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Potato psyllid and the South American desert plant *Nolana*: an unlikely psyllid host?

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Figure 1 . Carpet of blue *Nolana* flowers located in the natural home of this plant genus (coastal Chilean desert). Photograph taken by Gerhard Hüdepohl and used by permission (http://www.atacamaphoto.com/wp/wp-content/uploads/atacama-desert-in-bloom/paposo-flower-cactus.jpg).

Managing potato psyllid and zebra chip disease is complicated by the psyllid's ability to reproduce and develop on a large number of plant species. Most species of psyllids are limited to development on a few species of plants within a single genus or family. Potato psyllid is unusual in being able to develop on multiple species in multiple genera across two families of plants (Solanaceae: potato and relatives; Convolvulaceae: bindweeds and morning glories). This flexibility complicates efforts to manage potato psyllid, as it allows psyllids to build-up on plant sources outside of the actual crop. Indeed, we now have evidence that non-crop hosts contribute to residency of potato psyllid in regions that may otherwise not allow year-round presence. More worrisome, some non-crop species that support the psyllid are also hosts for the bacterium that causes zebra chip disease.

One component of our research is to examine non-crop species for suitability to potato psyllid and to the zebra chip pathogen. These studies are funded through the Northwest Potato Research Consortium, Washington State Department of Agriculture, and USDA-NIFA-SCRI. While our studies have targeted primarily weedy nightshades, we are also looking at ornamental Solanaceae that are planted in flower gardens, used as hedges, or grown as container plants. Our recent examination of matrimony vine (*Lycium*), summarized in an issue of **Potato Progress** (Horton et al. 2016), is an example of this research. Recently, we became aware of a taxon of ornamental plants being sold in North America for use in flower gardens or as container plants. The plants are in the genus *Nolana* (Chilean bellflower) now included within the Solanaceae. We added *Nolana* to our studies more as a curiosity than because of concerns that these ornamentals might contribute significantly to epidemiology of zebra chip disease. Indeed, as a South American endemic (see following section), *Nolana* has had no associational history with potato psyllid or the zebra chip pathogen, due to non-overlapping geographies. This absence of geographic overlap, combined with *Nolana*'s somewhat uncertain taxonomic proximity to potato, led us to wonder whether potato psyllid or the zebra chip pathogen would find these plants to be suitable hosts. As we show below, *Nolana* is indeed suitable to both the psyllid and the pathogen. We present our results here as a bit of an instructive tale for scientists and the potato industry that there is quite a bit about the biology of this insect and the zebra chip pathogen that we have yet to learn.

