Seed Production and Viability of Eight Porterweed Selections Grown in Northern and Southern Florida

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Abstract. Nettleleaf porterweed (Stachytarpheta cayennensis) is a potentially invasive ornamental plant in Florida. Plant growth, visual quality, flowering, and seed viability were assessed for nettleleaf porterweed and eight closely related alternatives planted in northern and southern Florida. In northern Florida, 'Mario Pollsa' porterweed (Stachytarpheta spp.), 'Violacea' porterweed (Stachytarpheta mutabilis), 'Naples Lilac' porterweed (Stachytarpheta spp.), 'Red Compact' porterweed (Stachytarpheta speciosa), and nettleleaf porterweed (Stachytarpheta cayennensis) achieved high flower ratings between 4 (average to good flowering) and 5 (abundant flowering, peak bloom) during 4 or more months. Also, jamaican porterweed (Stachytarpheta jamaicensis), 'Violacea' porterweed, 'Red Compact' porterweed, and nettleleaf porterweed achieved visual quality ratings between 4 and 5 (good to excellent quality) throughout most of the study. In southern Florida, the same cultivars received high flower ratings but generally for shorter periods of time. Also, 'Violacea' porterweed and 'Red Compact' porterweed consistently received visual quality ratings that were above 4 (good quality, very desirable). During the course of the 28-week study, nettleleaf porterweed produced the greatest number of spiked inflorescences with 39% to 80% seed viability. At both locations, 'Violacea' porterweed did not produce any viable seed and seed viability was less than 10% for 'Mario Pollsa' porterweed, coral porterweed (Stachytarpheta mutabilis), and 'Naples Lilac' porterweed.

The invasive plant management program in Florida has contracted over 190 research projects at a cost of \$19.8 million over the last 39 years (Schmitz, 2009). Despite these efforts, plant invasions continue to rise. The State of Florida is the second largest producer of ornamental plants in the United States with total industry sales in 2005 estimated at \$15.2 billion (Hodges and Haydu, 2006). Although the majority of introduced plants do not escape cultivation, some plants become exceptionally adaptable, regenerate prolifically, and eventually invade natural areas (Parker et al., 2007; Reichard and Hamilton, 1997; Williamson and Fitter, 1996). Consequently, the nursery and landscape industry has been an unintentional but significant contributor to the spread of invasive plants (Burt et al., 2007; Culley and Hardiman, 2009; Dehnen-Schmutz et al., 2007; Fox et al., 2003; Harrington et al., 2003; Li et al., 2004; Mack and Erneberg, 2002; Niemiera and Von Holle, 2009; Pemberton and Liu, 2009; Reichard and White, 2001). The same qualities that often prompt exotic ornamental introductions (short juvenility, long flowering, fast growth, ease of propagation) can be

detrimental generations later if invasion occurs (Caley et al., 2008). Desirable attributes of nettleleaf porterweed (Stachytarpheta cayennensis) are its long period of profuse and vibrantly colored flowers that attract butterflies and adaptability to a range of landscape conditions; yet a consequence of this is its ability to self-seed and readily naturalize in areas far beyond its planting. Introduced to the United States from Central and South America, nettleleaf porterweed has since escaped cultivation in Florida, Hawaii, and Puerto Rico (U.S. Department of Agriculture, 2008). In Florida, herbarium vouchers document its escape in two of the southern-most counties (Wunderlin and Hansen, 2009a). It has been found in 18 conservation areas in Florida (Gann et al., 2008) and is problematic in other parts of the world, including the Pacific Islands (Pacific Island Ecosystems at Risk, 2007) and Australia (World Wildlife Fund Australia, 2006). In Australia, it was ranked as an environmental weed with a score of 4, meaning it has naturalized and is known to be a major problem at three or fewer locations within a state or territory (Groves et al., 2005). Florida's Exotic Pest Plant Council (FLEPPC) designates porterweed as a Category II invasive, indicating that it has increased in abundance or frequency but has not yet altered Florida plant communities to the extent shown by Category I species (FLEPPC, 2007). In 2006, The University of Florida Institute of Food and Agricultural Sciences Status Assessment of Non-native Plants (Fox et al., 2008) recommended that porterweed be used with caution and managed to prevent its escape. These conclusions were footnoted to emphasize that there was insufficient evidence to fully validate the statement and that the status should be reassessed every 2 years (Fox et al., 2008).

