Paronychia erecta (Chapm.) Shinners (squareflower [Caryophyllaceae]) in coastal dunes of the Florida panhandle.

Effect of temperature, light, and seed provenance on germination of *Paronychia erecta* (squareflower): a native plant with ornamental potential

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ABSTRACT

Paronychia erecta (Chapm.) Shinners (squareflower [Caryophyllaceae]) is a perennial with attractive square-like inflorescences. We collected seeds from 3 locations (provenances) in northwest Florida including Navarre Beach (NB), Pensacola Beach (PB), and Perdido Key (PK) and subjected the seeds to seed fill tests (X-ray analysis), viability tests (tetrazolium staining), and germination experiments. In experiment 1, we determined effects of provenance (NB, PB, and PK) and temperature regimes (33/24, 29/19, 27/15, and 22/11 °C [91.4/75.2, 84.2/66.2, 80.6/59.0, and 71.6/51.8 °F] under a 12-h photoperiod) on germination speed and final germination proportion. In experiment 2, we determined effects of provenance (NB and PK) and photoperiod (0 or 12 h of light) on final germination (after 28 d). Seeds were 90 to 99% filled and 63 to 91% viable. In experiment 1, interactions of provenance × temperature were nonsignificant for final germination ($P = 0.052$) and germination speed ($t50$) ($P = 0.3129$), indicating the effects of provenance were similar across temperatures. Germination was high (94–99%) at 22/11, 27/15, and 29/19 °C and was reduced (27%) at 33/24 °C. Germination speed ($t50$) was quicker for 27/15 and 29/19 °C (10.3 and 11.0 d) compared to 22/11 °C (13.1 d). Seeds dry-stored for 21 d imbibed and germinated to 50% by 9 d, indicating a lack of physical and intermediate or deep physiological dormancy. Experiment 2 results revealed a significant provenance × photoperiod interaction ($P < 0.0001$) with 81 and 65% germination in light and 16 and 26% germination in dark for NB and PK, respectively. Results show promise for successful *P. erecta* seed propagation at average winter, spring, and fall Florida temperatures.

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KEY WORDS

seed viability, propagation protocol, landscapes and gardens, conservation, Caryophyllaceae, coastal dune

NOMENCLATURE

USDA NRCS (2020)
Wunderlin and others (2020)

Photos by the authors

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CONVERSIONS

(°C x 1.8) + 32 = °F
1 km = 0.62 mi
1 km² = 0.4 mi²
1 m = 3.3 ft
2.54 cm = 1 in
25.4 mm = 1 in
0.43 kg = 1 lb
1 ml = 0.034 oz

Interest and use of native plants in ornamental landscaping continues to grow as more and more consumers recognize the value in sustainable gardening. In a 5-y period, Brzuszek and others (2007, 2010) reported consumer interest of native plants increased from a minimal to a moderate level when given the choice of none, minimal, moderate, enthusiastic, and zealous categorical levels of interest. This finding is consistent with increased revenue of native plants. A survey of the Florida environmental horticulture industry revealed that native plants represented 15.9% of total nursery sales in 2015 (Hodges and others 2016); up from 7.8% in 2011 (Hodges and others 2011). Further, consumers are willing to pay more for plants labeled as native and noninvasive (Yue and others 2011a, 2011b, 2012), and a 14% price premium for pollinator-friendly landscape plants (Khachatryan and others 2017). While this increase is encouraging, native plants still represent only a small fraction of our ornamental industry. In a national survey, White and others (2018) identified slightly more than 800 active native plant vendors selling approximately 26% of all US native flora. Similarly, in Florida alone, we estimate that less than 25% of our 3300 native plant species are in cultivation (Florida Association of Native Nurseries 2020; Wunderlin and others 2020). Thus, great opportunity exists to evaluate whether native plants that are attractive in their natural settings can adapt to our modified urban landscapes and gardens. Major challenges to the promotion of native plants for wider landscape uses typically include a lack of species-specific propagation protocols (Wilde and others 2015), necessary consumer and industry education (Kauth and Pérez 2011), and identification of native plant candidates that are not only aesthetically pleasing and ecologically functional but also economically viable.

