

# Reports

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## Chewing sandpaper: grit, plant apparency, and plant defense in sand-entrapping plants

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**Abstract.** Sand entrapment on plant surfaces, termed psammophory or sand armor, is a phylogenetically and geographically widespread trait. The functional significance of this phenomenon has been poorly investigated. Sand and soil are nonnutritive and difficult for herbivores to process, as well as visually identical to the background. We experimentally investigated whether this sand coating physically protected the plant from herbivores or increased crypsis (e.g., decreased apparency to herbivores). We tested the former hypothesis by removing entrapped sand from stems, petioles, and leaves of the sand verbena *Abronia latifolia* and by supplementing natural sand levels in the honeyscented pincushion plant *Navarretia mellita*. Consistent with a physical defensive function, leaves with sand present or supplemented suffered less chewing herbivory than those with sand removed or left as is. To test a possible crypsis effect, we coated some sand verbena stems with green sand, matching the stem color, as well as others with brown sand to match the background color. Both suffered less chewing herbivory than controls with no sand and herbivory did not significantly differ between the colors, suggesting crypsis was not the driving resistance mechanism. Strong tests of plant apparency are rare; this experimental approach may be possible in other systems and represents one of few manipulative tests of this long-standing hypothesis.

**Key words:** *Abronia latifolia*; *external defenses*; *Navarretia mellita*; *physical defenses*; *plant apparency*; *plant defense*; *psammophory*; *sand armor*.

### INTRODUCTION

Many diverse plants entrap substrate, often sand, particles on their stems, petioles, and leaf surfaces with exudates or trichomes (Fig. 1; Appendix S1). Jürgens (1996) termed this adaptation “psammophory” (“sand-carrying”) and described the phenomenon’s occurrence in the flora of in the Namib Desert; Neinhuis et al. (1996) described the phenomenon mechanistically in members of the Amaryllidaceae and Hyacinthaceae. Danin (1996), Lev-Yadun (2007) and Farmer (2014) each independently described the phenomenon in Middle Eastern desert plants with Farmer terming it “sand armor.” In the Americas, many plants in dune or desert communities are psammophorous, perhaps none more so than the various *Abronia* species (Nyctaginaceae), known

colloquially as sand-verbenas. Table 1 lists over 200 species of psammophorous species from these references and our own observations. These include 88 genera in 34 families of both dicotyledons and monocotyledons across the globe; many more certainly occur in desert, dune, and dry Mediterranean ecosystems worldwide.

Jürgens (1996) presented several explicit hypotheses of the ecological and physiological benefits and costs of this extra-cuticular sand layer, including protection from physical abrasion in sandstorms, reduction of water loss, reduced surface temperature and reduced solar radiation (though potentially limiting photosynthesis). His null hypothesis was that the production of exudates for other purposes (e.g., protection or waste excretion) creates sand entrapment as a side effect. Beal (1878), Jürgens (1996), Neinhuis et al. (1996), Lev-Yadun (2007), and Farmer (2014) all independently hypothesized that the sand layer may protect the plant from herbivores, either by making tissues difficult or costly to consume (resistance) or difficult to find (crypsis).

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FIG. 1. Examples of sand coatings on plants. (1) *Abronia latifolia* (Nyctaginaceae) leaf and (2) stem; (3) *Navarettia mellita* (Polemoniaceae) basal leaves and (4) flower with Bombylid fly; (5) *Crassula alpestris* (Crassulaceae) photo A. Harrower; (6) *Strumaria bidentata* (Amartyllidaceae), photo E. Bihmann; (7) *Mimulus breweri* (Phrymaceae); (8) *Ifigia decumbens* (Asteraceae), photo N. Helme; (9) *Tripterocalyx micranthus*, photo R. Wolf; (10) *Tiquilia plicata* (Boraginaceae), photo S. Matson; (11) *Aliciella leptomeria* (Polemoniaceae), photo J. Andre; (12) *Pholisma sonora* (Boraginaceae), photo A. Bennett. All unlisted photos: E. LoPresti.

