

# Growth and Development of the Native *Ruellia caroliniensis* and Invasive *Ruellia tweediana*

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**Abstract.** Invasive species have disrupted thousands of acres of natural areas in Florida and appear to have a physiological competitive advantage over native species. The influence of light and temperature on germination was determined for the invasive Mexican petunia (*Ruellia tweediana* Griseb.) and native wild petunia (*Ruellia caroliniensis* Steud.). Seeds were collected and germinated in incubators with light or darkness at 15, 24, 33, and 30/20 °C. Light increased germination for each species, except at 15 °C (*R. caroliniensis*). For *R. caroliniensis*, highest germination (86% to 94%) occurred at 33 °C and 30/20 °C. Highest germination of *R. tweediana* (98% to 100%) occurred at 30/20 °C. Studies also were initiated to determine if *R. tweediana* has a competitive advantage over the native species when grown under wet and dry substrate conditions. Growth and development measurements after 8 weeks under controlled conditions revealed that *R. tweediana* grown in wet conditions had the greatest dry weight increase as compared to other treatments. *Ruellia caroliniensis* had higher specific leaf area when grown in wet or dry conditions, as compared to *R. tweediana*. Throughout the experiment, net CO<sub>2</sub> assimilation of *R. caroliniensis* grown under dry or wet conditions was consistently lower than that of *R. tweediana*. Shoot nitrogen and phosphorus use efficiencies were generally greatest for *R. tweediana* plants grown in wet conditions. For shoot nutrient content, significant species × moisture interactions occurred for measured phosphorus (P) and calcium (Ca). When grown in wet conditions, *R. tweediana* had less shoot P and Ca as compared to dry conditions. For root nutrient content, species × moisture interactions were insignificant for each measured nutrient, with the exception of potassium (K). Potassium use efficiency of *R. tweediana* roots grown in wet conditions was higher than that of *R. tweediana* grown in dry conditions and *R. caroliniensis* grown in wet conditions.

Environmental horticulture is the fastest growing segment of American agriculture. Florida is the second largest producer of ornamental plants in the U.S. with an estimated value of sales by the environmental horticulture industry of 9.908 billion dollars (Hodges and Haydu, 2002). As a national leader in ornamental plant production, the Florida environmental horticulture industry is faced with rising concerns about escaped nonnative ornamental plants displacing native species and ecosystems. About 1.9 million acres of Florida's remaining natural areas have been invaded by exotic plant species and >240 million dollars have been

spent in Florida to control invasive, exotic plant species since 1980 [Florida Exotic Pest Plant Council (FLEPPC), 2003]. Several factors, including highly disturbed habitats, tourism, concentrated populations, absence of freezes, and abundance of lakes, streams and wetlands, predispose the South Florida landscape to great invasibility (Simberloff, 1997). Invasive species damage natural areas, alter ecosystem processes, displace native species, hybridize with natives, and/or support other potentially damaging plants, animals, and pathogens (Randall and Marinelli, 1996).

Invasive plants characteristically share one or more of several characteristics, including 1) effective reproductive and dispersal mechanisms, 2) superior competitive ability, 3) few to no herbivores or pathogens, 4) ability to occupy a vacant niche, and 5) capability to alter a site by either significantly changing resource availability or disturbance regimes, or both (Gordon, 1998). Pattison et al. (1998) reported that overall, invasive Hawaiian rainforest species appear to be better suited than native species for capturing and using light resources, particularly in high light environments such as those characterized by relatively high levels of disturbance. Likewise,

Baruch and Goldstein (1999) reported that leaf nutrient concentration was generally higher for invasive species as compared to native species of the same genus in Hawaii.

Differences in seed production, conditions for seed germination, growth and carbon fixation, and nutrient use efficiency are all important predictors of invasive ability (Rejmánek, 1996). Although widely sold by the southeastern nursery industry, *R. tweediana* has escaped cultivation in Florida (Wunderlin and Hansen, 2003) and was designated recently as a category I invasive species by FLEPPC. By definition, FLEPPC classifies a plant species as category I when it has actively altered native plant communities through native species displacement, changed community structure or ecological functions, or hybridized with natives (FLEPPC, 2003). Because this is largely based on personal observations, research is needed to 1) help growers make an informed decision of a plant's potential to become invasive and 2) understand why it may have become invasive so that future invasions may be prevented.