We believe *Paronychia erecta* (Chapm.) Shinners (squareflower [Caryophyllaceae]) exhibits a suite of characteristics that lends itself to being an excellent candidate for ornamental use. Its ability to produce large numbers of attractive flowers from spring to fall and its low-growing, evergreen plant habit makes *P. erecta* ideally suited as ground cover or for mass plantings (Figure 1). Narrowly distributed and primarily found in sandy sites such as sand dunes in the Florida Panhandle (Wunderlin and others 2020) and in Alabama, Mississippi, and Louisiana (USDA 2020), *P. erecta* has been identified as an important food source for subspecies of the federally protected beach mouse (*Peromyscus polionotus* Wagner [Cricetidae]) (Moyers 1996) and is vital to coastal restoration and dune stabilization. This multistemmed herbaceous perennial species measures more than 1 m in width and approximately 10 cm in height. It has purple to green, oppositely arranged leaves that are up to 3 mm wide and small white flowers that group together in multibranched corymbs to form square-like inflorescences lending to its common name of squareflower. These flowers are perfect containing both male and female reproductive organs. The *P. erecta* fruiting structure, termed as a utricle, is a small, one-seeded indehiscent fruit with a thin, inflated pericarp. Like many other members of its genus, *P. erecta* seeds are ovoid to elliptical in shape, small, orange to brown in color, and wrapped in a persistent calyx (Figure 2).

Figure 1. Paronychia erecta (squareflower) in coastal dunes of the Florida panhandle having square-shaped inflorescence (A) and close-up view of flowers at pre-anthesis (closed bud) and anthesis (petals open and extended with brown anthers visible) (B).

To our knowledge, neither the sexual nor asexual propagation of this species has been reported, and it is not currently listed in Florida's native plant nursery directory (Florida Association of Native Nurseries 2020). Limited horticultural information exists on the seed propagation of closely related species. Namely, Rugel's nailwort (*Paronychia rugelii* (Chapm.) Shuttlw. ex Chapm.) can be easily propagated by seed that is commercially available through the Florida Wildflower Cooperative (unpublished data). The Florida endemic and endangered paper nailwort (*Paronychia chartacea* Fernald ssp. *chartacea*) can also be easily propagated by seed in simulated spring or fall temperatures (Steppe and others 2019). In nature it appears to be influenced by the presence of biological soil crusts and fire frequency (Hawkes 2004), also favoring intact scrub with higher germination in bare sand than in litter only or under shrubs (Stephens and others 2012). Germination knowledge of native species in their natural conditions can often inform

Figure 2. Fruit morphology of *Paronychia erecta* showing fruits (utricles) enclosed by persistent calyces (A), enlarged utricles with calyx removed (B), and dissected fruit (C) showing persistent calyx (Ca), utricle tissue (Ut), and seed (Sd) with endosperm and embryo. As a comparison, in first image (A), an arrow points to utricle without persistent calyx distinguished among nearby utricles with persistent calyces.

and guide propagation studies that are conducted in controlled environments and commercial substrates (Heather and others 2010; Trigiano and others 2018; Campbell-Martinez and others 2021; Hooton and others 2021).

Our overall objective of this study was to develop a seed germination protocol to ensure availability of the species for coastal dune restoration and to widely promote its production and use as a native ornamental. Specific objectives were to 1) explore seed collection and cleaning methods; 2) determine initial seed fill and seed viability; and 3) examine the effects of temperature, light (photoperiod), and seed provenance on germination of *P. erecta* collected from wild populations in the Florida panhandle.

Paronychia erecta spreading on coastal dunes.