Many lines of evidence suggest a direct effect of sand on herbivores. Farmer (2014) and Lev-Yadun (2007) justified this hypothesis by comparing sand to the many examples of crystalline structures in plants (phytoliths, raphides, etc.), containing silicon or calcium, that serve as defenses against herbivores. Sand or other substrate material is known to contribute to tooth wear in humans (Molnar et al. 1983), badgers (Da Silva and MacDonald 1989), many ungulates (Jurado et al. 2008) including livestock (Mayland et al. 1977), and rodents (Gomes Rodrigues et al. 2011). This factor may be an important driver in mammalian dental morphology (Janis and Fortelius 1988, Damuth and Janis 2011) and behavior; moles squeeze the soil out of earthworms “like toothpaste from a tube” before consuming them to reduce potential tooth wear (Gorman and Stone 1990). While untested, these examples support the hypothesis that sand coatings may reduce palatability to herbivores and damage to psammophorous plants.

Several artificially parallel cases occur in the applied literature. Nordlander et al. (2009) demonstrated that coating the stems of young conifers in sand (with an adhesive) increased plant survival by reducing pine weevil (Coleoptera: Curculionidae) damage. Similarly, Showler (2002) and Showler (2003) demonstrated that covering cotton plants in kaolin (a clay mineral) dust reduced oviposition by boll weevils (Coleoptera: Curculionidae: *Anthonomus grandis grandis*), and reduced feeding and oviposition, and caused significant mortality of beet armyworm caterpillars (Lepidoptera: Noctuidae: *Spodoptera exigua*). It is likely that, in the latter cases, the fine dust interfered with the epicuticular waxes on the insects (Ebeling 1971) as opposed to interfering with feeding or digestion.

Sand coating of plant parts may increase crypsis through the increase in substrate matching, allowing the plant to escape detection by herbivores (i.e., reducing its “apparency” sensu Feeny 1976). Several genera of desert spiders entrap sand grains with small “hairlettes” coming off of their dense body setae; this covering renders the spider almost invisible and presumably reduces predation (Duncan et al. 2007). While Feeny’s apparency hypothesis was proposed to explain interspecific plant variation, Rhoades and Cates (1976) suggested that intraspecific and even within-plant distributions of defenses could be understood by considering the predictability and availability of edible tissue to herbivores. Although these theories have been important in stimulating research in plant–herbivore interactions and have been cited over 1400 times (Endara and Coley 2011), they have rarely been tested explicitly. The dearth of direct tests results from a difficulty in unambiguously measuring “apparency” in most complex, real-world situations (Feeny 1991 cited in Stamp 2003).

We experimentally tested the broad hypothesis that a sand coating provides defense and the two mechanistic hypotheses. We chose two locally available psammophorous plants in northern California, representative of this widespread phenomenon, for experiments. We manipulated the sand coating and measured herbivory on *Abronia latifolia* (Nyctaginaceae) at the UC-Davis Bodega Marine Reserve (Sonoma County, California, USA) and *Navarettia mellita* (Polemoniaceae) at the UC-Davis McLaughlin Reserve (Lake County, California, USA). *Abronia latifolia* is a common dune plant along much of the California coast (Baldwin and Goldman 2012). The short glandular trichomes that coat almost the entire surface of stems, petioles, and the

Table 1. A list of sand-entrapping (i.e., psammophorous) plants in the literature and through our own observations.