As alternatives to the resident species (wild-type form) of nettleleaf porterweed, there are several other closely related species that have ornamental value such as coral porterweed (Stachytarpheta mutabilis), 'Violacea' porterweed (Stachytarpheta mutabilis), and several dwarf porterweed selections (Stachytarpheta speciosa) (Caldwell, 2005). In addition, there is a Florida native jamaican porterweed (Stachytarpheta jamaicensis) that is distinctively lower-growing with a more horizontal spread (Gilman, 2007; Hammer, 1994). The genus Stachytarpheta has undergone a series of taxonomic revisions that are further complicated by putative hybrids (Munir, 1992). In Florida, the Category II invasive nettleleaf porterweed reportedly hybridizes with the native jamaican porterweed and is documented as Stachytarpheta ×intercedens (Wunderlin and Hansen, 2009b). In Hawaii, Wagner et al. (1999) report that the hybrid resembles jamaican porterweed more closely than nettleleaf porterweed, but the corollas are darker in color than jamaican porterweed with a more erect habit and more ovate and darker green leaves. Wagner et al. (1999) also report that nettleleaf porterweed hybridizes with coral porterweed. Munir

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(1992) report that S. \times intercedens actually evolved by the hybridization of indian snakeweed (Stachytarpheta indica) and jamaican porterweed. Hybridization potential between native and invasive species of the same genus is of particular concern. For example, the FLEPPC Category I invasive lantana (Lantana camara) has extensively hybridized with all three distinct varieties of the Florida native pineland lantana (Lantana depressa), contaminating the endemic gene pool (Langeland and Craddock Burks, 1998). Schierenbeck and Ellstrand (2009) have reviewed numerous examples in which hybridization preceded the emergence of successful invasive populations. Controlled plant breeding has been used to develop numerous new noninvasive plants (with improved commercial traits) in several states, including North Carolina (Ranney, 2004), Connecticut (Li et al., 2004), and Florida (Czarnecki et al., 2008). Stachytarpheta is a genus of ≈ 133 species with six species recognized and taxonomically reviewed in Australia (Munir, 1992) and 79 species recognized and infragenerically classified in Brazil (Atkins, 2005). Dwarf and tall cultivars have been selected with flowers displaying various hues of blue, purple, pink, and red. There is a range of polyploids within the porterweed genus and even within some of its species (Sanders, 2001). The magnitude of effort needed to incorporate sterility into new porterweed breeding lines will depend on existing ploidy levels among cultivars. Relatively little is known about the ploidy level, vigor, flowering, and seed viability of cultivars grown in Florida, because they are routinely propagated by vegetative cuttings. The overall objective of this study was to evaluate horticultural attributes and potential invasiveness of the FLEPPC Category II invasive nettleleaf porterweed and seven closely related potential alternatives planted in northern Florida (Quincy, USDA Plant Hardiness Zone 8b) and southern Florida (Fort Pierce, USDA Plant Hardiness Zone 9b). Specific objectives include: 1) assessment of plant performance, growth, and flowering among cultivars; 2) determination of seed production, viability, and germination among cultivars; and 3) confirmation of ploidy number and potential for hybridization between the native and invasive species.

Materials and Methods

Plant material and field conditions. Eight porterweed species or cultivars were selected for this study based on local availability (Table 1). Seed- propagated jamaican porterweed and clonally propagated coral porterweed, 'Violacea' porterweed, 'Red Compact' porterweed, and nettleleaf porterweed were obtained as liners from Liner Farm Inc. (St. Cloud, FL) and finished in 3.8-L containers at the Indian River Research and Education Center (Fort Pierce, FL). In addition, clonally propagated 3.8-L 'Mario Pollsa' porterweed, 'Naples Lilac' porterweed, and 'J.P.'s Pink' porterweed were obtained from Boynton Botanicals (Boynton Beach, FL). Nine uniform 3.8-L plants of each selection were installed under full sun conditions in southern Florida (Fort Pierce) and northern Florida (Quincy) on 29 Apr. 2008. Plants were placed 1.5 m on center in beds covered with black landscape fabric. Plants were subirrigated by filling canals (southern Florida) or dripirrigated (northern Florida) as needed (generally three times per week in spring and fall and one time per week in summer). Plants were fertilized 6 weeks after planting with 57 g of 12-month 15N-3.9P-10K Osmocote Plus (Scotts Co., Marysville, OH) in the area 15 to 30 cm from the crown. Daily rainfall, temperature, and solar radiation were recorded by Florida Automated Weather Network monitoring stations located at each site. Field conditions for southern Florida were as follows: Ankona sand with 0.8% organic matter, pH 6.8, average monthly rainfall 18.8 cm, mean minimum and maximum temperatures 14.2 and 33.4 °C, respectively, and 80.9% relative humidity. Field conditions for northern Florida were as follows: Carnegie loamy fine sand with 2.6% organic matter, pH 4.7, average monthly rainfall 14.6 cm, mean minimum and maximum temperatures 9.3 and 33.7 °C, respectively, and 77.0% relative humidity.

Visual quality, flowering, and plant growth. Visual quality (plant color and form) was assessed monthly for each cultivar independently at each location. Assessments of foliage color and form were performed on a scale from 1 to 5 in which 1 = very poor quality, not acceptable, severe leaf necrosis or chlorosis, poor form; 2 = poor quality, not acceptable, large areas of necrosis or chlorosis, poor form; 3 = fair quality, marginally acceptable, somewhat desirable form and color; 4 = good quality, very acceptable and desirable color and form; and 5 = excellent quality, perfect condition, premium color and form, peak landscape performance.