MATERIALS AND METHODS

Seed Collection and Processing

We collected *P. erecta* seeds (utricles with persistent calyces) from 3 provenances (locations) within remnant back dunes in the northwest Florida panhandle including Navarre Beach (NB), Pensacola Beach (PB), and Perdido Key (PK), separated by approximately 15 to 50 km (Table 1). Seeds were collected from >200 individuals per provenance (Table 2) on 19 October

TABLE 1

Characteristics of seed collection provenance for Paronychia erecta *(squareflower).*

Provenance	Description	GPS Location
Navarre Beach (NB)	Intact back dunes of Santa Rosa Island (barrier island). Approximately 300–500 m inland from Gulf of Mexico.	30.378096 N, 86.896811 W
Pensacola Beach (PB)	Intact back dunes of Santa Rosa Island (barrier island). Approximately 200–400 m inland from Gulf of Mexico.	30.348300 N, 87.060495 W
Perdido Key (PK)	Disturbed area adjacent to unpaved road on back dune of Perdido Key (barrier island). Approximately 300 m inland from Gulf of Mexico.	30.297103 N, 87.444195 W

TABLE 2

Number of Paronychia erecta *(squareflower) plants sampled from 3 provenances (locations) in northwest Florida, approximate number of seeds isolated from plants after cleaning and seed weights, and percentage of calyxes filled and viable as determined through X-ray analysis (*n *= 100) and viability tests (*n *= 100).*

Provenance	Number of plants	Number of seeds	Seed weight (mg)	Seeds/lb	Seed fill (%)	Viability[z] (%)
Navarre Beach	220	7400	0.57	792,024	94	91
Pensacola Beach	227	9800	—	—	99	63
Perdido Key	223	3600	0.44	1,021,374	90	81

[z] Pre-germination viability analysis conducted using 1.0% tetrazolium solution at 30 °C for 12–18 h.

2018 and were harvested from ≤50% of floral material present per plant. Seeds were commercially cleaned at the Forest Service Seed Extractory (Bend, Oregon). During cleaning, seeds were passed through sieves, sorted on a single-deck vibratory table, and further separated by a continuous seed blower that sorted the material by weight.

Seed Weight, Fill, and Viability Tests

We weighed (mg) seeds from NB and PK provenances using a total of 10 replicates with 10 subsamples (n = 100 per provenance). Then an average weight per seed and seeds per lb was calculated. Using a third-party laboratory (US Forest Service National Seed Laboratory, Dry Branch, Georgia), an X-ray analysis (Faxitron Ultrafocus, Tucson, Arizona) was conducted on all 3 provenances to determine post-cleaning seed fill percentages (Figure 3). Once cleaned, seeds were air-dried and stored at room temperature (23–28 °C) in sealed glass containers. We examined pre-germination viability on 100 seeds using a tetrazolium (TZ) staining test adapted from the Association of Official Seeds Analysts (AOSA) rules for tetrazolium testing (Peters 2017) for all 3 provenances. Seeds were cut laterally and stained overnight (12 h) at 30 °C in a 1.0% tetrazolium (2,3, 5-triphenyl chloride) solution. Seeds were considered viable when firm embryos stained evenly red (Figure 3). We conducted post-experiment TZ tests on all non-contaminated and non-germinated seeds.

Experiment 1 (Provenance and Temperature)

On 9 November 2018, seeds (not surface sterilized) collected from NB, PB, and PK were placed in 11 × 11 × 4 cm transparent polystyrene germination boxes (Hoffman Manufacturing, Corvallis, Oregon) containing one sheet of germination paper on top of one sheet of blotter paper (Anchor Paper Company, St Paul, Minnesota) moistened with 15 ml of autoclaved, distilled water. We placed germination boxes in various germination chambers (Percival Scientific, Model I30VL, Perry, Iowa) with a 12-h photoperiod (76.08±7.54 µmol/$m^{-2}s^{-1}$) with 1 of 4 temperature regimes (33/24, 29/19, 27/15 °C, and 22/11 °C) in which warm temperatures corresponded with light. Experimental design was a randomized complete block design with a 3 (provenance) × 4 (temperature) full-factorial arrangement of treatments. The position in a chamber was treated as a blocking factor. A total of 50 seeds per germination box (experimental unit) was replicated 4 times per treatment. We monitored for germination and disease 3 times a week over the course of 28 d, and boxes were watered as needed with autoclaved, distilled water. Germination was counted as radicle emergence outside of the calyx. Seeds that germinated were removed from the boxes, as were seeds deemed contaminated that turned soft and mushy or had visible hyphal growth (due to disease). At the end of experimentation, calyxes were manually dissected and the number of empty seeds recorded. Final germination proportions were calculated as the number of germinated seeds divided by the number of filled, non-diseased seeds.