Family and Genus	Species
Acanthaceae	
<i>Monechma</i>	<i>cleomoides, mollissimum, spartioides</i>
<i>Petalidium</i>	<i>angustitubum</i>
Aizoaceae	
<i>Arenifera</i>	<i>pillansii</i>
<i>Psammodora</i>	<i>herrei, longifolia, modesta, nissenii</i>
Amartyllidaceae	
<i>Bokkeveldia</i>	<i>watermeyerii</i>
<i>Brunsvigia</i>	<i>bosmaniae</i>
<i>Namaquanula</i>	<i>bruce-bayeri, etesionamibensis</i>
<i>Strumaria</i>	<i>bidentata, hardyana</i>
Apiaceae	
<i>Lomiatum</i>	sp.
Asparagaceae	
<i>Chlorophytum</i>	<i>viscosum</i>
Asteraceae	
<i>Centaurea</i>	<i>pumilio</i>
<i>Chaenactis</i>	<i>steviooides</i>
<i>Dicoria</i>	<i>canescens</i>
<i>Diphormotheca</i>	sp.
<i>Helichrysum</i>	<i>gariepinum, pumilio, roseo-niveum</i>
<i>Hemizonia</i>	<i>congesta</i>
<i>Heterotheca</i>	<i>grandiflora</i>
<i>Holocarpha</i>	<i>virgata</i>
<i>Ifloga</i>	<i>decumbens, verticillata, spicata</i>
<i>Lasiopogon</i>	<i>glomerulatus</i>
<i>Lessingia</i>	spp.
<i>Leysera</i>	<i>tenella</i>
<i>Madia</i>	<i>elegans, gracilis, sativa</i>
<i>Podotheca</i>	<i>angustifolia</i>
<i>Rigiopappus</i>	<i>leptocladus</i>
Boraginaceae	
<i>Eucrypta</i>	spp.
<i>Phacelia</i>	<i>inyoensis, ivesiana, parishii, pulchella, stellaris</i>
<i>Pholisma</i>	<i>arenarium, sonora</i>
<i>Tiquilia</i>	<i>atacamensis, litoralis, plicata</i>
Brassicaceae	
<i>Eremobium</i>	<i>aegyptiacum</i>
<i>Savignya</i>	<i>parviflora</i>
Cactaceae	
<i>Ariocarpus</i>	<i>kotschoubeyanus</i>
<i>Pediocactus</i>	<i>sileri</i>
<i>Sclerocactus</i>	<i>spinosior</i>
Caryophyllaceae	
<i>Gypsophila</i>	<i>viscosa</i>
<i>Silene</i>	<i>antirrhina, laciniata, sedoides, succulenta, villosa</i>

Table 1 (continued)

Family and Genus	Species
<i>Spergularia</i>	<i>macrotheca, purpurea</i>
Chenopodiaceae	
<i>Atriplex</i>	spp.
<i>Chenopodium</i>	spp.
Colchicaceae	
<i>Hexacyrtis</i>	<i>dickiana</i>
Crassulaceae	
<i>Crassula</i>	<i>alpestris</i>
Cyperaceae	
<i>Lepidosperma</i>	<i>viscidum</i>
Euphorbiaceae	
<i>Croton</i>	<i>setigerus</i>
<i>Euphorbia</i>	<i>gummifera</i>
Fabaceae	
<i>Indigofera</i>	<i>argentea, colutea</i>
<i>Ononis</i>	<i>matrix, repens, serrata, variegata</i>
<i>Stylostanthes</i>	<i>viscosa</i>
Geraniaceae	
<i>Erodium</i>	<i>cicutarium</i>
<i>Geranium</i>	<i>viscosissimum</i>
Hyacinthaceae	
<i>Albuca</i>	<i>aspera, bontebokensis, bruce-bayeri, crudenii, dinteri, etesiogariensis, foetida, glandulosa, jacquinii, shawii, spiralis, viscosa, viscosella</i>
<i>Dipcadi</i>	<i>dinteri, vaginatum</i>
<i>Ornithogalum</i>	<i>albucooides, glandulosum, karachab-poortense, psammophorum, sabulsoum, scabrocostatum</i>
Iridaceae	
<i>Babiana</i>	sp.
<i>Hexaglottis</i>	sp.
Loasaceae	
<i>Mentzelia</i>	<i>albicaulis, leucophylla, tricuspis</i>
Molluginaceae	
<i>Limeum</i>	<i>arabicum, arenicolum, viscosum</i>
Nyctaginaceae	
<i>Abronia</i>	<i>alpina, ammophila, angustifolia, elliptica, fragrans, latifolia, macrocarpa, maritima, mellifera, nana, pogonantha, turbinata, umbellata, villosa</i>
<i>Allionia</i>	<i>incarnata</i>
<i>Boerhavia</i>	spp.
<i>Mirabilis</i>	<i>multiflora, domestic spp.</i>
<i>Tripterocalyx</i>	<i>micranthus</i>
Orobanchaceae	
<i>Castilleja</i>	<i>applegatei</i>
<i>Chloropyron</i>	<i>molle, palmatum, tencopensis</i>

Table 1 (continued)

