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Mesowear patterns in horses suggest that horse diets were influenced by Cenozoic climate and its impact on vegetation and habitat structure. Horses show evidence of increased dietary abrasion as soon as grasslands became more widely available, and there is no evidence of a delay toward the shift to grazing. The temporary increase in dietary abrasion among brachyodont anchitheres beginning in the early Miocene occurred during a time during which there is evidence for increasing abundance of C₃ grasslands. However, most fossil horse samples yield highly variable mesowear scores (Fig. 1E), suggesting that most paleopopulations were experiencing rather low levels of dietary abrasion, indicating that selection for increased crown height may have been weak or absent most of the time. The famous “Great Transformation” (7) in molar crown morphology leading to the subfamily Equinae probably originated during intervals of heavy selection pressure due to pronounced increases in dietary abrasion among populations that were pioneering new habitats. A few early Miocene samples from the Great Plains (purple arrows in Fig. 1, C and E), including *Parahippus*, the genus from which Equinae originated, demonstrate mesowear values that are equal to those of later Equinae and suggest levels of dietary

abrasion that may have been extreme for their comparatively brachyodont dentitions.

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Supporting Online Material

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Materials and Methods

SOM Text

Figs. S1 to S4

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References

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Paleoindian Seafaring, Maritime Technologies, and Coastal Foraging on California’s Channel Islands

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Three archaeological sites on California’s Channel Islands show that Paleoindians relied heavily on marine resources. The Paleocoastal sites, dated between ~12,200 and 11,200 years ago, contain numerous stemmed projectile points and crescents associated with a variety of marine and aquatic faunal remains. At site CA-SRI-512 on Santa Rosa Island, Paleocoastal peoples used such tools to capture geese, cormorants, and other birds, along with marine mammals and finfish. At Cardwell Bluffs on San Miguel Island, Paleocoastal peoples collected local chert cobbles, worked them into bifaces and projectile points, and discarded thousands of marine shells. With bifacial technologies similar to those seen in Western Pluvial Lakes Tradition assemblages of western North America, the sites provide evidence for seafaring and island colonization by Paleoindians with a diversified maritime economy.

By about 13,000 years ago, Paleoindians were widespread in North America, with terrestrially focused Clovis sites found throughout the continent, especially in interior settings (1). Although a few Terminal Pleistocene sites have been found along the Pacific Coast of Peru (2, 3) and seaweeds have been dated to ~14,000 years ago at Monte Verde II in Chile (4), little is known about Paleoindian settlement, economies, and technologies along the coastlines of North America (5). Rising postglacial sea levels and coastal erosion may be responsible for this gap, but traces of early coastal set-

tlement might still be present in areas of steep bathymetry near geographic features that attracted Paleoindian peoples inland and away from now-submerged Terminal Pleistocene coastlines (6).

California’s Northern Channel Islands (Fig. 1), separated from the mainland by an oceanic strait a minimum of 7 to 20 km wide since the Last Glacial Maximum, have long been a source of claims for ancient human settlement (7). They have relatively impoverished terrestrial flora and fauna but a wealth of marine resources including seaweeds, marine mammals, shellfish, finfish, and seabirds. Human bones from the Arling-

ton Springs site on Santa Rosa Island have been dated to ~13,000 ± 200 calendar years ago (cal BP) (6–8), and a low-density shell midden at Daisy Cave on San Miguel Island dates to ~11,500 ± 200 cal BP (6), but these sites yielded no diagnostic artifacts and few faunal remains. This led some to question the fully maritime character and technological affiliation of these early Channel Island peoples (9).

Until ~10,000 years ago, the Northern Channel Islands were still connected as one large island, Santarosae. Since 13,000 cal BP, sea levels have risen by ~70 m, shrinking the size of the islands by ~65%, shifting shorelines as much as 10 km, and submerging Terminal Pleistocene coastlines where early maritime peoples most likely lived (10). By examining caves, springs, tool-stone outcrops, and other geographic features that attracted ancient maritime peoples away from Santarosae’s paleoshorelines, we have identified >50 shell middens and other sites dated

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from ~10,200 to 8000 cal BP, suggesting that a substantial human population existed on the islands in the Early Holocene (6, 11). Here, we describe three Terminal Pleistocene sites—a stratified site on Santa Rosa sealed beneath 2.5 m of alluvium and two large surficial sites on San Miguel containing five shell midden loci—that provide evidence for a diversified maritime economy and a sophisticated technology. Colonizing the Northern Channel Islands at this time required a sea voyage of 9 to 10 km (10).