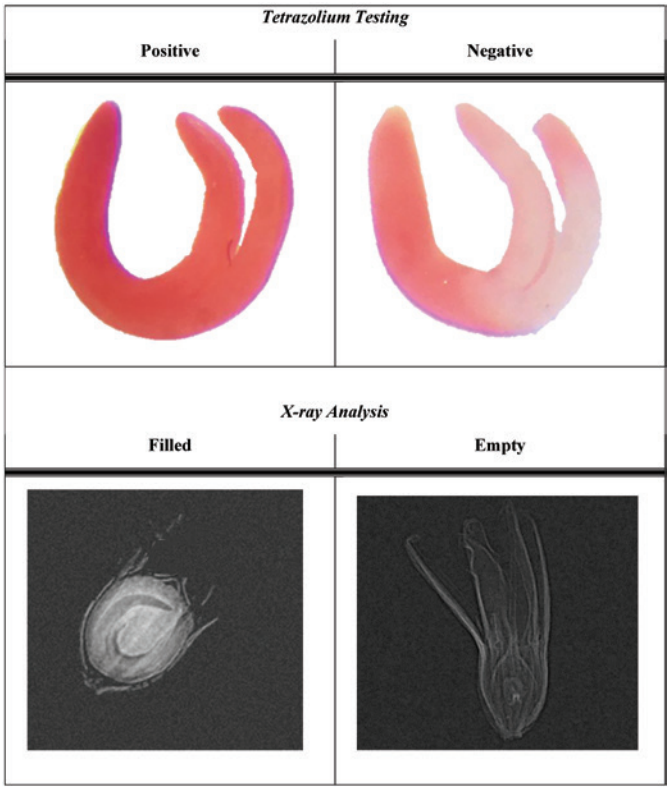

Figure 3. Examples of positive and negative viability staining (1% tetrazolium solution overnight at 30 °C) (*top*) and filled and empty seed shown through X-ray images (*bottom*) of *Paronychia erecta*.

Experiment 2 (Provenance and Photoperiod)

Seeds were placed in germination boxes as described in Experiment 1 within a germination chamber set at 27/15 °C on 8 September 2019 and 3 October 2019 in 2 separate replicate experimental runs. Seeds collected from either NB or PK had a 0- or 12-h photoperiod of 76.08±7.54 μmol/$m^{-2}s^{-1}$ during daily high temperatures. We achieved darkness (0-h photoperiod) by double wrapping Petri dishes with aluminum foil. Experimental design was a randomized complete block design with a 2 (provenance) × 2 (photoperiod) full-factorial arrangement of treatments. The position in chamber and experimental run were treated as blocking factors. A total of 25 seeds per germination box (experimental unit) was replicated 4 times for each treatment. We recorded germination and disease once after 24 d, and a germination proportion (number of germinated seeds / (25 – number of diseased seeds)) was calculated for each Petri dish.

Experimental Design and Data Analysis

We analyzed main effects and their interactions using generalized linear mixed models procedure (PROC GLIMMIX in SAS 9.4). A Kenward-Rogers approximation was used for computing the denominator degrees of freedom for the fixed-effects tests. Position in the growth chamber was considered a random effect in both experiments, and the experimental run was coded as a random effect for Experiment 2. Differences between means for significant main effects and interactions ($P \leq 0.05$) were computed using the ilink option of the LSMEANS statement.