This study was designed to characterize growth, developmental and reproductive differences between a native and invasive species of *Ruellia*. Specific objectives of this project were to 1) quantify seed production and determine the influence of light and temperature on germination of *R. tweediana* and *R. caroliniensis* and 2) compare growth rate, biomass accumulation, photosynthetic rate and nutrient use efficiency of each species grown in simulated dry and wet soil moisture conditions. These moisture conditions were chosen to better understand the potential risks and impacts associated with the nonnative species in both upland and wetland environments.

## Materials and Methods

**Plant species.** A native plant of Mexico, *R. tweediana* is an herbaceous perennial with flowers distinctly pedunculate and borne solitary or in a few flowered cymes from leaf axils (Wunderlin, 1998). The wildtype form that has escaped in natural areas of Florida is inferior to the cultivated forms, with smaller purple flowers, thinner leaves and less desirable growth habit. It is commonly found on riparian sites but has been reported on drier sites as well (Wunderlin and Hansen, 2003). Leaves are 12.4 to 16.0 cm long. Fruit is an elongated capsule 0.4 cm wide × 2.2 cm long with brown seeds, 2 mm wide. Flower and seed stages alternate year-round in Florida. *Ruellia caroliniensis* is a smaller, less upright perennial varying from 31 to 52 cm tall, depending on growing conditions. Bluish-purple flowers occur in early spring and extend into late summer. Leaves are oval, 6.7 to 7.5 cm long. Flowers are succeeded by seed capsules 0.4 cm wide × 1.3 cm long with brown seeds, 2.5 mm wide. *Ruellia caroliniensis* is widespread throughout Florida, occurring in varied habitats including sandhills, flatwoods and hammocks (Wunderlin and Hansen, 2003).

**Seed production and germination.** Five uniform seedlings of *R. caroliniensis* and *R. tweediana* were transplanted in 3.8-L pots, and randomized on benches. After 12 weeks, plants

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were transferred to 11.4-L pots. All plants were top-dressed at a standard rate of 45 g /pot of 15N–3.9P–10K Osmocote Plus (The Scotts Co., Marysville, Ohio) and watered as needed. Seed capsules were collected daily before capsules opened during May thru January. The number of seed pods were recorded per plant per day and the number of seeds in each capsule were counted and weighed to obtain an estimated seed count per month.

Collected seeds were allowed to dry and naturally dehiscence at room temperature (22 to 25 °C) for 2 weeks before use in germination experiments. Seeds with visible indication of pathogen or insect damage were removed and not used in the experiments. Individual treatments for all incubator germination experiments consisted of five replications of 25 seeds placed on two sheets of Reeve Angel filter paper (Whatman Inc., Clifton, N.J.) in 9 cm petri-dishes. Filter paper was moistened with 10 mL nanopure (reverse osmosis/deionized) water. All dishes were sealed with Parafilm to prevent desiccation and placed in temperature- and light-controlled chambers equipped with fluorescent lamps (model 818; Precision Scientific, Winchester, Va.). Seeds were placed in light or darkness at 15, 24, 33 and 30/20 °C. The 30/20 incubator was set at 30 and 20 °C during the light and dark period, respectively. A 12-h photoperiod was maintained in each chamber with a photosynthetic photon flux of 22 to 30  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . Dishes assigned to dark treatments were wrapped in two layers of heavy-duty aluminum foil and remained unopened until the final day of the experiment. Germination of seeds exposed to light was monitored daily for a period of 28 days. A seed was considered germinated when the radicle protruded 2 mm from the seedcoat. At the end of the germination period, T50 (days until 50% final germination in light), final germination percent and radicle length were recorded.

**Plant growth and development.** A separate experiment was conducted to compare the growth, nutrient content/use efficiency, and photosynthesis of *R. tweediana* and *R. caroliniensis* grown in high (wet) and low (dry) moisture conditions. Seeds of each species were germinated in a soilless germination medium (Fafard, Inc., Apopka, Fla.) for 45 d (four leaf pairs). Uniform seedlings were rinsed to remove substrate and transplanted into 3.8-L pots filled with acid-washed sand. Sand was acid washed by saturating with a 0.2 N solution of HCl overnight, followed by rinsing with reverse osmosis water until a pH of 5.5 to 6.0 was achieved. Ten plants per treatment were randomized in a plant growth room equipped with metal halide lamps (Hydrofarm, Inc., Petaluma, Calif.) and rotating fans. The light intensity (bench level) was adjusted to  $450 \pm 20 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  with a 12-h photoperiod. Plants were maintained in dry (18% to 28%) and wet (82% to 100%) moisture conditions for 8 weeks. Soil (sand) moisture content was measured twice daily using a HydroSense time domain reflectometer (Campbell Scientific, Inc. Logan, Utah). A linear regression model was calculated using measurements taken from a series of test containers with sand at known volumetric water contents ranging from 0% to 100%. Moisture levels were adjusted to dry