CA-SRI-512W was identified on the northwest coast of Santa Rosa Island by two of the authors (J.M.E. and T.C.R.) in 2008. Situated east of the mouth of Arlington Canyon, where

the ~13,000-year-old Arlington Man skeletal remains were found in 1959 (7, 8), the site is located adjacent to the modern coast on an uplifted marine terrace ~20 m above sea level (masl). Comparison of sea level curves (12) to local bathymetric maps suggests that the site was ~5 to 7 km from the coast and ~75 masl when it was occupied. CA-SRI-512W contains a deeply buried paleosol, 30 to 40 cm thick, exposed in the eroding sea cliff (fig. S1), sealed beneath 2.5 m of alluvium containing at least five overlying soil horizons. Because the Northern Channel Islands are nearly devoid of burrowing animals, the stratigraphy of CA-SRI-512W is exceptional. Well-preserved bird bone and charcoal samples from the deeply buried paleosol—

four of them embedded in the same soil matrix as chipped stone tools, other artifacts, and the remains of marine fauna—produced AMS ^{14}C dates ranging from ~12,000 to 11,350 cal BP (Table 1), with a most likely age range of ~11,800 to 11,500 cal BP.

At CA-SRI-512W, we collected 52 small stemmed Channel Island Barbed (CIB) points (13), 15 crescents, and numerous bird bones (table S1) from the slope below the Terminal Pleistocene paleosol. Fourteen CIB points or preforms and four crescents were found in situ in five test pits excavated in the Terminal Pleistocene paleosol. Chipped stone crescents are a relatively rare artifact found with stemmed points in some early California, Great Basin, and Columbia Plateau sites (14, 15). Other tools found in situ include biface preforms, flake tools, abundant chipped stone tool-making debris, several abraded bone tool fragments, and a large piece of red ochre with a deep groove cut across it (Fig. 2). The chipped stone tools are made primarily from local island cherts, but one piece of obsidian tool-making debris was found in situ. Geochemical analysis of this artifact indicates that it came from the West Sugarloaf flow of the Coso Volcanic Field (fig. S2) in eastern California, more than 300 km to the northeast, which suggests that Channel Island peoples participated in long-distance trade nearly 12,000 years ago.

More than 5000 bone fragments were recovered from the five test units at CA-SRI-512W, many of them burned. The faunal assemblage is dominated by birds, including several species of waterfowl and seabirds such as Canada goose (*Branta canadensis*), snow goose (*Chen*

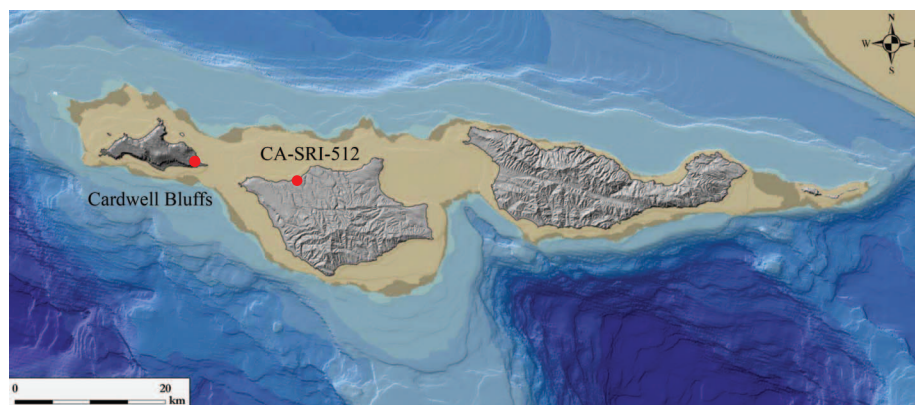


Fig. 1. Map showing the locations of CA-SRI-512 and Cardwell Bluffs sites relative to reconstructed Terminal Pleistocene paleogeography, including -60 m (dark tan) and -50 m (light tan) submarine contours that approximate paleoshorelines at ~12,500 and 11,000 cal BP.

Table 1. AMS ^{14}C Dates from CA-SRI-512W, CA-SMI-678, and CA-SMI-679. All dates are for single shell or charcoal fragments, measured via accelerator mass spectrometry (AMS); calendar age ranges, expressed at 1σ , were calculated in CALIB 6.0 (24), using a ΔR of 225 ± 35 for marine samples. UF, ultrafiltration. (See supporting online material for more details.)