RESULTS

Seed Weight, Fill, and Viability Tests

Seeds of NB weighed more than seeds of PK (0.57 compared to 0.44 mg/seed) (Table 2). There were a calculated 792,024 and 1,021,374 seeds/lb for NB and PK, respectively. Seed fill determined by X-ray analysis was high (≥90%) across all provenances. Pre-germination viability varied between the 3 locations (NB, PB, and PK). Seeds from NB, PB, and PK had pre-germination viability of 91, 63, and 81%, respectively.

Experiment 1 (Provenance and Temperature)

Provenance and temperature influenced final germination ($P = 0.0002$ and $P < 0.0001$) and *t*50 ($P < 0.0001$ and $P < 0.0001$) (Table 3). Final germination percentages were higher for seeds collected from NB and PK (80–82%) compared to PB (73%) (Figure 4A) and were higher for seeds at 22/11, 27/15, and 29/19 °C (≥94%) compared to 33/24 °C (27%) (Figure 4B). Germination speed (*t*50) was quicker from seeds collected from NB and PK (10.5±0.45 and 11.3±0.62 d) compared to PB (12.7±0.28 d) (Figure 4A) and was quicker for 27/15 and 29/19 °C (10.3±0.45 and 11.0±0.43 d) compared to 22/11 °C (13.1±0.30 d) (Figure 4B). Germination began by 7 d and was ≥59% by 14 d for all provenances. Germination was high (≥76%) by 14 d for 22/11, 27/15, and 29/19 °C.

TABLE 3

Effects of provenance (Navarre Beach, Pensacola Beach, and Perdido Key), temperature (22/11, 27/15, 29/19 and 33/24 °C), and their interaction on final germination and germination speed (time to 50% of total germination, t50) of Paronychia erecta *(squareflower).*

Effect	Num df	Den df	*F* value	*P* value
Final germination (%)				
Provenance	2	36	10.17	0.0002
Temperature	3	36	456.16	<0.0001
Provenance × Temperature	6	36	2.32	0.0542
*t*50 (days)				
Provenance	2	24	14.33	<0.0001
Temperature	2	24	27.15	<0.0001
Provenance × Temperature	4	24	1.26	0.3129