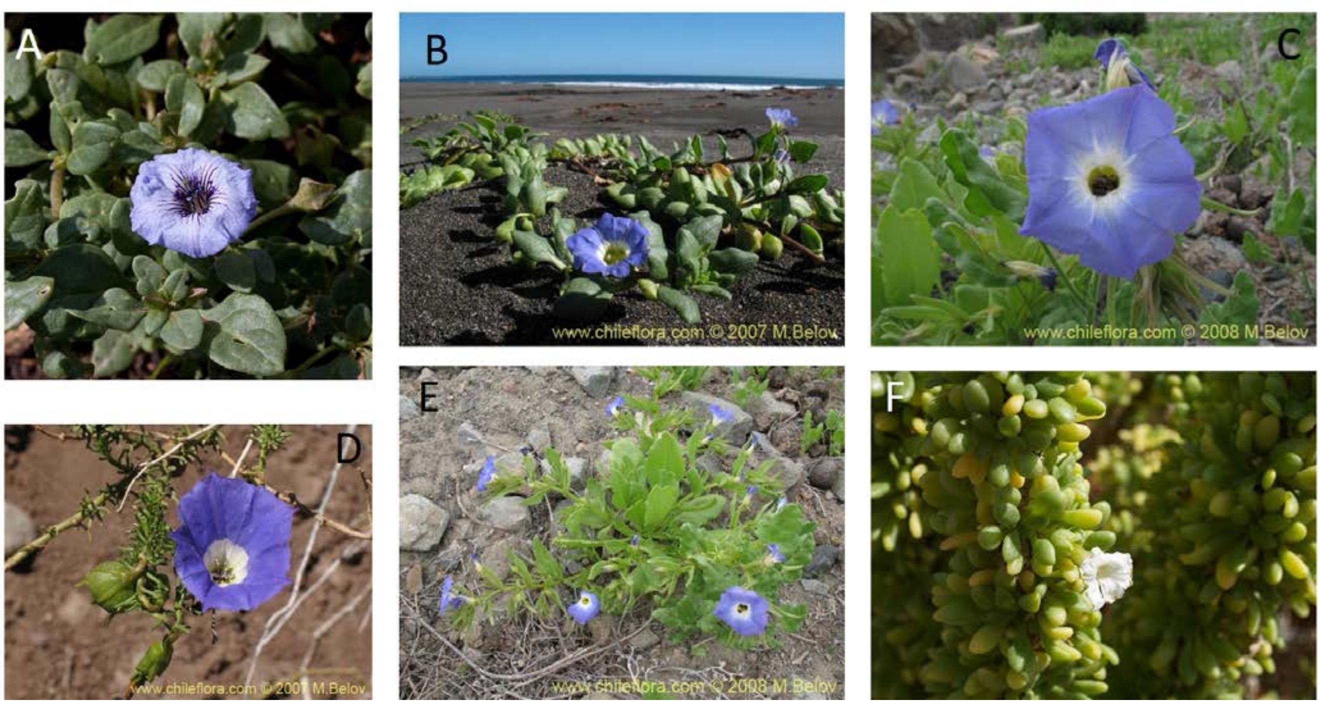

Figure 2. (A) *Nolana humifusa*; (B) *Nolana prostrata*; (C and E) *Nolana elegans*; (D) *Nolana* sp.; (F) Galápagos endemic *Nolana galapagensis*. See **Bibliography** for photo credits.

What is *Nolana*? *Nolana* is a genus of succulent herbaceous annuals or perennial shrubs in the Family Solanaceae (Fig. 2). The genus name, *Nolana*, is from the Latin *nola* – meaning “a little bell” – referring to the bell-shaped form of its flowers. Common names include Chilean bellflower, little bells, bluebird, and cliffhanger. A great deal of historical uncertainty has followed this genus with respect to its higher taxonomy. Some morphological traits of these plants, most notably characteristics of its fruit, are unlike Solanaceae, and at one time *Nolana* was placed in its own family, the Nolanaceae. However, characteristics of its flowers combined with molecular work have *Nolana* now placed in the Solanaceae. Interestingly, the closest relatives of *Nolana* appear to be the matrimony vines (*Lycium*), which are important host plants for potato psyllid in the desert southwest of the US and northern Mexico.

Nolana has an extraordinary distribution and ecology. The genus includes ~85 species limited naturally in distribution within a narrow stretch of South American coast in Peru and Chile (Fig. 3A; modified from Dillon et al. 2009). This area is one of the most arid regions on earth, but is home to *Nolana* and other like-adapted plants. These plant communities survive by efficient use of moisture provided by the coastal fogs (known as garúa or Camanchaca) that blanket this region (Fig. 3BC). Typical weather conditions are interrupted every 4-7 years by El Niño events, when heavy rainfall and warm temperatures prompt a massive bloom response by these desert plants, leading to replenishment of seed banks (Dillon et al. 2009). Plants subsist in patches of vegetation called “lomas” (fog oases or mist oases; http://en.wikipedia.org/wiki/Lomas), each lomas essentially an “island of vegetation among a virtual ocean of desert” (Dillon et al. 2009). A given lomas formation may contain one to a dozen species of *Nolana* surviving in co-existence. Outside of this coastal range, *Nolana* occurs only in a few isolated locations in the inland Andes, and as a single endemic species in the Galápagos Islands located ~500 miles west of coastal Ecuador. The species in the Galápagos (*Nolana galapagensis*; Fig. 2F) is a largish shrub, and its succulent leaves possibly are fed upon by the marine iguanas endemic to the Galápagos (http://www.sacha.org/famil/nolana/n_galap.htm).

Potato psyllid and the zebra chip pathogen: assays with *Nolana*. The natural distribution of *Nolana*