Site (CA number): Locus and provenance	Material dated	Lab number	Measured age	Calibrated age range (cal BP)
SRI-512W: A6 paleosol	Goose bone (XAD extract)	UCIAMS-59871	$10,000 \pm 30$	11,600–11,355
SRI-512W: A6 paleosol	Goose bone (XAD extract)	UCIAMS-59872	$10,045 \pm 40$	11,700–11,405
SRI-512W: burned stump on slope below A6	<i>Ceanothus</i> charcoal	Beta-261353	$10,090 \pm 50$	11,820–11,410
SRI-512W: A6 paleosol	Goose bone (UF)	OS-68030	$10,150 \pm 40$	11,970–11,730
SRI-512W: A6 paleosol	Charred twig	UCIAMS-60751	$10,155 \pm 30$	11,960–11,760
SRI-512W: below A6	<i>Ceanothus</i> charcoal	OS-75147	$10,200 \pm 45$	12,010–11,820
SMI-678: Locus A, 0–5 cm	<i>Haliotis rufescens</i>	OS-59534	$10,650 \pm 40$	11,635–11,350
SMI-678: Locus A, Unit 4, 5–10 cm	<i>Haliotis rufescens</i>	OS-75990	$10,700 \pm 50$	11,730–11,400
SMI-678: Locus B, Unit 1, 0–5 cm	<i>Haliotis rufescens</i>	OS-80130	$10,650 \pm 40$	11,635–11,350
SMI-678: Locus B, 0–5 cm	<i>Haliotis rufescens</i>	OS-63090	$10,650 \pm 55$	11,655–11,340
SMI-678: Locus B, surface	<i>Haliotis rufescens</i>	OS-76006	$10,750 \pm 40$	11,915–11,440
SMI-678: Locus C 0–5 cm	<i>Haliotis rufescens</i>	OS-59413	$10,650 \pm 40$	11,635–11,350
SMI-678: Locus C, Unit 1, 0–10 cm	<i>Haliotis rufescens</i>	OS-63089	$10,500 \pm 50$	11,310–11,190
SMI-678: Locus C, Unit 1, 10–20 cm	<i>Haliotis rufescens</i>	OS-76002	$10,850 \pm 50$	12,060–11,755
SMI-678: Locus D, probe 0–5 cm	<i>Mytilus californianus</i>	OS-76005	$10,850 \pm 50$	12,060–11,750
SMI-678: Locus D, 0–5 cm	<i>Mytilus californianus</i>	OS-76003	$10,900 \pm 50$	12,180–11,915
SMI-678: Locus D, 10–20 cm	<i>Chlorostoma funebris</i>	OS-76004	$10,900 \pm 45$	12,170–11,925
SMI-678: D, Unit 1, 0–5 cm	<i>Mytilus californianus</i>	OS-80129	$10,950 \pm 45$	12,240–12,000
SMI-679SE: Tegula feature	<i>Chlorostoma funebris</i>	OS-63091	$10,750 \pm 55$	11,990–11,430
SMI-679SE: Tegula feature	<i>Mytilus californianus</i>	OS-76008	$10,800 \pm 45$	11,955–11,710
SMI-679SE: Unit 1, 0–5 cm	<i>Haliotis rufescens</i>	OS-80131	$10,800 \pm 45$	11,955–11,710
SMI-679SE: Unit 1, 15 cm	<i>Haliotis rufescens</i>	OS-80171	$10,800 \pm 40$	11,950–11,720
SMI-679SE: Tegula feature	Charred twig	OS-70638	$10,900 \pm 45$	12,920–12,630

caerulescens), cormorant (*Phalacrocorax* spp.), and albatross (*Phoebastria albatrus*). The CIB points and chipped stone crescents seem likely

to have been used to hunt birds, but pinniped and undifferentiated marine mammal bones were also recovered, along with smaller numbers of

bones from rockfish (*Sebastes* spp.), greenling (*Hexagrammidae*), sculpin (*Cottidae*), surfperch (*Embiotocidae*), and the herring/sardine family



Fig. 2. Paleocoastal artifacts from CA-SRI-512W. Channel Island Barbed (CIB) points at left and three crescents in center column are from slope below eroding A6 paleosol; sawn red ochre (lower center), abraded bone tool fragments (upper right), projectile points, and crescents at right were found in situ in test units. Scale bar, 1 cm per square. [Photo by J. Erlandson]