Family and Genus	Species
<i>Orobanche</i>	<i>californica, cooperi, parishii, valida</i>
Onagraceae	
<i>Camissonopsis</i>	<i>cheiranthifolia, pallida</i>
Phrymaceae	
<i>Mimulus</i>	<i>bigeloveii, breweri, douglasii, fremontii, laynae, mohavensis, nanus, pillosus, rattanii, torreyi</i>
Plantaginaceae	
<i>Collinsia</i>	<i>corymbosa, tinctoria</i>
<i>Stemodia</i>	<i>viscosa</i>
Poaceae	
<i>Distichlis</i>	<i>spicata</i>
<i>Stipagrostis</i>	spp.
Polemoniaceae	
<i>Aliciella</i>	<i>latifolia, leptomeria, lottiae, micromeria, monoensis, triodon</i>
<i>Collomia</i>	<i>diversifolia, tinctora</i>
<i>Eriastrum</i>	<i>filifolium</i>
<i>Gilia</i>	<i>austro-occidentalis, brecciarum, cana, latiflora, malior, tenuiflora</i>
<i>Ipomopsis</i>	<i>depressa, gunnisonii, polycladon</i>
<i>Navarretia</i>	<i>mellita, pubescens, sinistra</i>
<i>Polemonium</i>	<i>micranthum, viscosum</i>
Polemoniaceae	
<i>Chorizanthe</i>	<i>pungens</i>
<i>Eriogonum</i>	<i>viscidulum</i>
Scrophulariaceae	
<i>Anticharis</i>	<i>glandulosa</i>
<i>Chaenorhinum</i>	<i>minus</i>
<i>Nemesia</i>	<i>viscosa</i>
<i>Peliostomum</i>	<i>viscosum</i>
<i>Sutera</i>	<i>fruticosa, maxii, pallida, sessilifolia, tristis</i>
Solanaceae	
<i>Nicotiana</i>	<i>glauca, spp.</i>
<i>Petunia</i>	<i>domestic, axillaris, exserta, integrifolia</i>
<i>Schizanthus</i>	<i>hookeri</i>
Turneraceae	
<i>Piriqueta</i>	<i>morongii</i>
Xanthorrhoeaceae	
<i>Trachyandra</i>	<i>bulbinifolia, divaricata</i>
Zygophyllaceae	
<i>Fagonia</i>	<i>arabica, glutinosa, mollis</i>

Note: See Appendix S1 for further information and references.

bottoms of leaves, entrap sand while the tops of leaves remain sparsely sandy (Fig. 1). The perennial *A. latifolia* is grazed by snails (*Helix aspersa*; personal observation), deer mice (*Peromyscus maniculatus*; Osborne and Sheppe

1971), possibly deer (as in Crete et al. 2001) and a seasonally common leaf-mining caterpillar (Heliodinidae: *Lithariapteryx abroniaeella*; personal observation).

*Navarretia mellita*, as well as several congeners, is densely glandular and often become covered by sandy substrate; it is a ruderal species endemic to California, occurring in small patches along roadsides, in ditches, and eroded areas. These patches are usually small (1–50 individuals) and likely ephemeral. The entire glandular inflorescence, including the spiky bracts, is consumed by a mammalian browser and the damage is consistent with that of black-tailed jackrabbits (personal observation).

## MATERIALS AND METHODS

### *Abronia sand reduction experiment*

In order to experimentally determine whether entrapped sand, at natural density, defended *A. latifolia*, we performed an experimental sand removal. In the dune ecosystem, it is difficult to determine which leaves belong to the same plant, as the majority of the plant is below-ground and connected via an extensive and deep root runner system. Therefore, for our experimental unit, we chose and labeled 30 pairs of nearest-neighbor stems (lying on the ground, not growing up through vegetation) with a roughly equal number of leaves that were initially free of herbivore damage. On 14 October 2014, we selected pairs of stems along a line transect, alternately assigning one stem of each pair to a control treatment and the other to a manipulation. For each manipulated stem, we gently brushed off sand from petioles and upper and lower leaf surfaces with a soft wet sponge. As to not risk plant damage during manipulation, we did not attempt to remove all sand; however the reduction in sand cover from the treatment was visually apparent (Fig. 2). We assessed herbivore damage and reimposed treatments on 26 October and 23 November and collected final data on 12 December. We noted a small amount of mechanical damage on both control and manipulated plants that was likely due to handling or mammals (e.g., humans, deer) trampling the plants; we did not include these instances in analyses.