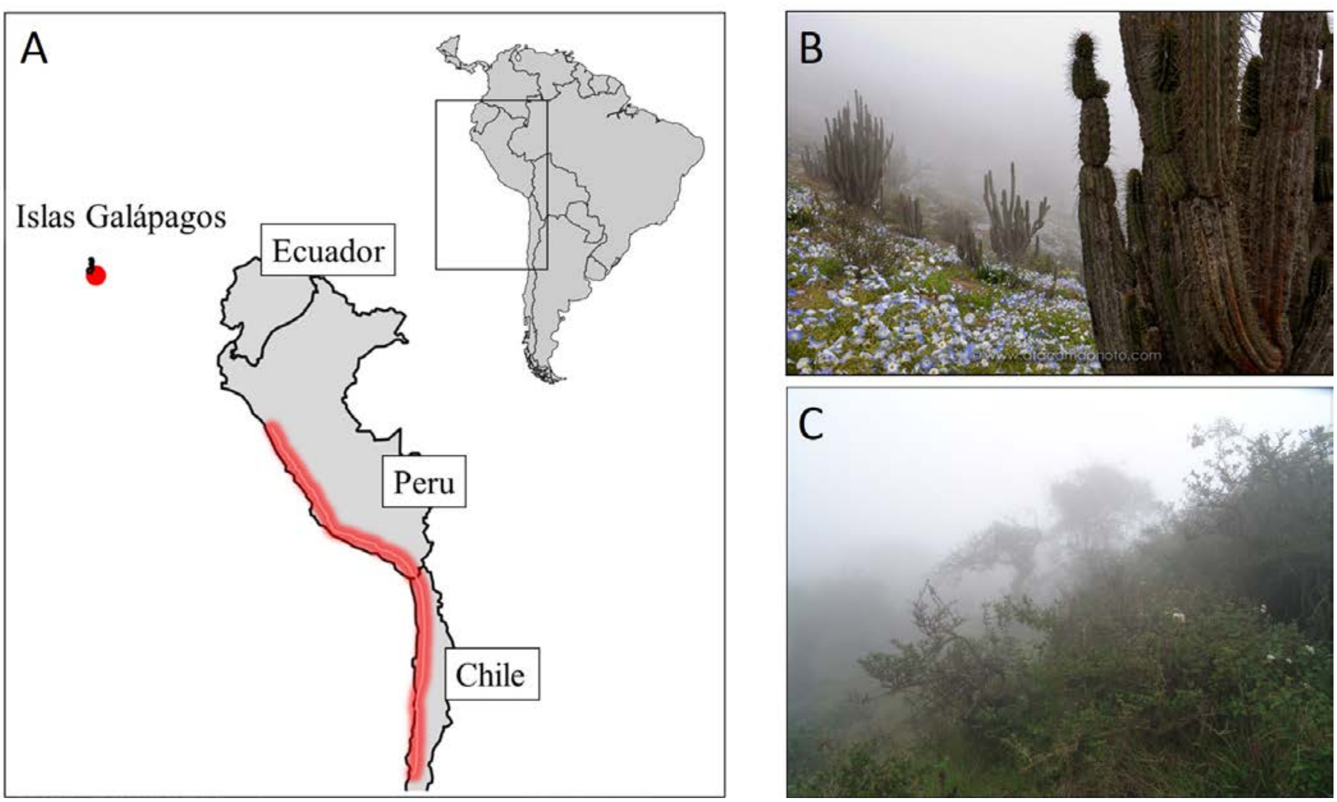

Figure 3. (A) Natural distribution of the genus *Nolana* (desert coasts of Peru and Chile); (B) carpet of blue *Nolana* flowers in an Atacama Desert "lomas", National Reserve, Paposo, Chile, showing foggy mist in background; (C) fog oasis at the Atiquipa Lomas, Peru. Photo credits provided in **Bibliography**.

is outside the geographic range of potato psyllid, whose southern limits in Central America are well north of the northern natural limits of *Nolana*. There is additionally no evidence that the zebra chip pathogen occurs in Chile or Peru. Despite the lack of geographical overlap with *Nolana*, however, both the psyllid and the zebra chip pathogen are shown here to develop on *Nolana*. **Methods**. Seed of ornamental bell flower (*Nolana humifusa*, *Nolana paradoxa*) is available through several outlets in the U.S. and Canada. We obtained seed of *Nolana humifusa* (Chilean bellflower) in 2015 from J.L. Hudson, Seedsman (http://www.jlhudsonseeds.net). The seed was germinated in potting soil diluted 1:1 with sand in four inch pots. Plants were grown in a greenhouse until 4-6 inches tall (Fig. 4A), and then moved into a constant temperature room (72 ^{o}F) for assays. Potato (Ranger Russet) was grown under the same conditions and used as control plants. ***Assay with potato psyllid***. Psyllids of the NW haplotype were added to plants and allowed to deposit eggs. Adults were removed and eggs were counted. Hatchlings were allowed to complete development to the adult stage. We calculated two measures: (1) egg-to-adult survival (%) and (2) egg-to-adult development times (days). ***Assay with the zebra chip pathogen***. A second set of plants was challenged with infective psyllids to determine if *Nolana* supports development of the zebra chip pathogen. Visual symptoms associated with infestation of the plant were monitored. Leaf tissues were then examined with PCR to confirm that visual symptoms were indeed associated with presence of the pathogen.