Fig. 3. Chert projectile points from CA-SMI-678 and CA-SMI-679. Center column, five eccentric crescents (top to bottom: SMI-679-39, -214, -67, -5, and -341). Left columns, Amol points (top to bottom, column 1: 678-58, 679-24, 679-256; column 2: 678-722, 679-28, 678-38). Right columns, CIB points (column 4, top to bottom: 679-255, 679-216, 679-300; column 5: 679-215, 678-101, 678-86). SMI-678-722 was found in situ within shell midden stratum dated to ~12,240 to 11,750 cal BP. Scale bar, 1 cm per square. [Photo by J. Erlandson]



(Clupeidae) (table S3). On the slope below the site, we found a burned tibiotarsus fragment from an extinct flightless goose, *Chendytes lawi* (16). No marine shells have been recovered from CA-SRI-512W.

The relatively small size of this Paleocoastal site (which is exposed for about 60 m along the modern sea cliff), along with the density and diversity of artifacts and faunal remains, suggests that it served as a seasonal hunting camp, probably occupied by fairly mobile hunter-gatherers. The abundance of geese implies that the site was occupied in winter (17), but it may also have been used in other seasons. Situated just east of Arlington Canyon, the largest drainage on Santa Rosa Island, the site may have been located downwind (south-east) of a broad, marshy canyon bottom. Wetlands in this canyon would have been an ideal location to hunt waterfowl and seabirds attracted to the island by the lack of large terrestrial predators.

Near Cardwell Point on San Miguel Island, naturally occurring chert cobbles can be found scattered across a raised marine terrace at 65 to 75 masl. Here we identified two large and heavily eroded lithic scatters (CA-SMI-678 and -679) that were situated ~1 to 2 km from the coast and ~125 masl during the Terminal Pleistocene. At the Cardwell Bluffs sites, in an area ~500 m long and 300 m wide, we collected more than 400 whole or broken bifaces (table S2) and identified remnants of five discrete shell middens where faunal remains and artifacts were found in situ. AMS ¹⁴C dates from well-preserved marine shells from four middens at CA-SMI-678 ranged from ~12,250 to 11,200 cal BP. Four dates on marine shells from a small midden at CA-SMI-679 average ~11,850 cal BP. A charred twig from this midden, dated to ~13,000 cal BP, may indicate an earlier human occupation contemporary with Arlington Springs. Because of potential problems with natural wildfires and the clearer cultural origin of the marine shells, however, we believe that the shell dates better estimate the age of the CA-SMI-679 midden.

Stratigraphic profiles at CA-SMI-678 and CA-SMI-679 demonstrate that portions of the sites were once buried under a thin sheet of dune sand, probably until the 19th to 20th centuries when overgrazing by introduced livestock caused heavy erosion. On eroded surfaces, Paleocoastal artifacts were found in several clusters interspersed with intact site remnants, suggesting that multiple occupations of the sites occurred over a millennium or more. Twelve test pits excavated in intact site remnants produced thousands of chipped stone artifacts, nearly 10 kg of marine shell (tables S4 and S5), but no animal bone.

The chipped stone bifaces from Cardwell Bluffs ranged from preforms to finished or broken projectile points (Fig. 3). Preforms consisted primarily of bifaces broken during manufacture of points or knives, whereas the finished artifacts were mostly basal point fragments that appear to have been discarded during repair of hunting gear. We collected 31 crescents, including lunate forms and “eccentric” varieties with notches and projections

on one side. Stemmed points were more abundant, including 32 CIB points of various sizes and shapes, some with elongated stems and pronounced barbs, others with shorter stems or barbs and serrated blade margins. We also recovered 23 Amol points, a previously unknown stemmed point type that lacks barbs although most examples have serrated blade margins. Variation in the two stemmed point types may result from the reworking and recycling of broken points. Most of the points, preforms, and bifaces come from eroded site surfaces, but many were found around the margins of the dated shell middens, and three bifaces and an Amol point were found in situ in the ~12,100-year-old shell midden at CA-SMI-678D.

The marine shell from CA-SMI-678 demonstrates that Paleoindians harvested a variety of shellfish from rocky intertidal and kelp forest habitats, including red abalone (*Haliotis rufescens*), giant chiton (*Cryptochiton stelleri*), mussel (*Mytilus californianus*), black turban snail (*Chlorostoma [Tegula] funebris*), and crabs (table S4). The abundance of red abalone and giant chiton, and the near absence of black abalone (*H. cracherodii*), suggests that sea surface temperatures were cooler than today. An 11,850-year-old basin-shaped midden feature at CA-SMI-679, ~1 m in diameter and 5 to 15 cm thick, was dominated by black turban shells, a small intertidal gastropod easily gathered but laborious to process. Pitted stones found nearby were probably used as anvils to crack turban shells and extract their meat. A more extensive shell midden about 3 to 4 m to the west contained a more balanced shellfish assemblage (table S5) similar to that of CA-SMI-678.

