines many aspects of bryophyte ecology, which allows them to grow on habitats that rooted plants cannot. *Dudleya* species display genetically controlled adaptations that allow them to colonize these moss-dominated microhabitats. Depicted here is *Anacolia menziesii* in Laguna Beach, which provides a germination substrate for the threatened *Dudleya stolonifera* on otherwise barren rock surfaces.

Figure 9. Absorption and retention of moisture by rock-inhabiting lichens and moss crusts may be vital to *Dudleya* species occupying steep rock surfaces, especially during drought, since these species can absorb moisture from dew or mist in the absence of rainfall. In Laguna Beach, *Dudleya stolonifera* has the ability by rapid production of roots to absorb the moisture captured and retained by moss (*Bryum* sp.) growing on sheer rock. The water is stored in the succulent leaves and spongy tissue of the caudex.

Figure 10. The rapid absorption of moisture and particulates associated with aerosols appears to an important function of the pincushion lichens growing on rock outcrops, which directly benefit the recruitment of *Dudleya* species in these barren, soil-free habitats. The importance of the biological functions of lichens documented in forest and woodland habitats in terms of nutrient and moisture capture may be transferable to these cliff and rock communities.

Figure 11. Biological soil crusts stabilize soil surfaces and reduce erosion, improve percolation and soil moisture storage, enhance vascular plant seedling establishment, and improve soil fertility by nitrogen fixation. Biological crusts dominated by the lichens *Diploschistes scruposus* (white) and *Placidium squamulosum* (brown) enhance seedling recruitment and survival of *Dudleya multicaulis* on clayey soils at this site in the Santa Ana Mountains, Orange County.

Figure 12. Impacts to populations of *Dudleya verityi* occurred following the Green Meadows fire of 1993 in Ventura County. Re-colonization of this *Dudleya* on several charred outcrops occurred after seed nests consisting of regenerating foliose (*Xanthoparmelia* [green] and *Physcia* [gray]) and fruticose (*Niebla*) lichens were re-established, approximately between 1999-2000. The pinholes and grooves or cryptogamic imprints provide a micro-foothold for lichen re-establishment on barren rock, which leads to further colonization by the *Dudleya*.

(Boonpragob et al. 1989). Acidic gaseous forms of nitrogen (HNO_3, HNO_2) are also likely important in southern California as well (T.H. Nash III, pers. communication). See the following publications dealing with lichens and air pollution in southern California for additional reference (Nash and Sigal 1980; Sigal and Nash 1983; Blum et al. 1989; Boonpragob and Nash 1991; Nash and Sigal 1998).

In the summer-dry Mediterranean climate of southern California, dry deposition is the primary pathway for accumulation of these pollutants in the lichens (Boonpragob and Nash 1990). However, van Dobben and ter Braak (1999) documented that not all lichens can be used as general pollution indicators, since some species may not be sensitive to all types of pollutants. Pollution index values that reflect variations in traffic densities and lichen species sensitivities would be expected to correlate specific degrees of urbanization with air pollution (Levin and Pignata 1995), and should be developed in southern California if we are to understand the distribution of many lichen species. Individual species of bryophytes also differ in response to air pollution, especially to mineral ions of chromium, nickel, copper or sulfur (Norris 2003), but may not be as vulnerable to damage from nitrogen oxides. Accordingly, the mosses could be expected to play a greater role in seedling recruitment of *Dudleya* on rock and cliff habitats if the lichens become threatened by air pollution. However, like the canary in the mine, bryophytes can alert us to very subtle changes at very local scales (Shevock 2001), such as changes in moisture regimes owing to habitat alterations.

Fire is devastating to soil crust organisms (Johansen et al. 1984), and damage to saxicolous crusts has been poorly studied (Garty 1992). Hebert and Meyer (1984) observed that saxicolous crustose lichens can survive rangeland fire, and die only if touched by flame or sparks. Little is known about the post-fire re-colonization of epiphytic lichens in the southwest (Romagni and Gries 1997). Management programs that incorporate frequent prescribed burns could impact late-successional epiphytic lichens (Bowler and Riefner 2000), and these practices could also damage cliff and rock cryptogamic communities. However, no quantitative data are available regarding the response of epiphytic lichens, rock-inhabiting biological crusts, or soil crust organisms to fire in southern California. Accordingly, an assessment of fire damage to these organisms and associated post-fire re-colonization should be incorporated into a long-term monitoring program. Our general observations suggest that the fruticose lichens are most easily damaged, and the crustose lichens and turf forming mosses the least, as fire sweeps over outcrops. Severe impacts to some populations of *Dudleya verityi* occurred following the Green Meadows fire of 1993 in Ventura County. Re-colonization of *Dudleya* on several charred outcrops occurred after seed nests consisting of foliose and fruticose lichens were re-established, approximately between 1999-2000 (Riefner, pers. observation; Figure 12). The increased severity of fire in southern California scrub habitats has likely contributed to the destruction of many rock and soil crust communities, which have not been studied.