Observations of flower initiation, flowering period, and seed set were recorded monthly. Flowering was assessed on a scale from 1 to 5 in which 1 = no flowers or flower spikes; 2 = flower spikes visible, but no open

Table 1. Nomenclature and	plant d	lescription	of eight	porterweed	cultivars. ^z

Common name	Species/cultivar	Foliage and inflorescence description
Nettleleaf porterweed	Stachytarpheta cayennensis" (synonym: S. urticifolia)	Upright, medium-sized plant reaching 1.0 to 1.5 m, distinct and prominent leaf veins, glossy green foliage, small dark blue-purple flowers borne on thin spike open in clusters of 3 to 5. Reportedly more cold-hardy than other porterweeds (K. Kastenholz, personal communication). Plant hardiness zone 9b-10b. Polyploid.
Jamaican porterweed	Stachytarpheta jamaicensis	Native to Florida. 0.5 to 1.0 m high, mounding, low-growing plant of horizontal habit. Small blue-purple flowers are produced either singly or 3 to 5 in a cluster on a thickened spike to 12 inch long or more. Plant hardiness zone 9a–11. Polyploid.
'Mario Pollsa' porterweed	Stachytarpheta 'Mario Pollsa'	Larger selection growing to 2 m, lavender flowers in clusters of 3 to 5 are produced on long erect spikes; pubescent leaves and spikes; collected in South America by Mario Pollsa and brought into the United States by Ron Boender (Butterfly World, Coconut Creek, FL) (K. Kastenholz, personal communication). Polyploid.
Coral porterweed	Stachytarpheta mutabilis	To 2 m, fast-growing, large coral flowers open in clusters of 8 to 10 in succession along large arching spike. Flowers appear almost pink when temperatures are very high; leaves and sepals highly public ent. Polyploid.
'Violacea' porterweed	Stachytarpheta mutabilis 'Violacea' (S. frantzii)	To 2 m, fast-growing, large dark violet blooms open in clusters of 10 to 15 in succession along large arching spike; leaves and spikes highly pubescent. Polyploid.
'Naples Lilac' porterweed	Stachytarpheta 'Naples Lilac'	To 2 m or more, purple flowers in clusters of 3 to 5 are produced on long, erect pubescent spikes. Cross between nettleleaf porterweed and 'Violacea' porterweed, created by Thomas Hucker (Former Director of Naples Botanical Garden, FL) (Kastenholz, personal communication). Polyploid.
'J.P's Pink' porterweed	Stachytarpheta speciosa 'J.P's Pink'	Compact form reaching only 0.5 to 1.0 m, true pastel pink flowers with white centers oper in clusters of 5 to 8 along thin spike; more cold-sensitive than other cultivars. Found as a sport of 'Red Compact' porterweed at J.P.'s Nursery, West Palm Beach, FL (K. Kastenholz, personal communication). Diploid.
'Red Compact' porterweed	Stachytarpheta speciosa 'Red Compact'	Compact form reaching only 0.5 to 1.0 m, lighter green foliage, bright red flowers open in clusters of 4 to 6 along thin spike. Diploid.

²Plant hardiness zone is based on the U.S. Department of Agriculture zone map (USDA, 2003) and observations in Florida. Foliage and inflorescence descriptions are based on personal observations in northern and southern Florida. Ploidy level was determined by flow cytometry (see "Materials and Methods"). ⁹Nettleleaf porterweed is listed by the Florida Exotic Pest Plant Council (FLEPPC) as a Category II invasive in south Florida (FLEPPC, 2007). flowers; 3 = one to several spikes with open flowers; 4 = many spikes with open flowers, average to good flowering; and 5 = abundant flowering, peak bloom. Each month, completely senesced brown spikes (containing mature seed) were removed from each plant and counted. To calculate total seed production per plant, seeds were manually removed and counted from 10 representative spikes from each cultivar. Total spike number was multiplied with this value to estimate total seed production per plant during the 28week growing season at each location. At the termination of the study (Week 28, 10 Nov. 2008), growth indices were calculated for each plant as an average of the measured height (measured from crown to natural break in foliage) and two perpendicular widths [(height + width1 + width2)/3]. Although monthly field data were no longer collected after 28 weeks (termination of the experiment), plants were allowed to overwinter at each location merely to assess cold hardiness. After winter and the last frost-free day (at 46 weeks), plants were heavily pruned and regrowth was documented after 6 weeks to verify cold hardiness among cultivars and sites.