Along with Daisy Cave and Arlington Springs, these Paleocoastal sites are preserved because they were situated on upland landscapes distant from submerged Terminal Pleistocene shorelines—interior localities where Paleocoastal people were attracted by sources of tool stone, fresh water, shelter, and possibly a marsh near CA-SRI-512. The artifact assemblages from CA-SRI-512W and Cardwell Bluffs provide a window into the technologies used by maritime Paleoindians on California’s Channel Islands. Early projectile point technologies along the southern California Coast were long thought to have been relatively crude (18, 19), but the finished points and crescents from these island sites are finely made—thin and highly symmetrical, with delicate barbs, serrations, or notches. Although the faunal assemblages from Cardwell Bluffs and CA-SRI-512W are very different, together they demonstrate that Paleocoastal peoples on the Northern Channel Islands took advantage of a diverse array of marine and aquatic resources, including shellfish, waterfowl and seabirds, sea mammals, and finfish.

If Arlington Springs is included, the earliest Paleocoastal Channel Island sites are contemporary with Clovis and Folsom sites of the continental interior (6, 8, 20). The island sites provide evidence for Terminal Pleistocene seafaring, island colonization, and a diversified maritime economy, adding to the variability of Paleoindian adapta-

tions in the Americas. The stemmed points and crescents dated as early as 12,200 cal BP link these early island assemblages to those found in interior Western Pluvial Lakes Tradition (WPLT) sites found around many lakes and marshes in North America’s Far West (15). Stemmed point fragments have also been recovered in the basal levels of Paisley Caves, dated to ~14,300 cal BP (21), and the Paleocoastal stemmed points and crescents from the Channel Islands seem unlikely to be descended from Clovis. Such WPLT assemblages may provide a logical technological link among Terminal Pleistocene stemmed point traditions of Northeast Asia (22), the Pacific Northwest, and possibly early stemmed point traditions widely distributed in South America (23).

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Materials and Methods

Figs. S1 and S2
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Pseudomonas sax Genes Overcome Aliphatic Isothiocyanate–Mediated Non-Host Resistance in *Arabidopsis*

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Most plant-microbe interactions do not result in disease; natural products restrict non-host pathogens. We found that sulforaphane (4-methylsulfinylbutyl isothiocyanate), a natural product derived from aliphatic glucosinolates, inhibits growth in *Arabidopsis* of non-host *Pseudomonas* bacteria in planta. Multiple *sax* genes (*saxCAB/F/D/G*) were identified in *Pseudomonas* species virulent on *Arabidopsis*. These *sax* genes are required to overwhelm isothiocyanate-based defenses and facilitate a disease outcome, especially in the young leaves critical for plant survival. Introduction of *saxCAB* genes into non-host strains enabled them to overcome these *Arabidopsis* defenses. Our study shows that aliphatic isothiocyanates, previously shown to limit damage by herbivores, are also crucial, robust, and developmentally regulated defenses that underpin non-host resistance in the *Arabidopsis*-*Pseudomonas* pathosystem.

Non-host resistance is the ability of most plant species to resist microbes or viruses that are successful pathogens on other plants. It is the most prevalent form of plant disease resistance, is durable and effective against a broad range of potential pathogens, but our understanding of its molecular basis is still poor (1–3). Plants generate a huge diversity of natural products, with multiple roles in defense, communication, and development (4). Preformed natural products provide chemical barriers to phytopathogenic fungi (5–7) and are deterrents in plant-herbivore interactions (8). However, their role in restricting bacterial host range remains obscure, as do the bacterial mechanisms involved in breaching natural product-mediated host defenses. To better understand fundamental host-pathogen biology and to inform the development of sustainable field resistance to major crop diseases (9), we sought to define plant components conferring non-host resistance as well as strategies used by virulent pathogens to overcome resistance barriers.