or wet specifications using Nanopure water. Plants were initially fertilized with 200 mL of full strength Hoagland's nutrient solution (Hoagland and Arnon, 1938) followed by 50 mL of 20% Hoagland's weekly thereafter. At 8 weeks, plants were harvested and leaf area, leaf greenness, plant height (stem length), flower number and root and shoot dry weights were recorded. Leaf area was measured using a leaf area meter (LI-3000A; LI-COR, Lincoln, Nebr.). Leaf greenness was measured on the 5th, 6th, 7th, and 8th leaf from the apex of each plant using a SPAD-502 chlorophyll meter (Minolta Camera Co., Osaka, Japan). Shoots were severed at the crown and roots were hand-washed thoroughly. Shoot to root ratios were determined after shoots and roots were dried for 48 to 72 h at 70 °C in a drying oven. Specific leaf area (SLA) was calculated by dividing total leaf area by leaf dry weight. Specific stem length (SSL) was calculated by dividing stem length by stem dry weight.

**Photosynthetic efficiency and nutrient uptake.** Net  $\text{CO}_2$  assimilation (photosynthesis) was measured on young, fully expanded leaves. Measurements were taken from the 3rd and 4th fully open leaf from the apex of each plant at 0, 2, 4, 6, and 8 weeks using a CIRAS portable infrared gas analyzer (PP Systems, Haverhill, Mass.). Measurements performed on leaves with slightly less than 2.5  $\text{cm}^2$  area were recalculated and normalized using PP Systems software (RECALCRS.BAS version 3.0).

At 0 and 8 weeks, total nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) were analyzed within leaf, stem and root tissues (Pioneer Laboratory, Fort Pierce, Fla). Samples were dried for 48 to 72 h at 70 °C and ground to a powder with a ball mill grinder. To generate enough tissue for nutrient analysis, a composite tissue sample was obtained by mixing two individual subsamples together. Nutrient use efficiency (NUE) was calculated for shoot and root N, P, and K as (shoot dry weight + root dry weight)/[(shoot dry weight  $\times$  nutrient concentration in shoots) + (root dry weight  $\times$  nutrient concentration in roots)] as described by Koutroubas et al. (2000).

**Statistical analysis.** For the germination study, a split block experimental design with temperature as the main block and light as the split-plot was used with each treatment replicated five times. Data were subjected to analyses of variance (ANOVA) using the Statistical Analysis System (SAS Institute, 1999). Since temperature  $\times$  light interactions were significant, means were separated by an interaction Fisher's LSD,  $P = 0.05$ .

For the plant growth and development study, a  $2 \times 2$  (species  $\times$  moisture) factorial set of treatments within a completely randomized block experimental design with 10 replications per treatment was used. Data were subjected to analysis of variance (ANOVA). Main effect means of species and moisture were subjected to an F test and significant species  $\times$  moisture interaction means were subjected to Duncan's multiple range test,  $P = 0.05$ .

## Results and Discussion

**Seed production and germination.** Each *R. caroliniensis* capsule contained an average of 5.2 seeds. Peak production occurred in July and production continued through October (Fig. 1). Each *R. tweediana* capsule contained an average of 20.6 seeds. Production of seed was similar or higher than that of *R. caroliniensis* during every month except June, when seed production was lower (Fig. 1). Peak seed production of *R. tweediana* occurred in August but production continued through December. Perrins et al. (1992) reported that the length of the flowering period was longer in weedy species as compared to nonweedy species. Long flowering periods may allow a greater accessibility to pollinators and a greater chance of seed set (Reichard, 1997).