Seed germination and viability. Mature inflorescences were removed from each plant at each site and cleaned by hand using a dehulling trough (Hoffman Manufacturing, Inc., Albany, OR). Immature seeds or seeds with visible indication of pathogen or insect damage were discarded. Cleaned seeds were gravity air-dried at 22 °C for 48 to 72 h before analysis. In accordance with the Tetrazolium Testing Handbook, Contribution No. 29 Association of Official Seed Analysts rules (Peters, 2000), pregermination viability tests were replicated twice on a subset of 100 seeds per cultivar from both sites. Seeds were pretreated by allowing them to imbibe between moist blotter paper overnight at room temperature. Seeds were then cut longitudinally and stained for 18 to 24 h at 30 to 35 °C in 1.0% tetrazolium (2, 3, 5-triphenyl chloride) solution with positive staining patterns confirming seed viability (Mid-West Seed Service Inc., Brookings, SD). An additional 400 seeds per cultivar from both sites were subjected to germination tests (four replications of 100 seeds per test) at 30/20 °C (8-h photoperiod at 30 °C followed by 16 h darkness at 20 °C) for 28 d (Mid-West Seed Service Inc.). Seeds were arranged in germination boxes (containing two layers of moistened blue blotter paper) that were placed in incubators equipped with cool-white fluorescent lamps. Germination readings were taken at Day 14 with a final count at Day 28. Ungerminated seed were subjected to postgermination viability tests (as described previously) and used to report percent germination of viable seeds.

Using a subsample of seed collected from cultivars grown in Fort Pierce, an additional experiment was conducted to determine temperature effects on seed germination. Cleaned seeds were treated with 0.6% sodium hypochlorite for 5 min, rinsed three times with deionized water, and soaked overnight in aerated water. Floating seeds were discarded. Individual treatments consisted of four replications of 50 seeds per cultivar in 10.9×10.9 -cm transparent polystyrene germination boxes (Hoffman Manufacturing, Inc., Albany, OR) containing two sheets of germination paper (Hoffman Manufacturing Inc.) moistened with 15 mL deionized water. Germination boxes were placed in temperature- and light-controlled chambers equipped with cool-white fluorescent lamps (Model 818; Precision Scientific, Winchester, VA). Germination boxes were placed in 20/10, 25/ 15, 30/20, and 35/25 °C. The photoperiod was administered by providing 12 h light at 20, 25, 30 or 35 °C (photosynthetic photon flux was 22 to 30 μ mol·m⁻²·s⁻¹ at shelf level) followed by 12 h dark at 10, 15, 20, or 25 °C, respectively. Germination of seed was monitored daily for a period of 28 d. An additional 5 to 10 mL of deionized water was added to germination boxes as needed. A seed was considered germinated when radicle emergence was 2.0 mm or greater. At the end of the germination period, final germination percentage (FGP) and T50 (days to 50% of FGP) were determined per germination box.

Ploidy analysis and hybridization potential. Ploidy level of the porterweed cultivars was analyzed by flow cytometry (Viloria and Grosser, 2005). Several young, recently matured leaves were collected from containerized stock plants and a small piece of leaf tissue (≈ 0.5 cm²) was chopped thoroughly using a sharp razor blade in Cystain ultraviolet Precise P extraction buffer (Partec GmbH, Münster, Germany). The homogenate was incubated for 1 min and then filtered through a Partec 30-µm Cell-Tric disposable filter (Partec GmbH). Staining buffer (HR-B; Partec GmbH) was added to the suspension of nuclei and the samples were analyzed on a ploidy analyzer (PA-1; Partec GmbH) following the manufacturer's recommendations.

To assess the hybridization potential between the invasive nettleleaf and the native jamaican porterweed, manual crosses were performed between nettleleaf porterweed \times jamaican porterweed and the reciprocal. One 3.8-L plant for each porterweed was grown in a greenhouse. For each plant, three flower spikes were selected and tagged. As flower buds matured sequentially along the spike, they were emasculated before anther dehiscence. The corolla and attached anthers were removed by pulling them gently, and the exposed stigma was pollinated. For identification, each pollinated flower was marked by coloring the remaining sepal on the spike with a permanent marker. This process was repeated during a period of 10 d, completing ≈ 20 pollinations per spike to a total of 55 pollinations for nettleleaf porterweed × jamaican porterweed and 62 pollinations for the reciprocal cross.

Four weeks after pollinations were completed, tips of the pollinated flower spikes were cut to prevent further flowering and promote ripening. Spikes were harvested when they were brown and brittle and could be detached easily from the plant. This began ≈ 80 d after pollination for nettleleaf porterweed and 110 d for jamaican porterweed. Putative hybrid seeds were cleaned and germinated at 25/15 °C for 2 weeks before transfer to the greenhouse for phenotype evaluation.

Experimental design and statistical analysis. The field experiments were conducted similarly in northern and southern Florida. A randomized complete block experimental design was used with eight cultivars placed in three-plant plots replicated three times (blocks). Visual quality and flowering data were collected monthly for each plant. At 28 weeks, growth data were collected on each plant sample, subjected to analysis of variance (ANOVA), and significant means separated by least significant difference (LSD) at P = 0.05. For the first germination study, data were subjected to ANOVA and significant cultivar means separated by LSD at P = 0.05. For the second germination study, a split block experimental design was used with temperature as the main block and cultivar as the split plot. Percentage data were transformed by a sqrt arcsine before conducting an ANOVA within temperatures. Transformed means were separated by a Duncan's multiple range test (P = 0.05). Untransformed cultivar means are presented in tables.