### *Abronia apparency manipulation*

To determine whether sand protected plants physically or because of increased crypsis due to attached sand, we conducted an experiment manipulating the cryptic effect of the sand coating. On 20 April 2015, we tagged 25 sets (blocks) of three apical stems lying on sand with four or more leaves each. In each set, we assigned each stem to one of three treatments: (1) a sand removal as in the previous experiment, (2) an addition of colored green sand (Michaels Co., Irving, Texas, USA) to more closely match the stem color, or (3) an addition of tan sand, of the same grit as the green, closely matching the background color. We predicted (1) that sand treatments



FIG. 2. *Abronia latifolia* experiments. Top: leaf cluster pair after treatments imposed. On the left is the sand reduction treatment, note especially the bare petioles (compare to Fig. 1); on right is control. Below: washed (left), brown sand (center), and green sand (right) treatments in the apparency experiment. Photos: E. LoPresti

would receive less herbivory than the washed stem and (2) the more cryptic (e.g., less apparent) brown sand treatment would receive less herbivory than the green sand treatment. We checked these plants for damage and reimposed treatments on 5 May and 15 May and collected the final measurements on 3 June 2015.

#### *Navarretia* soil addition experiment

To determine whether substrate-entrapment reduced herbivory on inflorescences of *N. mellita*, we conducted a substrate addition experiment. The spiky, delicate, and complex architecture of this plant did not permit the removal of appreciable amounts of substrate without damaging the plant; the small patch size of all patches we located prevented an additional apparency manipulation. Therefore, we tagged 37 plants (all plants in the patch with >1 inflorescence and no prior damage) on 7 June and alternately assigned them to a control group and a substrate addition group (mean number of inflorescences  $\pm$  1 SE, control  $6.0 \pm 0.8$  and in substrate addition  $6.1 \pm 1.1$ ). Plants in the substrate addition treatment received a gentle

shower of substrate, much of which was entrapped on the glandular trichomes (a photograph is in Appendix S1). We refreshed treatments on 4 July and 20 July and recorded damaged and intact inflorescences on 6 August, when many fruit were dehiscent.

#### Statistics

All statistical analyses were performed using R version 3.0.2 (R Development Team 2013). As *Abronia* stems differed in number of leaves over time, because of both growth and senescence, we used a binomial mixed model to analyze the number of leaves damaged (of total leaves), with both date and pair (block in apparency experiment) as varying intercepts and treatment as a fixed effect. We used likelihood ratio tests to determine whether this model fit the data better than a null model including only the random effects but not treatment. For the *Navarretia* experiment and the *Abronia* leaf miner, where herbivory occurred rarely, we analyzed the categorical response to the treatments (herbivory/no herbivory) using a chi-square test with a Yates' correction for small sample size.

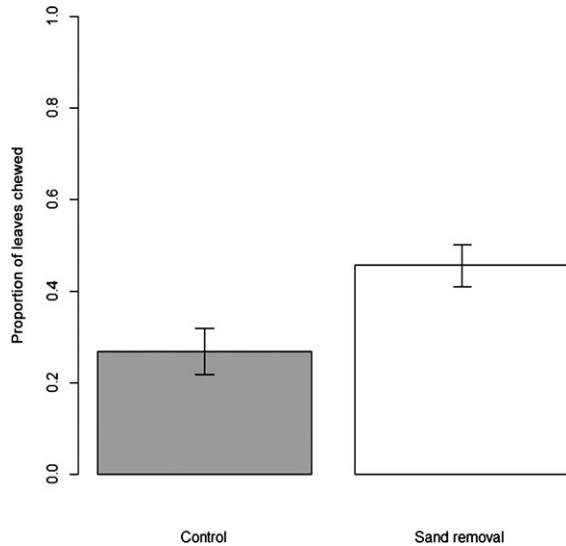


FIG. 3. Proportion of *Abronia latifolia* leaves with chewing herbivore damage. For ease of visualization, these results are presented as a proportion, averaged within each treatment for each plant and date; statistics were done on binomial data.