Results. Psyllids readily deposited eggs on *Nolana* (Fig. 4B). Survival and development rates of immatures were similar to rates on potato and on other plant species known to support potato psyllid (Fig. 5). Egg-to-adult development on *Nolana* required ~25 days, only 1 day longer than needed to develop on potato, and 7-9 days more rapidly than shown on jimson weed (*Datura*) or matrimony vine (*Lycium*). About 60% of eggs deposited on *Nolana* successfully produced adult psyllids. Results for plant species other than potato (blue bars in Fig. 5) are from ongoing screening trials (Cooper and Horton unpubl.). *Nolana* was also an excellent host for the zebra chip pathogen. Plants challenged with infective psyllids gradually began turning a purplish color, combined with a characteristic curling of leaves (Fig. 4C). PCR confirmed presence of the pathogen in plants. *Nolana* plants that were challenged with uninfected psyllids failed to develop these visual symptoms.

Figure 4. (A) *Nolana humifusa* in preparation for bioassay. (B) Adult potato psyllids and eggs on *Nolana humifusa*. (C) Visual symptoms associated with successful transmission of the zebra chip pathogen to *Nolana humifusa*.

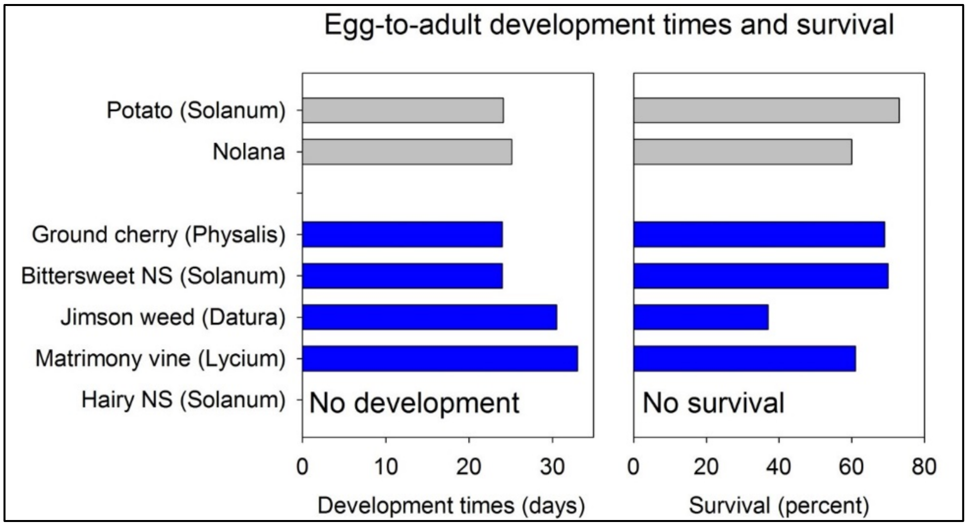

Figure 5. Results of assay with *Nolana humifusa*, showing development times in days (left panel) and nymphal survival (right panel; percent surviving to adulthood). Gray bars are from current assays; blue bars show the same measurements for psyllids on plant taxa screened previously by Cooper and Horton (unpubl.).

Discussion

Nolana has long been appreciated as an attractive plant for flower gardens, so its availability today through seed sellers should not be surprising. Bellflowers have been in gardens of Europe since the mid-1700s as introductions from South America. Seed of *Nolana prostrata* arrived in Spain from Peru in the mid-1700s, and from there made it to England in 1761 (Loudon 1842). A second species, *Nolana paradoxa*, was present in English gardens by the 1820s (Loudon 1842). Species of *Nolana* from Peru and Chile were part of botanical gardens in South Australia as long ago as the 1870s (Schomburgk 1878), possibly from seed that had arrived from England. *Nolana* also has a history in eastern North America, as shown by its presence in colonial gardens of the 1700s. A Boston newspaper from 1760 advertises seed of *Nolana prostrata* for sale (Earle 1901), the seed presumably descending from plants in England and carried to the New World by colonists. Bernard McMahon, a nurseryman who arrived in the colonies from Ireland in 1776, established his Philadelphia seedhouse in 1802 and produced a catalog (possibly America's first seed catalog) advertising over 700 species or varieties of seeds and roots – this list included seed of *Nolana prostrata* (Chappell 2000), again presumably descended from *Nolana* in England. Gardens of contemporary Colonial Williamsburg in Virginia that have been designed to duplicate Williamsburg gardens from colonial times may often include *Nolana humifusa* (Loeb et al. 2015), the species which we used in our assays. While similar historical accounts are not available for the western US, the widespread availability of *Nolana* through nurseries indicates that these ornamentals have current popularity. Indeed, there are reports that one of these species, *Nolana paradoxa*, has escaped cultivation and is now growing naturally in some areas of southern California (http://nathistoc.bio.uci.edu/Plants%20of%20Upper%20Newport%20Bay%20(Robert%20De%20Ruff)/Nolanaceae/Nolana%20acuminata.htm; Roberts 1998).