Results and Discussion

Visual quality and plant growth. Visual quality of porterweed varied by location and cultivar (Fig. 1A; Table 2). In both locations, peak visual quality values (very good to excellent) were recorded from April to June and August to October for most of the cultivars with the exception of coral porterweed that gradually declined in northern Florida and 'J.P.'s Pink' porterweed that sharply declined and eventually died in northern and southern Florida. Warm and wet conditions in July [resulting in temporary leaf rust (Puccinia spp.)] and cold temperatures in November contributed to lower visual quality readings during these months in both locations. Overall, nettleleaf porterweed, jamaican porterweed, 'Naples Lilac' porterweed, and 'Red Compact' porterweed had similarly high visual quality ratings in northern Florida (Table 2). In southern Florida, 'Violacea' porterweed, nettleleaf porterweed, and 'Red Compact' porterweed had the highest overall visual quality ratings (Table 2). In northern Florida, coral porterweed and 'J.P.'s Pink' porterweed had the lowest overall visual quality ratings. In southern Florida, 'Mario Pollsa' and 'J.P.'s Pink' porterweed had the lowest overall visual quality ratings.

Of the porterweed cultivars evaluated in northern and southern Florida, after 28 weeks, 'Mario Pollsa' porterweed was the tallest (106 cm) followed by 'Naples Lilac' porterweed (103 cm) (data not presented). 'Naples Lilac' porterweed had the greatest growth index at both sites, because plants were significantly wider than the other cultivars (Table 2). It is of interest to note that on average, porterweed cultivars were 1.2 to 1.8 times larger in northern Florida than in southern Florida after 28 weeks. After completion of the study, frost killed aboveground portions of all plants during the winter in northern and southern Florida. In northern Florida, spring regrowth was not observed for any of the plants regardless of cultivar. In southern Florida, winter survival (and subsequent regrowth) was 100% for jamaican porterweed, 'Violacea' porterweed, 'Naples Lilac' porterweed, and nettleleaf porterweed. Less winter survival was observed for 'Mario Pollsa' porterweed (78%), coral porterweed (67%), 'Compact Red' porterweed (56%), and 'JP's Pink' porterweed (0%). This indicates that regardless of species, porterweed performs as an annual in northern Florida. In southern Florida,

porterweed can generally be used as a perennial, but dwarf cultivars may be less hardy or vigorous.

Flowering. Porterweed flowers continually and indeterminately. Although flower performance varied by cultivar and location, there were at least some flowers (and usually many) on each plant throughout the duration of the study (Fig. 1B; Table 2). Regardless of cultivar or site, peak flowering times generally were in late spring to early summer (May to June) and again in the early fall (September to October) (Fig. 1B). Within 28 weeks, plants in northern Florida produced an average of 3.4 times more flower spikes than plants in southern Florida. Average number of spent flower spikes from a single plant ranged from 49 (coral porterweed) to 651 (nettleleaf porterweed) in northern Florida or 26 (coral porterweed) to 203 (nettleleaf porterweed) in southern Florida. Overall, 'Naples Lilac' porterweed and 'Red Compact' porterweed had similarly high flower ratings (4.25 and 4.07, respectively) in northern Florida (Table 2). In southern Florida, nettleleaf porterweed, 'Naples Lilac' porterweed, and 'Red Compact' porterweed had the highest overall flower ratings (3.97, 3.88, and 3.81, respectively) (Table 2). At both locations, coral porterweed and 'J.P.'s Pink' porterweed had the lowest flower ratings. This information can be useful from a nursery and landscape perspective as well as from an invasive perspective because length of the flowering period has been found to be greater in weedy species as compared with nonweedy species (Perrins et al., 1992). Long flowering periods may allow greater accessibility to pollinators and a greater chance of seed set (Reichard and Hamilton, 1997).



Fig. 1. (Continued on next page)



Fig. 1. Monthly visual quality (color and form) and flowering of eight porterweed cultivars grown for 28 weeks in northern (**A**) and southern (**B**) Florida. Visual quality (**A**) was rated 1 (very poor) to 5 (excellent). Flowering (**B**) was rated 1 (no flower spikes) to 5 (abundant flower spikes). Mean values ± sE are shown (n = 3).

Table 2. Growth index, average monthly flower rating (scale 1–5), and average monthly visual quality rating (scale 1–5) of eight porterweed cultivars grown for 28 weeks in northern and southern Florida.