Significant light  $\times$  temperature interactions occurred for germination and radicle length of *R. caroliniensis* and *R. tweediana* (Table 1). Highest germination of *R. caroliniensis* was achieved at 30/20 °C in light. At lower temperatures, seed germination of *R. caroliniensis* either did not occur (15 °C) or was reduced (24 °C). Provision of light increased germina-

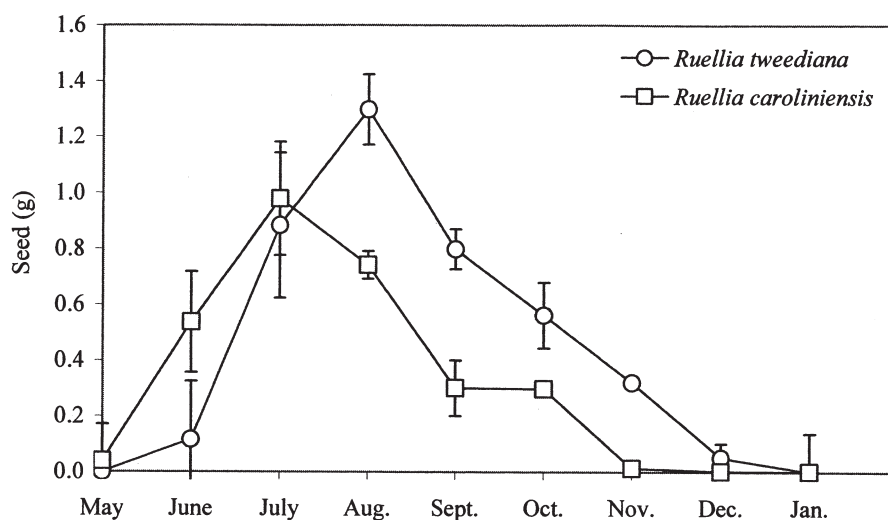


Fig. 1. Monthly seed production of *Ruellia caroliniensis* (RC) and *Ruellia tweediana* (RT). Data were collected daily from five plants per cultivar of identical age and presented as means  $\pm$  standard error.

Table 1. Final germination percent, radical length, and number of days to 50% of final germination percent (T50) of seed collected from the wildtype *Ruellia tweediana* (Florida invasive<sup>2</sup>) and *Ruellia caroliniensis* (Florida native). Plants were grown under identical conditions before seed collection. Seed was germinated with and without light in petri dishes placed in incubators set at 15, 24, 30/20, and 33 °C. T50 is reported only for seeds that germinated in light.

Temp (°C)	Light	<i>R. caroliniensis</i>			<i>R. tweediana</i>		
		Germination (%)	Radical length (cm)	T50	Germination (%)	Radical length (cm)	T50
15	Yes	0.0	0.0	---	63.2	3.9	7.60
15	No	0.0	0.0	---	56.8	2.9	---
24	Yes	52.0	3.4	4.4	44.0	5.2	3.0
24	No	4.8	0.9	---	40.8	2.7	---
33	Yes	89.6	3.2	3.0	57.6	3.2	3.0
33	No	86.4	2.7	---	20.8	2.1	---
30/20	Yes	94.4	3.9	4.2	100.0	4.2	3.0
30/20	No	93.6	3.0	---	97.6	2.6	---
LSD <sub>(0.05)</sub>		0.1	0.7	0.7	0.2	0.5	0.4
Light		**	**	---	**	**	---
Temperature		**	**	**	**	**	**
Light × temperature		**	**	-	**	**	---

<sup>2</sup>Designated by the Florida Exotic Pest Plant Council as a category I invasive plant (FLEPPC, 2003).

\*\*Significant F test at  $P = 0.01$ .

tion at 24, 33, and 30/20 °C. Radicle length of *R. caroliniensis* was generally greater when seeds were germinated in light, except at 33 °C (Table 1). The least number of mean days to achieve 50% germination was observed at 33 °C (Table 1). For *R. tweediana*, germination varied from 20.8% to 100%, depending on light and temperature (Table 1). Highest germination (97.6% to 100%) occurred at 30/20 °C with or without light when temperatures fluctuated between day and night. Several weed species germinate over a wide range of temperatures (Balyan and Bhan, 1986; Susko et al., 1999) and germination at a given temperature regime frequently differs when seeds are exposed to light or dark (Akanda et al., 1996). Seeds that do not require light for germination may be representative of seeds that germinate when shaded by litter, burial, or leaf canopy (Susko et al., 1999). While the most weedy species of *Echium* in Australia germinated far more quickly than two less weedy species (Forcella et al., 1986), Rejmánek and Richardson (1996) found no differences between percent germination of invasive and noninvasive *Pinus* species. Clearly, seed germination is only one of the important components for characterizing a plant's invasive potential, as numerous related traits may not fully explain the success of a particular species in a given environment. Based on vouchered specimens of species collected in natural areas and submitted to herbariums, *R. tweediana* has

escaped cultivation in 26 counties across Florida (Wunderlin and Hansen, 2003). Germination data suggests that this species can germinate under a variety of conditions throughout the entire state of Florida. Germination data also suggests the likelihood of continuous emergence of these seedlings throughout the year.