## RESULTS

### *Abronia* field sand reduction

The experimental sand reduction roughly doubled chewing herbivory compared to controls on the same dates (Fig. 3). A model that included treatment as a fixed effect (plus date and pair as random effects) fit the data significantly better than the random intercept-only model (likelihood ratio test,  $\chi^2 = 16.4$ ,  $df = 1$ ,  $P < 0.001$ ). This model predicted 111% (95% CI, 35%–159%; treatment coefficient  $z = 3.57$ ,  $df = 176$ ,  $P < 0.001$ ) more herbivory for the stems in the sand removal treatment. The noted herbivory was primarily small holes both in center and margins of leaves, often with the lower epidermal layer still intact. We could not conclusively assign this damage to any single herbivore; in our experience both arthropod and molluscan herbivores could produce this type of damage.

### *Abronia* apparency manipulation

Contrary to prediction, both sand treatments (green and brown) suffered less herbivory than the sand-removal treatment (Fig. 4). The model incorporating treatment and the random effects of date and block (of all three treatments) fit significantly better than a model incorporating only the random effects (likelihood ratio test,  $\chi^2 = 34.3$ ,  $df = 2$ ,  $P < 0.001$ ). Tukey post hoc comparisons of the treatments showed no difference between the two sand treatments ( $P > 0.33$ ). A model incorporating sand presence fit the data better than that of color (AIC 259, 261, respectively) and predicted an increase of 146% (79–240%,  $z = 5.64$ ,  $P < 0.001$ ) in the incidence of leaf damage for a sand addition. We also analyzed the damage

by mining caterpillars (*Lithariapteryx abroniaella*), as they were more common during this spring experiment, though still uncommon: of the total of 225 observations after the first week, we only noted leaf miners in 56 instances. This herbivore was unaffected by our sand treatments, of 25 replicates per treatment, 28% (7) with brown sand, 40% (10) with green sand, and 36% (9) with sand-removal stems had mines, a nonsignificant difference (two-tailed chi-square test,  $\chi^2 = 0.82$ ,  $df = 2$ ,  $P = 0.66$ ).

### *Navarretia* soil addition experiment

Plants that received soil addition had a lower incidence of inflorescence removal (1/19 plants, 5%) than control plants (8/18 plants, 44%), a significant result (two-tailed chi-square with Yates' correction,  $\chi^2 = 5.7$ ,  $df = 1$ ,  $P = 0.02$ ). They matured 14% more inflorescences per plant than controls, despite having only 1.8% more inflorescences when the experiment began. All damage observed was from a mammalian browser, likely black-tailed jackrabbit, which removed entire inflorescence heads (a tight cluster of flowers). We did not calculate whether the amount of plant tissue removed was greater in the control plants, as the comparison was to only one damaged sand-addition plant. Descriptively, that sand addition plant lost 33% of its inflorescences to damage (2/6); the eight damaged control plants lost a similar percentage (mean 34%, range 6–100% removal).

## DISCUSSION

We found that substrate entrapment served as an external physical defense in all tests with *Abronia* and *Navarretia*. Sand and other substrate stuck onto plant

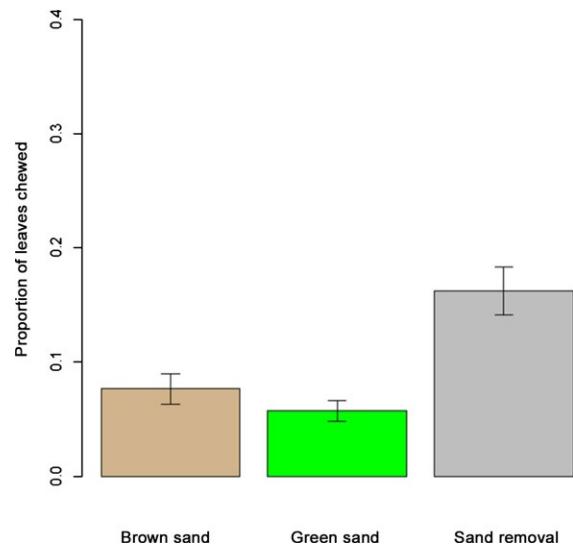


FIG. 4. Proportion of *Abronia latifolia* leaves with chewing herbivore damage. For ease of visualization, these results are presented as a proportion, averaged within each treatment for each plant and date; statistics were done on binomial data.

surfaces made that tissue less preferred by mammalian herbivores in these tests, decreasing observable damage to leaves in *Abronia* and increasing inflorescence survival in *Navarretia*. Similarly, externally feeding gastropod and insect herbivores cannot easily avoid masticating and ingesting the sand and avoided tissues that were coated with sand.