	Growth index		Avg flow	ver rating ^z	Avg visual quality rating ^y	
Species/cultivar	Northern Florida	Southern Florida	Northern Florida	Southern Florida	Northern Florida	Southern Florida
Nettleleaf porterweed	129.04	76.30	3.79	3.97	4.03	3.88
Jamaican porterweed	123.04	67.30	3.21	3.14	4.17	3.63
'Mario Pollsa' porterweed	140.89	104.44	3.81	3.60	3.39	3.13
Coral porterweed	101.33	96.74	2.49	2.62	3.03	3.42
'Violacea' porterweed	137.48	92.07	3.80	3.38	3.72	4.03
'Naples Lilac' porterweed	184.15	118.44	4.25	3.88	3.82	3.50
'J.P.'s Pink' porterweed	53.30	46.15	2.58	2.78	2.93	2.86
'Red Compact' porterweed	94.70	58.81	4.07	3.81	4.05	4.22
LSD $(0.05)^{x}$	26.36	14.02	0.34	0.32	0.37	0.43

^zBased on a flowering scale of 1 to 5 in which 1 = no flowers and 5 = abundant flowering or peak bloom.

^yBased on a visual quality scale (foliage and form) of 1 to 5 in which 1 = very poor quality and 5 = excellent quality.

^xLeast significant difference (LSD) at P = 0.05 level.

Seed production, viability, and germination. Within 8 to 12 weeks, each of the eight cultivars evaluated produced fruit characterized as an oblong-linear schizocarp splitting at maturity into two mericarps (Munir, 1992). However, there were significant differences in the actual embryo development (and hence viability) among cultivars. In northern Florida, jamaican porterweed had the greatest seed viability (78%) followed by 'J.P.'s Pink' porterweed (43%), 'Red Compact' porterweed (41%), and nettleleaf porterweed

(39%) (Table 3). In southern Florida, jamaican porterweed and nettleleaf porterweed also had the greatest seed viability (93% and 80%, respectively) compared with the other cultivars. The greater seed viability of nettleleaf porterweed (FLEPPC Category II invasive) in southern Florida compared with northern Florida is of interest. A suite of factors has been found to influence variation in seed dormancy, including population, year, mother plant condition (Andersson and Milberg, 1998), and temperature and soil moisture during seed maturation (Peters, 1982). Yet, location did not appear to influence seed viability of the other seven cultivars in this study. At both locations, seed viability was less than 10% for 'Mario Pollsa' porterweed (7% to 10%), coral porterweed (7% to 8%), 'Violaceae' porterweed (0%), and 'Naples Lilac' porterweed (1% to 2%) (Table 3).

Pregermination viability data generally correlated with percent germination within 28 d, indicating that seeds from most cultivars do not possess a physical or physiological dormancy as defined by Baskin and Baskin (2001) and that seeds are not decaying during the germination period. However, at both locations, seeds produced from the dwarf cultivars ('J.P.'s Pink' porterweed and 'Red Compact' porterweed) were 42% to 52% dormant (Table 3). Dormancy was not alleviated when seeds of these cultivars were germinated at a wide range of temperatures (20/10, 25/15, 30/20, and 35/25 °C) (Table 4). It is likely that these cultivars require additional stratification or scarification treatments before germination.

More than 75% of nettleleaf porterweed seed (collected in southern Florida) germinated at 20/10, 25/15, 30/20, and 35/25 $^{\circ}$ C (Table 4). Several weed species have been

Table 3. Percent viability and germination of seed collected from eight porterweed cultivars grown in northern and southern Florida.^z

Northern Florida ^v								
Species/cultivar	Pregermination viability ^x (%)	Germination ^w (%)	Dormant (%)	Total viable (%)	Germination of viable seed (%)			
Nettleleaf porterweed	38.5 b	32.8 b	6.3 c	39.0 d	84.0 a			
Jamaican porterweed	77.5 a	60.3 a	17.8 b	78.0 a	77.2 ab			
'Mario Pollsa' porterweed	9.5 c	3.5 c	6.5 c	10.0 e	35.0 bc			
Coral porterweed	6.5 c	1.5 cd	5.5 c	7.0 f	21.4 cd			
'Violacea' porterweed	0.0 d	0.0 e	0.0 d	0.0 h	0.0 d			
'Naples Lilac' porterweed	0.5 d	1.3 cde	0.3 d	1.5 g	75.0 a			
'J.P's Pink' porterweed	42.5 b	0.8 de	42.3 a	43.0 b	1.8 d			
'Red Compact' porterweed	40.5 b	0.3 de	40.8 a	41.0 c	0.6 d			
Southern Florida ^v								

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	Pre-germination	Germination ^w	Dormant	Total viable	Germination of
Species/cultivar	viability ^x (%)	(%)	(%)	(%)	viable seed (%)
Nettleleaf porterweed	79.5 a	69.3 b	1.0 de	70.3 b	98.8 a
Jamaican porterweed	92.5 a	84.5 a	8.5 c	93.0 a	90.9 b
'Mario Pollsa' porterweed	6.5 c	11.0 c	0.0 e	11.0 e	100.0 a
Coral porterweed	8.0 c	0.8 e	7.3 c	8.0 e	9.4 de
'Violacea' porterweed	0.0 d	0.0 e	0.0 e	0.0 g	0.0 e
'Naples Lilac' porterweed	1.5 cd	0.8 e	1.3 d	2.0 f	37.5 c
'J.P's Pink' porterweed	46.0 b	4.5 d	41.5 b	46.0 d	9.8 d
'Red Compact' porterweed	56.5 b	4.8 d	52.3 a	57.0 c	8.3 d

^zSeeds were subjected to an 8-h photoperiod at 30 °C followed by 16 h darkness at 20 °C.