Danin et al. (1983) and Garty (1992) introduced the concept of the "cryptogamic footprint," which is the micro-relief on rock surfaces (pinhead holes and microgrooves) created by living lithobiontic microorganisms (rock-inhabiting unicellular green algae, cyanobacteria, free-living micro-fungi, and endolithic lichens) during pre-fire periods. These imprints trap and accumulate moisture, minute particles of ash and soil, and organic materials that provide a micro-site foothold that stimulate post-fire recovery of new communities of cryptogams on the same substrates.

Natural plant communities usually develop an extensive underground network of mycorrhizal fungi that interconnect root systems. This network of roots and hyphae perform and mediate numerous important ecosystem functions for their host plants, including enhanced water and nutrient uptake and enhanced seedling development. Little work has been completed regarding the mycorrhizas of *Dudleya.* In southern California, only *Dudleya greenei* has been found to be a host for mycorrhizal fungi (Koske and Halvorson 1989), but few *Dudleya* species have been tested. Recent investigations at the pebble plains in the San Bernardino Mountains have found that *D. abramsii* Rose ssp. *affinis* K. Nakai, which grows in open-habitat soils densely permeated with mycorrhizal hyphae (Riefner and St. John 2000), is not a host. Mycorrhizal relationships of the threatened cliff-dwelling *Dudleya* species, especially those associated with moss crusts, have not been examined.

Parke and Linderman (1980) believe that moss species may promote the survival of vesicular-arbuscular mycorrhizal fungi (VAMF) during periods that are unsuitable for host plant growth. Therefore, mosses may provide for the maintenance of an adequate supply of VAMF inoculum to enable vascular plant colonization of inhospitable habitats. This moss/mycorrhizal relationship could be very important for the rare and threatened *Dudleya* species associated with bryophytes. Woodward et al. (1999) propose incorporating symbiotic associates such as mycorrhizal fungi into monitoring programs, because of their importance to their hosts, which represents a collective effort to obtain resources. Identifying this relationship, however, may be problematic in *Dudleya.* Certain *Dudleya* species studied by Mulroy (1976) and Dodero (1995) produce "rain roots" for rapid uptake of water. These presumably drought-deciduous fine roots may be in a decomposed condition, or unsuitable for mycorrhizal evaluation at most times of the year, and therefore, may require a special protocol for identification (St. John, pers. communication).

Woodward et al. (1999) also propose incorporating other measures such as identifying keystone species (organisms that have strong interactive effects with other species) in such a program. *Niebla ceruchoides* may be a keystone to enhanced seedling establishment of some *Dudleya* species on fog-swept cliffs, and similarly, the mosses may be key to recruitment success of *Dudleya* species on inland shaded cliffs and outcrops. Qualitative and quantitative research has identified that other cryptogams are potential keystone species: the reindeer lichen, *Cladonia rangiformis* Hoffm. of lowland heath communities in the United Kingdom (Newsham et al. 1995), the cyanobacterium, *Microcoleus vaginatus*, in southern California vernal pools (Riefner and Pryor 1996), and the moss genus *Sphagnum* in Canadian peatlands (Rochefort 2000). There is a serious gap in our knowledge of the life histories of the lower plants and lichens of southern California, and other essential relationships between cryptogamic species and vascular plants may be discovered. Unfortunately, there is not a list of specific traits or a protocol to identify keystone species. Accordingly, selecting measures of resilience, persistence, process, and organization is a logical starting point at which to begin a long-term monitoring program (Woodward et al. 1999) of habitats supporting rare *Dudlyea* species.

Further experiments could be designed that would indicate if these *Dudleya* species have developed a resistance to specific lichen substances known to inhibit vascular plant growth, which could help explain their association with the lichen micro-bushes and other properties of the substratum (John W. Thomson, pers. communication). Finally, quantitative data are needed to document the frequency with which *Dudleya* germinates and sprouts within *Niebla* thalli and bryophyte mats in natural conditions.

CONCLUSION

Currently, experimental data are severely limited with regards to air pollution effects of individual lichen and moss species, keystone species associations, damage to crust organisms by changes in the fire ecology, and other factors that could impact populations of rare *Dudleya* species in southern California. Establishment of baseline conditions is needed while viable populations of these lichen, bryophyte, and *Dudleya* associations are still available for study.

Lichens, mosses, fungi, and the algae have not been adequately taken into account by preservation efforts in southern California. Although they are essential to healthy ecosystems, academic botanists, consulting biologists, and land managers have largely overlooked these organisms; they clearly deserve greater attention by resource agencies (Faber 1998; Shevock 1998). Development and implementation of a monitoring program for the *Dudleya* – cryptogamic associations in southern California could address the goals proposed by Eldridge (2000) by creating a broad-based awareness of cryptogams, their habitats, and their benefits to biodiversity.

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