**Plant growth and development.** Significant species × moisture interactions occurred for stem and root dry weight (Table 2). Under wet conditions, *R. tweediana* had greatest stem dry weight with total dry weight increases of 60% to 83% more than other treatments. In a study comparing invasive and native Hawaiian rainforest species, the relative growth rates of invasive species were on average 2.5-fold higher than those of natives (Pattison et al., 1998). Leaf dry weight did not differ between species but native plants had higher leaf areas than nonnative plants and plants grown in wet conditions had greater leaf areas than plants grown in dry conditions. Plants that produce a smaller leaf area generally allocate more carbon to roots, thus increasing the potential for nutrient acquisition (Sage and Percy, 1987). Under wet conditions, *R. tweediana* had higher root DW than other treatments. Under wet conditions, *R. caroliniensis* and *R. tweediana* had similar shoot to root ratios that were greater than other treatments. Regardless of moisture conditions, SSL and SLA were greater for *R. caroliniensis* than *R. tweediana*. Specific leaf area has been positively related

to growth and efficiency and it is thought that a greater SLA may increase the capacity of a plant to assimilate CO<sub>2</sub> because more leaves are produced for a given mass of carbon invested in photosynthetic tissues (Lambers and Poorter, 1992; Reich et al., 1997). However, in our study the SLA of *R. tweediana* was ≈1.3 times less than that of *R. caroliniensis*. Initial plant height (day 0) of *R. tweediana* was higher than that of *R. caroliniensis* (Fig. 2). Effects of moisture treatments on plant height were apparent by week 4 and more pronounced by week 8, as shown by *R. tweediana* plants grown in wet conditions that were 1.9 to 2.8 times taller than plants of other treatments.

**Photosynthetic efficiency.** At 0, 2, 4, 6, and 8 weeks, net CO<sub>2</sub> assimilation (*A*) was higher for *R. tweediana* than *R. caroliniensis* (Fig. 3). Moisture conditions did not affect *A* of *R. caroliniensis* throughout the experiment. For *R. tweediana*, *A* was higher when plants were grown under dry conditions as compared to wet conditions at 2, 4, and 6 weeks. At 8 weeks, however, plants that were grown in wet conditions assimilated more carbon than plants grown in dry conditions. Most CO<sub>2</sub> was incorporated into stems and roots as evidenced by the dry weight measurements (Table 2). Increased plant height and root biomass may offer *R. tweediana* a competitive advantage over *R. caroliniensis* under similar conditions for capturing light resources and increasing access to nutrient

Table 2. Plant growth characteristics of *Ruellia caroliniensis* and *Ruellia tweediana* grown in dry (18% to 28% moisture) and wet (82% to 100% moisture) conditions for 8 weeks.

<i>Ruellia</i> species	Substrate moisture condition	Leaf greenness (SPAD)	Leaf area (cm <sup>2</sup> )	Leaf dry wt (g)	Stem dry wt (g)	Root dry wt (g)	Total plant dry wt increase (g)	Shoot to root ratio	Specific stem length (cm·g <sup>-1</sup> )	Specific leaf area (cm <sup>2</sup> ·g <sup>-1</sup> )
<i>caroliniensis</i>		31.6	91.9	0.65					67.9	
<i>tweediana</i>		36.5	76.0	0.72					36.4	
	Dry	34.7	69.1	0.56					62.1	
	Wet	33.4	98.9	0.81					42.1	
<i>caroliniensis</i>	Dry				0.13 c	0.92 b	1.60 b	0.73 c		144 a
<i>caroliniensis</i>	Wet				0.27 b	0.73 c	1.83 b	1.46 a		139 a
<i>tweediana</i>	Dry				0.34 b	0.84 bc	1.69 b	1.08 b		104 b
<i>tweediana</i>	Wet				0.92 a	1.20 a	2.93 a	1.49 a		109 b
Species		**	*	NS	**	**	**	*	**	**
Moisture		NS	**	**	**	NS	**	**	**	NS
Species × moisture		NS	NS	NS	**	**	**	*	NS	*

NS, \*, \*\* Nonsignificant or significant F test at  $P = 0.05$ , or 0.01, respectively. Significant interaction means separated by Duncan's multiple range test.