^yMean separation was conducted by Duncan's multiple range test on transformed means. Different lowercase letters within columns are significantly different (P = 0.05).

*Performed on a subset of 200 seed (two replications of 100).

"Performed on 400 seed (four replications of 100). Remaining seeds that did not germinate were subjected to viability tests and used to calculate viable seed germination percentages.

Table 4. Final germination percent and number of days to 50% of final germination (T50) of seed collected from eight porterweed cultivars grown in southern Florida.^z

	Germination (%) ^y			T50 (days)				
Species/cultivar	20/10	25/15	30/20	35/25	20/10	25/15	30/20	35/25
Nettleleaf porterweed	75.5 a	79.5 a	80.5 a	88.0 a	21.3 b	8.8 cd	7.0 cd	5.0 c
Jamaican porterweed	43.0 b	85.5 a	83.5 a	48.0 b	16.5 c	8.0 cd	7.0 cd	4.0 c
'Mario Pollsa' porterweed	10.5 c	9.0 b	11.5 b	7.5 cd	12.5 d	5.5 d	4.0 d	4.0 c
Coral porterweed	2.5 d	9.5 b	6.0 bc	10.5 c	22.3 b	12.0 bcd	7.5 cd	9.8 b
'Violacea'porterweed	0.0 e	0.0 c	0.0 d	0.0 e	x	x	x	x
'Naples Lilac' porterweed	1.5 d	1.5 c	1.0 d	3.5 d	26.0 a	19.0 a	19.5 a	14.7 a
'J.P's Pink' porterweed	0.0 e	0.5 c	7.5 bc	9.5 c	x	16.0 ab	16.8 ab	14.3 a
'Red Compact' porterweed	0.0 e	0.5 c	3.0 cd	10.5 c	x	14.0 abc	12.0 bc	14.8 a

^zSeeds were germinated with light (12-h photoperiod) in germination boxes placed in growth chambers set at 20/10, 25/15, 30/2,0 and 35/25 °C for 28 d.

^yPerformed on 200 seed (four replications of 50). Mean separation was conducted by Duncan's multiple range test on transformed means. Different lowercase letters within columns are significantly different (P = 0.05).

*T50 could not be calculated as a result of zero percent germination.

shown to germinate over a wide range of temperatures (Balyan and Bhan, 1986; Susko et al., 1999); and the consensus of comparative studies is that alien invaders germinate earlier, better, or at a wider range of conditions (Pyšek and Richardson, 2007). The jamaican porterweed also had high germination at 25/15 and 30/20 °C, but germination was dramatically reduced by 50% and 43% at the lowest (20/10 °C) and highest (35/25 °C) temperature treatments, respectively. Although not an objective of this study, it is of interest to note that germination of jamaican porterweed seed was considerably less if germination experiments are performed in darkness. At 25/15 and 30/20 °C, germination in the dark was 61% and 91% less, respectively, than seeds that received 12 h of light (data not presented). However in contrast, nettleleaf porterweed had similarly high germination with light (80% to 81%) or without light (78% to 83%) at 25/15 and 30/ 20 °C (data not presented). Seeds that do not require light for germination in petri dishes may be more capable of germinating in nature when shaded by leaf litter or a tree canopy or after burial in the soil (Baskin and Baskin, 2001).

With the exception of jamaican porterweed and nettleleaf porterweed, all other cultivars had 11.5% or less germination. The least number of mean days to achieve 50% of total germination varied with temperature and cultivar (Table 4). At 20/10 °C, T50 values ranged from 13 d ('Mario Pollsa' porterweed) to 26 d ('Naples Lilac' porterweed), whereas at 35/25 °C, T50 values were lower ranging from 4 or 5 d (nettleleaf porterweed, jamaican porterweed, and 'Mario Pollsa' porterweed) to 14 or 15 d ('Naples Lilac', 'J.P.'s Pink', and 'Red Compact' porterweed). Germination rate can be a useful measure of the speed or velocity of germination because germination patterns can be different even if final germination percentages are almost identical (Hartmann et al., 2002). In addition, invasiveness has been positively correlated with the rate of germination (Forcella et al., 1986).

Average number of seeds per inflorescence spike varied widely among cultivars with 'Red Compact' porterweed having the largest number of seeds per spike and 'Mario Pollsa' porterweed having the least number of seeds per spike (Table 5). The flowers of porterweed are semi-immersed in depressions or furrows in the rachis of the spike making it possible to estimate total seed production, even after dehiscence. In other studies, stem count has been used to predict the number of inflorescences and the inflorescence length has been used to predict the number of seed capsules (Ebeling et al., 2007). Also, seed capsule weight has been used to project number of seeds per plant (Wilson et al., 2004b). In the present study, percent germination was included in the equation to estimate potential seedling progeny. If calculating the average number of seeds per plant with projected germination (60% to 85%) under optimal conditions,

Table 5. Average number of seeds per flower spike, average number of spikes per plant, and average number of potential seedlings per plant of eight porterweed cultivars grown for 28 weeks in northern and southern Florida.