We observed that extracts from naive *Arabidopsis* plants inhibited the growth of most pathogens of *Pseudomonas syringae* for which *Arabidopsis* is not a host. In contrast, *P. syringae* pathovars *maculicola* (*Psm*) ES4326 and *tomato*

(*Pst*) DC3000, which are pathogenic on *Arabidopsis*, grew well on rich media supplemented with host extract from Col-0 (Table 1) or other accessions (table S1). Using *Arabidopsis*-*P. syringae* as a model system to dissect plant resistance to non-host pathogens, we screened a *Psm* ES4326 genomic library for genes conferring resistance in *Escherichia coli* to *Arabidopsis* extracts (Table 1) (10). A single operon, designated *sax* (survival in *Arabidopsis* extracts), allowed *E. coli* to grow on *Arabidopsis* extracts. In *E. coli*, *saxA* and *saxC* are together necessary for resistance: The absence of either resulted in susceptibility, whereas the absence of *saxB* reduced bacterial growth on extracts (fig. S1A). *SaxA* has a predicted secretory signal peptide (11) and, although related to class B β -lactamases (12, 13), it is unable to confer resistance to eight representative β -lactam antibiotics (fig. S2A), indicating that *SaxA* activity is distinct. *SaxB* is related to isochorismatase. *SaxC* is a highly conserved member of the AraC/XylS family of transcriptional regulators found in diverse prokaryotes and involved in carbon metabolism, stress response, and pathogenesis (14). Analysis of 35 plant-associated *P. syringae* genomes showed that only *Arabidopsis* pathogens have *saxA*-like genes with $\geq 90\%$ nucleic acid sequence identity to *Psm* ES4326 *saxA* (table S2 and fig. S3).

Non-host resistance is durable, and hence it is unlikely to be overwhelmed by a single mechanism. Indeed, deletion of *saxAB* genes in *Pst* DC3000 or *Psm* ES4326 had little impact on bacterial growth in *Arabidopsis* extracts (Table 1). To identify additional protective mechanism(s), we screened for compromised bacterial growth in *Arabidopsis* extracts after transposon mutagenesis of *Pst* Δ *saxAB* (10). Two putative multidrug re-

sistance (MDR) efflux genes were identified, with a third similar system revealed in *Pst* DC3000 by genome analysis (10); these were designated *saxF*, *saxD*, and *saxG*, respectively (fig. S1B). They form a subgroup among the nine resistance-nodulation-division (RND) efflux systems predicted in the *Pst* DC3000 genome (15), which function to extrude a wide range of substrates including antibiotics and host-derived molecules (16). We sequentially deleted *saxF/D/G* from the *Pst* Δ *saxAB* background, which resulted in progressively increased sensitivity (Table 1); hence, these genes were required for robust resistance to *Arabidopsis* extracts. Deletion of *saxAB*, *saxF/D/G*, or *saxAB/F/D/G* did not impair growth in rich medium (Fig. 1A), indicating that they are not essential. Thus, *sax* genes have distinct but complementary roles in *Pseudomonas* resistance to *Arabidopsis* extracts.

We purified the *Arabidopsis* antimicrobial compound restricting non-host *Pseudomonas*

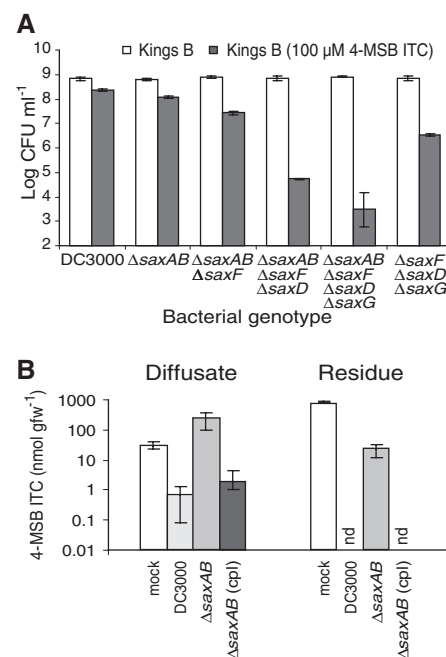


Fig. 1. *sax* genes in *Pst* DC3000 protect against *Arabidopsis*-derived isothiocyanates. (A) *sax* genes are synergistically required for bacterial resistance to isothiocyanates. Bacterial strains were inoculated into Kings B medium with or without sulforaphane and grown overnight. (B) Bacterial infection released sulforaphane (4-MSB ITC) into apoplastic diffusates. *Arabidopsis* leaf discs were vacuum-infiltrated with bacteria [optical density at 600 nm (OD_{600}) = 0.1] and incubated at 23°C for 48 hours before analysis. Data are means \pm SD; cpl, episomal complementation with the *sax* operon; gfw, gram fresh weight; nd, not detected.

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