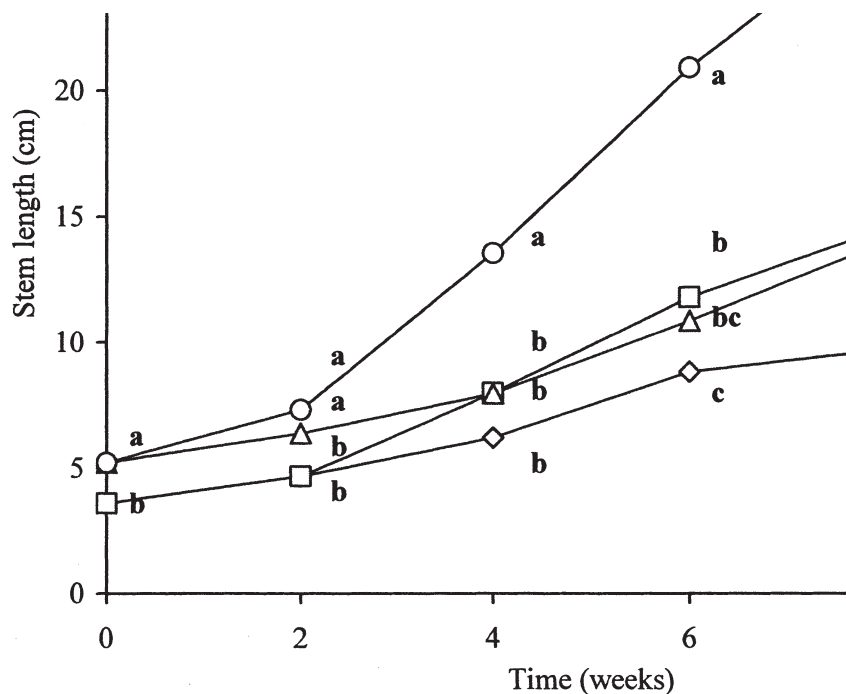


Fig. 2. Average plant height (stem length) of *Ruellia caroliniensis* (RC) and *Ruellia tweediana* (RT) grown in dry (18% to 28% moisture) and wet (82% to 100% moisture) conditions for 8 weeks. Treatment means within each week designated with a similar letter are nonsignificant.

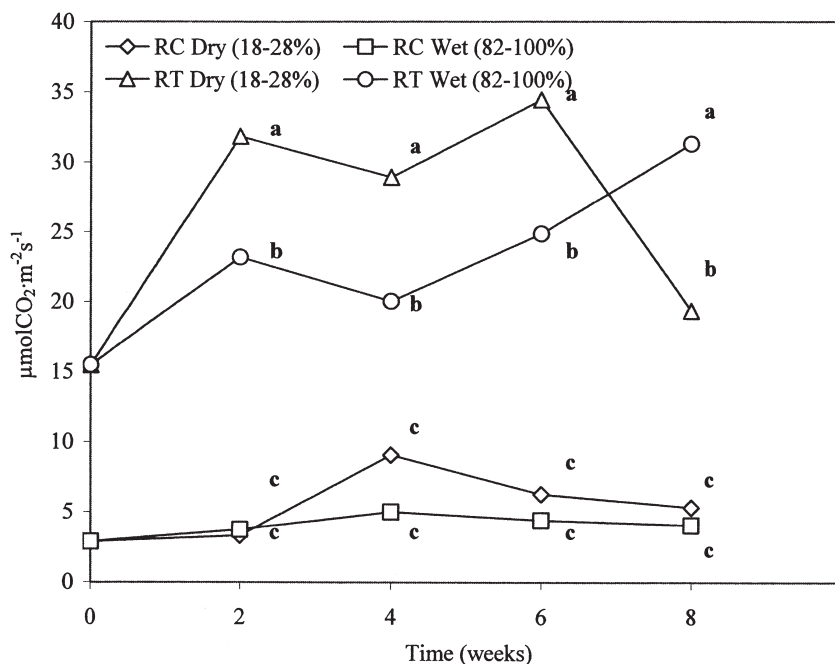


Fig. 3. Net CO<sub>2</sub> assimilation of *Ruellia caroliniensis* (RC) and *Ruellia tweediana* (RT) grown in dry (18% to 28% moisture) and wet (82% to 100% moisture) conditions for 8 weeks. Treatment means within each week designated with a similar letter are nonsignificant.

and water supplies. Invasive species that have similar reproductive potentials, growth form, and susceptibility to herbivory as that of native species likely capture limiting resources more efficiently (Vitousek, 1986) thus promoting faster growth rates. Several researchers have compared net CO<sub>2</sub> assimilation rates between native and invasive plants (Baruch et al., 1985; Baruch and Goldstein, 1999; Pattison et al., 1998; Williams and Black, 1993). In these studies, invasive species showed higher *A* than

native species. Baruch and Goldstein (1999) reported that the higher *A* of invasive species was likely a result of higher leaf N and higher SLA. However, in our study, N shoot content did not differ between species and SLA was greater for *R. caroliniensis* than *R. tweediana*.