	Avg no. of seeds per		mber of er plant ^z	Potential seedlings per plant ^y	
Species/cultivar	spike (n = 10)	Northern Florida	Southern Florida	Northern Florida	Southern Florida
Nettleleaf porterweed	189	651	203	40,300	26,600
Jamaican porterweed	399	531	131	127,400	44,200
'Mario Pollsa' porterweed	101	283	97	1,000	1,100
Coral porterweed	179	49	26	100	40
'Violacea' porterweed	297	226	53	0	0
'Naples Lilac' porterweed	147	467	99	900	100
'J.P's Pink' porterweed	248	140	66	300	700
'Red Compact' porterweed	427	413	115	400	2,300

^zValue represents spent flower spikes produced during the 28-week trial.

^yCalculated using germination percentages from respective sites.

jamaican porterweed has the potential to produce over 127 thousand seedlings in northern Florida and over 44 thousand seedlings in southern Florida (Table 5). Nettleleaf porterweed (with 33% to 70% germination) has the potential to produce over 40 thousand seedlings in northern Florida and 26 thousand seedlings in southern Florida. This information is useful, because length of flowering period does not necessarily indicate high seed production, and high seed production does not necessarily indicate high germination. For example, 'Dartmoor' butterfly bush (Buddleja davidii × Buddleja davidii var. nanhoensis) continually flowered (50% to 75% canopy coverage) throughout much of a study in west and south Florida (Wilson et al., 2004a) yet produced relatively few seeds compared with the other butterfly bush cultivars (Wilson et al., 2004b). Likewise, in another study, 'Little Kitten' japanese silver grass (Miscanthus sinensis) had the highest number of inflorescence panicles in southern Florida but less than half of the seeds were viable, and of these, only 54% germinated (Wilson and Knox, 2006). As Mandák (2003) points out, percentage of seed germination is only one important factor to consider when fully characterizing the invasive potential of plants. Seed bank establishment, seed dispersal, resource allocation, physiological and morphological adaptations to specialized environments, life history traits, and propagule pressure all contribute to plant invasiveness (Baruch and Goldstein, 1999; Pemberton and Liu, 2009; Pyšek and Richardson, 2007; Reichard and Hamilton, 1997; Rejmánek, 2000).

Ploidy identification and hybridization potential. 'Red Compact' and 'J.P.'s Pink' porterweed were determined to be diploids (Table 1). The C value of the other porterweed cultivars was two to 2.5 times that of 'Red Compact' or 'J.P.'s Pink', indicating that these cultivars might be tetraploids or pentaploids. It is known that there is a range of polyploids and aneuploids in the porterweed genus (Fedorov, 1974; Sanders, 2001). Therefore, the ploidy level of these cultivars (except for 'Red Compact' and 'J.P.'s Pink') should be considered tentative without further confirmation from mitotic and/or meiotic chromosome counting.

Manual pollinations between nettleleaf porterweed and jamaican porterweed were successful. Fruit set in each of the three pollinated flower spikes for S. jamaicensis \times S. urticifolia ranged from 10% to 20% with an average of 16.1%, and from 12.5% to 22.2% for the reciprocal with an average of 16.4%. Because each fruit contains two seeds, a total of 20 and 18 seeds were obtained for each cross. In addition, under greenhouse conditions, it was observed that both nettleleaf porterweed and jamaican porterweed plants had fruit set from self-pollination. Thirty self-pollinated seeds per plant were harvested to be used as controls to compare germination rates and morphology with the putative hybrid progenies. Future work will evaluate putative hybrid seedlings using morphological markers that distinguish both parents to confirm their hybrid origin.

The results of this study suggest 'Naples Lilac' porterweed (which was essentially seed-sterile) performed as well, if not better than, nettleleaf porterweed (a Category II invasive in Florida that produces abundant, viable seed). Other female sterile or almost sterile alternatives with good flowering and visual quality were 'Mario Pollsa' porterweed and 'Violacea' porterweed. The dwarf 'Red Compact' porterweed outperformed and lived longer than the dwarf 'J.P.'s Pink' porterweed. The native jamaican porterweed was much more prostrate and overall had less flower impact than the invasive nettleleaf porterweed but was ranked similarly in visual quality. Variation in ploidy level was found among porterweed cultivars. Although not straightforward as a result of its floral biology (autogamy, small flower size, inflorescence structure, and long fruit maturation time), manual cross-pollination between the native and invasive porterweed appears to be possible. The ecological risks associated with native gene pool contamination and the availability of highly ornamental, sterile, closely related porterweed alternatives suggest limiting the production and use of nettleleaf porterweed in Florida.

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