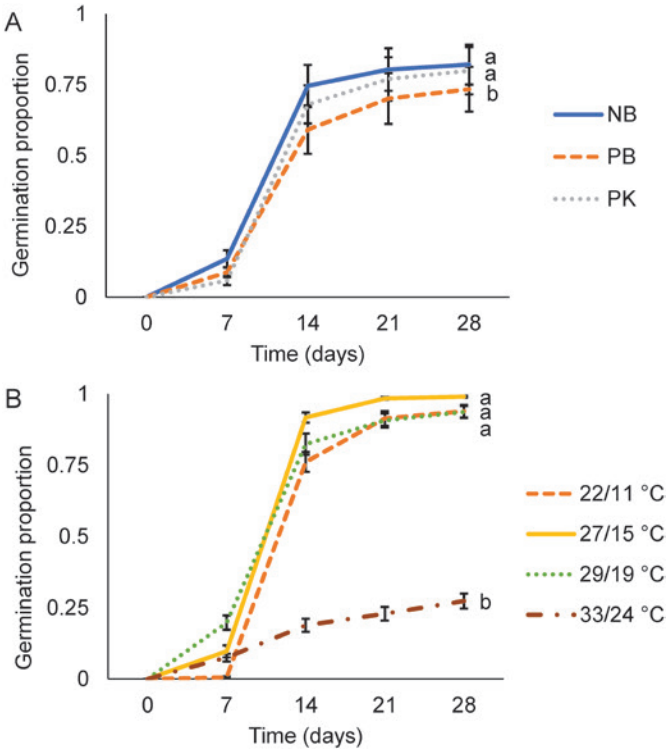

Figure 4. Germination proportion across time of *Paronychia erecta* from 3 provenances in the Florida panhandle (NB = Navarre Beach, PB = Pensacola Beach, PK = Perdido Key) (A) subjected to 4 seasonal temperature treatments (22/11, 27/15, 29/19, and 33/24 °C (B). Seeds were placed in growth chambers with light (12-h photoperiod) for 28 d. Higher temperatures coincide with diurnal light conditions. Within each treatment (provenance or temperature), means with the same letters do not differ ($P \leq 0.05$) at final germination after 28 d.

Experiment 2 (Provenance and Photoperiod)

Photoperiod affected germination but the effect was not similar across populations as is indicated by a significant ($P \leq 0.0001$) provenance × photoperiod interaction (Table 4). Germination was higher in light (81 and 65%) compared to dark (16 and 25%) for NB and PK, respectively; however, more germination occurred in the dark for PK compared to NB (Figure 5). Disease was ≤5% for each treatment (Figure 5).

DISCUSSION

Paronychia erecta seeds sorted using standard commercial methods resulted in a filled seed percentage of ≥90% acceptable for commercial propagation. Pre-germination viability tests using AOSA standard tetrazolium staining methods underestimated the germination potential of seeds for all provenances. Refined methodology is needed for accurate viability predictions using tetrazolium staining techniques for *P. erecta*.

Like several species in Caryophyllaceae, seeds of *P. erecta* germinate to high percentages (>70%) without any seed pretreatments (Maschmeyer and Quinn 1976; Stephens and others 2012; Baskin and Baskin 2014; Murru and others 2015). *Paronychia erecta* achieved >75% germination within 2 wk under a range of temperatures. Seeds prefer moderate (27/15 and 29/19 °C) and cooler temperatures (22/11 °C) as compared to warm temperatures (33/24 °C), though optimal temperature ranges for germination may vary slightly by seed provenance. Regardless, very high (≥98%) germination was observed for seeds at 27/15 °C after 4 wk in contrast to *P. chartacea*, which had higher germination (86 compared to 57%) at cooler temperatures (22/20 °C) compared to moderate temperatures (27/22 °C) (Stephens and others 2012).

Paronychia erecta germination is promoted by exposure to light although some germination occurs in the dark. This finding is consistent with results of *P. chartacea*, which had reduced emergence (<10%) in low to no light (5 or 20 mm of sand burial) compared to approximately 25% emergence in light (0 mm sand burial) during field studies (Petrü and Menges 2004). Additionally, high germination (86%) of *P. chartacea* was observed under germination chambers mimicking natural light cycles (Stephens and others 2012).

Based on the results herein, seed propagation of *P. erecta* was quickly and easily achieved in the greenhouse by the authors using several standard propagation procedures. Cleaned seeds were precisely direct-sown on top of propagation substrate using semi-automated seedling machinery and grown within a commercial facility (Figure 6). Additionally, non-cleaned seed (that is, seed with chaff) can be lightly, evenly sprinkled over potting mix or germinated within a communal flat under intermittent mist, and resultant seedlings can be transplanted into larger containers post-emergence (Figure 7). *Paronychia erecta* seeds emerge within a few weeks in greenhouse propagation systems and can be quickly moved into larger containers, or

TABLE 4

Effects of provenance (Navarre Beach, Pensacola Beach, and Perdido Key), light (12-h photoperiod or darkness), and the interaction of provenance and photoperiod on final germination of Paronychia erecta *(squareflower).*

Effect	Num df	Den df	*F* value	*P* value
Provenance	1	28	1.07	0.3104
Photoperiod	1	28	319.88	<0.0001
Provenance × Photoperiod	1	28	25.10	<0.0001