Sand-entrapment is a common plant trait (Table 1; Appendix S1). LoPresti et al. (2015) list over 110 genera of sticky plants that entrap insects. Insect entrapment is far rarer than substrate-entrapping trichomes in plants (*personal observation*; we listed in Table 1 only those species that we had directly observed or had a reference for). Many plants that do not entrap insects entrap substrate, a striking example being the doveweed, *Croton* (formerly *Eremocarpus*) *setigerus*, which catches substrate in its complex branching trichomes, especially when growing near dirt roads. The amount of substrate entrapped, its location on the plant, and the herbivore communities vary widely among plant species and the effectiveness of this putative defense will vary concordantly. For example, the *Abronia* leaf miner was unaffected by the sand treatments, in contrast to externally feeding leaf chewers. External and internal defenses may act differently on different guilds of herbivores (LoPresti 2015); internally feeding herbivores (such as leaf miners) may be less affected by surface defenses given their unique ability to avoid them.

In the sand color manipulation on *Abronia*, we found no significant differences between the colors, though both were associated with less herbivory than the removal control. This negative result suggests that any difference in apparency was not the driving factor in dictating herbivory (as the two sand coatings differed in apparency from the removal and each other, in different directions). This negative result complements the simple removal experiment, suggesting the result was caused by the physical properties of the sand itself, not mimesis. The apparency hypothesis has been prominent in theoretical discussions of plant defense but has received relatively few strong empirical tests (but see Strauss and Cacho 2013, Strauss et al. 2015). Our results failed to support an important role of apparency. Stamp (2003) suggests that the plant apparency hypothesis has not been widely tested because of the difficulty of measuring apparency (the classic comparison is an apparent tree vs. a small ruderal weed). Our test manipulated the apparency of individual stems, an approach that could be performed with other substrate-entrapping plants, of which there are many.

Jürgens (1996) lists at least eight distinct hypotheses for psammophory; these non-mutually exclusive hypotheses have not been tested in this or any other system and several, in our opinion, are likely for *Abronia* and *Navarretia* (making the trait pleiotropic). Sandstorms are practically nonexistent in either field site in this study, though wind-blown substrate (a potentially abrasive force) is common, and it is likely that this is how most of the entrapped substrate accrues on both plants. Evolutionary

selective pressures across the numerous plants in Table 1 have varied through time and space, and many of Jürgens's astute hypotheses demand testing in field settings. Psammophory is likely to have several potential costs. These costs may occur at several levels: investment costs (e.g., production and excretion of sticky exudates) as well as performance costs (e.g., decreased photosynthesis because of light blocked by sand) and ecological costs (e.g., decreased apparency to pollinators or other mutualists). Neither these costs nor other possible benefits have been quantified in psammophorous plants and deserve investigation in future studies. Psammophory will likely be effective only in suitable habitats. A comparative approach (Agrawal 2007) could shed light on the evolutionary forces that have shaped this trait, especially in a genus such as *Navarretia*, where many species are not glandular or substrate-entrapping. (To the best of our knowledge, all *Abronia* species are sand covered under normal circumstances).

This study represents the first experimental support for the long-standing hypothesis that a sand covering protects plants from herbivory, reducing tissue loss in both species tested, and increasing a fitness proxy in *Navarretia*. Herbivore resistance is but one possible function of psammophory and careful experimental testing of this and alternative hypotheses is needed. In all three experiments, the effect size of a sand coating as a defensive mechanism was relatively large compared to many other plant defenses in the literature. This result is consistent with meta-analyses and reviews that have concluded that external defenses, particularly physical ones, can be extremely potent and may be undervalued by ecologists (Carmona et al. 2011, LoPresti 2015).

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