**Nutrient content and use-efficiency.** Significant species × moisture interactions occurred for P and Ca content measured in shoot tissue (Table 3). When grown in dry conditions, *R. tweediana* had high shoot P as compared to other

treatments. In wet conditions, *R. tweediana* had far less shoot P and Ca than other treatments. Although the species × moisture interaction was insignificant for shoot N, moisture alone affected shoot N, with plants grown in dry conditions having higher N than plants grown in wet conditions. Leaf N content has been closely related to leaf greenness (chlorophyll content) (Wood et al., 1992). Although, the moisture effect on leaf greenness (as indicated by SPAD leaf readings) was insignificant, leaves of *R. tweediana* were greener than that of *R. caroliniensis* (Table 2). No significant species × moisture interactions occurred for measured root nutrients, with the exception of K root content, which was similarly high for *R. caroliniensis* grown in wet conditions and *R. tweediana* grown in dry conditions (data not shown). For total nutrient content (shoot and roots), significant species × moisture interactions occurred for P, K, and Ca (data not shown).

Mooney et al. (1978) showed that leaf N content on a dry weight basis varied little between diverse growth forms of *Eucalyptus* species in nature and that leaf N increased as the habitat became drier. Nitrogen and P concentrations in leaves are important determinants of growth potential (Baruch and Goldstein, 1999; Chapin, 1980). Generally, low leaf concentrations of N and P are characteristic of plants with relatively high nutrient use efficiency. *Ruellia tweediana* grown in wet conditions generally had higher shoot N and P-use efficiencies and higher root K-use efficiency than other treatments (Fig. 4). Baruch and Goldstein (1999) reported that the photosynthetic nitrogen use efficiency of invasive species was 15% higher than that of native species in Hawaii. Plants with a competitive advantage would be expected to produce more biomass per unit of nutrient taken up. Koutroubas et al. (2000) showed that plant species that more efficiently used limiting nutrients tended to dominate in herbaceous plant communities. Under typical wetland conditions in parts of southern Florida, *R. tweediana* might be expected to out-grow and out-compete the native species based on increased incorporation of these nutrients into plant biomass, especially if the nutrient supply is limited.

In summary, our studies show that *R. tweediana* plants have reproductive qualities characteristic of invasive plants such as a long flowering and seed production period, no requirement for scarification or stratification of seeds, low T50, and high germination occurring over a broad range of temperatures with and without light. The results in this study also suggest that the native and exotic *Ruellia* species have different strategies for assimilating carbon and utilizing nutrients in low and high moisture environments. Under wet conditions in controlled laboratory experiments, *R. tweediana* exhibits several traits that favor efficient use of resources and high growth rates. While this information alone does not allow for concise prediction of the environmental risks associated with potentially invasive exotic species, it does give insight into the competitive advantages *R. tweediana* may have over *R. caroliniensis* in wet and dry moisture environments.

Table 3. Plant shoot macronutrient content of *Ruellia caroliniensis* and *Ruellia tweediana* grown in dry (18% to 28% moisture) and wet (82% to 100% moisture) conditions for 8 weeks.

<i>Ruellia</i> species	Moisture	Concn (mg·g <sup>-1</sup> )				
		N	P	K	Ca	Mg
<i>caroliniensis</i>	---	13.30		15.77		3.823
<i>tweediana</i>	---	12.28		15.87		2.120
	Dry	13.78		15.02		4.215
	Wet	11.80		16.62		1.728
<i>caroliniensis</i>	Dry		1.028 b		33.03 ab	
<i>caroliniensis</i>	Wet		1.081 b		40.50 a	
<i>tweediana</i>	Dry		1.202 a		28.99 b	
<i>tweediana</i>	Wet		0.675 c		14.95 c	
Species		NS	**	NS	**	NS
Moisture		*	**	NS	NS	*
Species × moisture		NS	**	NS	**	NS

NS,\*,\*\*Nonsignificant or significant F test at  $P = 0.05$ , or  $0.01$ , respectively. Significant means separated by Duncan's multiple range test.