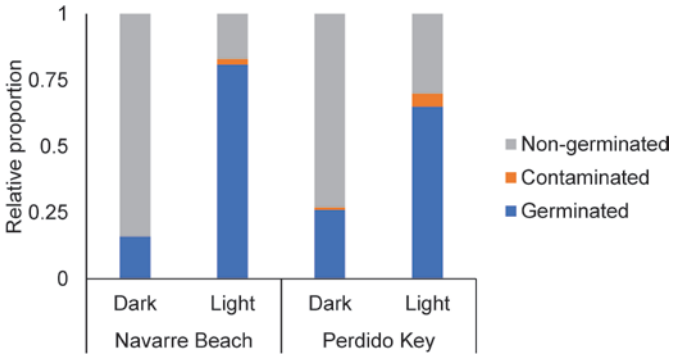

Figure 5. Relative proportion of non-germinated, contaminated, and germinated seeds of *Paronychia erecta* (squareflower) exposed to light (12-h photoperiod) or dark and collected from two provenances (Navarre Beach and Perdido Key) in the Florida panhandle. Seeds were placed in a 27/15 °C growth chamber for 24 d with the higher diurnal temperature coinciding with daily light treatment.

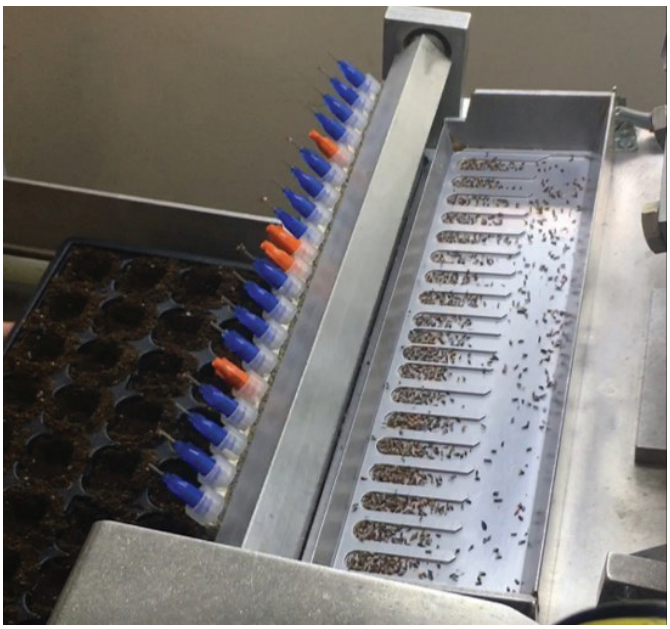

Figure 6. Semi-automated machine seeding *Paronychia erecta* into propagation flats within a commercial propagation facility in Pensacola, Florida.

Figure 7. 12-wk-old seedlings of *Paronychia erecta* grown under an intermittent mist system. Dried fruiting material was crushed and spread across the top of potting mix (MetroMix 830) within 72-cell plug flats.

Plug flats of *Paronychia erecta*.

held in plug flats for months, and can be overwintered in outdoor container nursery production.

CONCLUSIONS

Unique, long-lasting, square-shaped inflorescences; evergreen rosette form; and the ability of *P. erecta* to grow in dry, hot, salty, nutrient-poor soils make it an attractive native plant for use in ornamental, low-input landscaping. It can be used as an evergreen ground cover in managed landscapes and as an important wildlife food in coastal dune restoration projects. *Paronychia erecta* is quickly and easily propagated from seed using standard propagation procedures. Seeds of *P. erecta* should be collected in the fall when the fruiting and subtending stem tissue turn brown and begin to dry. Seeds are orthodox and may be stored for at least 1 y when air-dried and stored at room temperature. Sow seeds on top of well-drained soilless media during the spring, fall, or winter to produce finished liners in 12 wk. For year-round propagation and nursery production in the absence of seeds, future work is needed to investigate asexual propagation of *P. erecta* and to optimize container production. Additionally, future information regarding production of transplant-ready plants from plugs is needed, particularly looking at the feasibility of growing this crop under standard greenhouse and nursery conditions.

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