While there is no historical association between potato psyllid and *Nolana*, due to a lack of geographic overlap between potato psyllid and natural populations of *Nolana*, widespread availability of this ornamental in potato growing and other regions of North America prompted us to examine these plants for suitability to the psyllid. Our results showed that *Nolana* supports establishment and growth of the insect as well as the bacterium that causes zebra chip disease in potatoes. It may not be all that surprising that potato psyllid developed on this plant, as this insect has shown the ability to develop on other Solanaceae with which it has no evolutionary history (e.g., the European import bittersweet nightshade). Additionally, potato psyllid has had a long history with apparently close relatives of *Nolana*, namely plants in the genus *Lycium*, and this historical association may have “prepared” the psyllid to survive on *Nolana*. We are less able to explain success of the pathogen in *Nolana*. There is no reported evidence that the zebra chip pathogen occurs within the geographic range of *Nolana*, nor have we been able to transmit the bacterium to the *Nolana*-related *Lycium* in repeated laboratory trials. Our results do provide a bit of a caution to the potato industry that plant species grown for ornamental purposes in western North America, including species not previously known to support potato psyllid, may nonetheless be potential reservoirs of the psyllid and the zebra chip pathogen.

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Photographs

Web-links to photographs used in this article are provided here. Unless otherwise stated, permission for use of photographs is authorized under Creative Commons license. Photographs in Figure 4 were taken by co-authors of this article.

Figure 1. Carpet of blue *Nolana* flowers, Atacama Desert; photograph by Gerhard Hüdepohl and used by permission (http://www.atacamaphoto.com/wp/wp-content/uploads/atacama-desert-in-bloom/paposo-flower-cactus.jpg).

Figure 2. (A) *Nolana humifusa*; photograph by Denis Prévôt (https://commons.wikimedia.org/wiki/File:Nolana_humifusa_-_Fleur.jpg). (B-D) *Nolana prostrata*, *Nolana elegans*, *Nolana* sp.; photographs by M. Belov (http://www.chileflora.com/Florachilena/FloraEnglish/PIC_FAMILIES_SIMPLE_Nolanaceae.php). (E) *Nolana galapagensis*; photograph by Brian Gratwicke (http://commons.wikimedia.org/wiki/File:Nolana_galapagensis_1.jpg).

Figure 3. (B) *Nolana* flowers in an Atacama Desert "lomas", National Reserve, Paposo, Chile; photograph by Gerhard Hüdepohl and used by permission (http://www.atacamaphoto.com/search/index.php?/Themes/atacamacactus/D2X3041.jpg). (C) Fog oasis, Peruvian coastal desert; photograph by Dr. Luis Balaguer (https://commons.wikimedia.org/wiki/File:A_fog_oasis_at_the_Atiquipa_Lomas,_Peru.jpg)

End piece photograph: Atacama Desert in bloom; photograph by P. Pardo Ávalos/ESO (https://www.eso.org/public/images/poposo-flor_9644)

Other resources consulted in writing this article

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Discussion of garúa and Camanchaca fogs and cloud banks that blanket the coasts of Chile and Peru, providing moisture for coastal desert vegetation: https://en.wikipedia.org/wiki/Camanchaca; https://en.wikipedia.org/wiki/Gar%C3%BAa

Brief discussion of lomas formations: https://en.wikipedia.org/wiki/Lomas

The *Globodera* Alliance Coordinated Agricultural Project (GLOBAL Project) -brings researchers, extension professionals, potato industry, and regulators together to eradicate *Globodera spp.* that threaten U.S potato production.Worldwide, *Globodera pallida* and *Globodera rostochiensis* — also known as potato cyst nematodes — are considered to be the most economically important pests of potato and if left uncontrolled, can cause up to 80 percent yield loss.

Attached are the GLOBAL Project's newsletters (in English and Spanish), which examine issues concerned with biology and control of these obligate plant parasitic nematodes.

To learn more and receive updates on GLOBAL project visit: www.globodera.org

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The 50th Annual University of Idaho Potato Conference and 39th Ag Expo will be held on the Idaho State University campus in Pocatello, January 16-18, 2018.

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For more information and a link to registration, see:
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