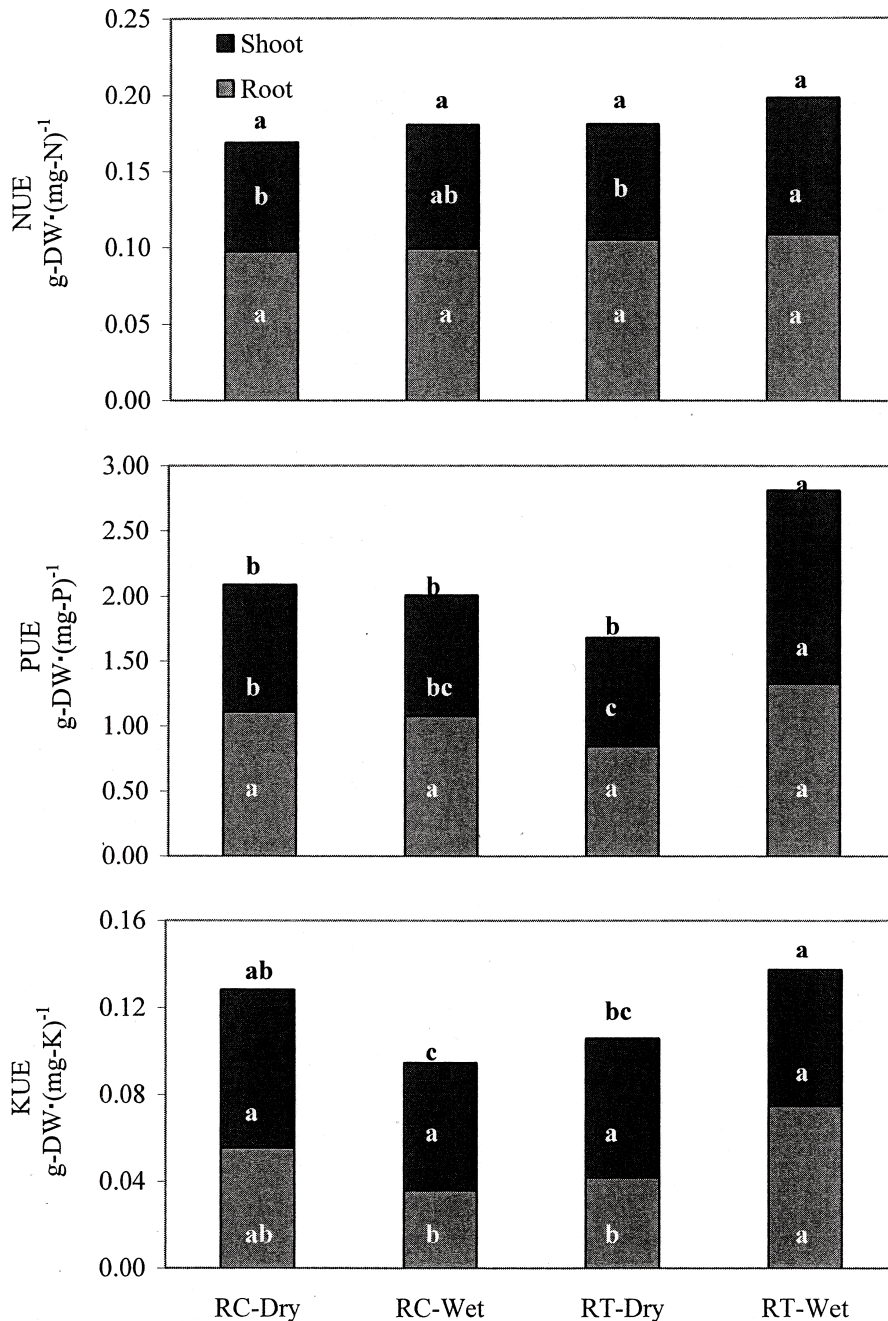


Fig. 4. Nitrogen (NUE)-, phosphorus (PUE)- and potassium (KUE)-use efficiencies of *Ruellia caroliniensis* (RC) and *Ruellia tweediana* (RT) grown in dry (18% to 28% moisture) and wet (82% to 100% moisture) conditions for 8 weeks. Means for shoots, roots and whole plants designated with a similar letter are nonsignificant, compared across treatments.

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