

Habitat Differences in Morphology and Reproductive Allocation in *Guettarda scabra* (Rubiaceae)

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ABSTRACT To understand reproductive allocation in a common woody plant of Everglades rockland habitats, we compared vegetative and reproductive traits of *Guettarda scabra* (L.) Vent. (Rubiaceae), in three habitats of Long Pine Key, Everglades National Park, Florida (pineland, hammock, and hammock edge). Plants in the pineland were shorter, with smaller leaves, and allocated more resources to sexual reproduction; plants in the hammock were taller, had larger leaves, and allocated more resources to vegetative growth. Hammock-edge plants were intermediate in height, had leaves intermediate in size, but had more leaves overall than plants in pineland or hammock. Pineland and hammock-edge plants produced many more fruits than hammock plants, with pineland plants having the largest fruit-to-leaf ratio. We interpret these differences as both a response to increased competition for light in the hammock, as well as to effects of fire in the pineland, with this species displaying greatest flowering, fruiting, and reproductive success in open pineland habitat.

Key words: Everglades, fire, Florida, flower, fruit, leaf, native, rockland, succession.

INTRODUCTION Within a plant genotype, there is flexibility, or plasticity, of certain traits in response to environmental variation. Phenotypically plastic traits extend the range of environments in which a species can exist (Sultan 2000), and can affect interactions that species and individuals have with others (Agrawal 2001). Some plants show seasonal variation in plastic traits that can be ecologically advantageous and evolutionarily adaptive (Kitajima et al. 1997, Winn 1999).

Variable morphological (plastic) traits include the size of vegetative parts and pubescence of foliage, as well as the numbers of shoots, leaves, flowers, and fruit. Other traits, such as leaf shape and floral characteristics, show less response to environmental factors. Douglas (1981) found that intraspecific competition in *Mimulus primuloides* Benth. growing at low altitudes reduced plant size, whereas plant size was limited by severe climate at high altitudes. *Polygonum*

cascadense W.H. Baker plant size varied significantly among habitats (Hickman 1975), a plastic response to moisture availability. Fruit production is influenced by moisture availability at different sites (Hickman 1975, Aker 1982), and resource availability affects seed production (Wyatt 1981). Shading has also been shown to limit fruit set (Willson and Price 1980) and fruit filling (Pate et al. 1980).

Marked differences in size and structure can be seen in leaves produced in sun and in shade in many species (Ashton and Berlyn 1992, Buisson and Lee 1993, Chazdon and Kaufman 1993, Lee et al. 2000). Sun leaves are smaller and thicker, developing under high light conditions; shade leaves are larger and thinner, to maximize their light reception in low light conditions. Plant morphology, too, can shift with change in the ratio of red:far red light, which decreases as sun grades to shade (Buisson and Lee 1993, Van Hinsberg and Van Tienderen 1997, Jones and Koptur 2015).

The pine rocklands of south Florida are a fire-successional habitat with a diverse understory (Possley et al. 2008); this habitat is the most

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imperiled in the state (G1 conservation status, Natureserve 2015), due to extensive destruction for human use because it occurs on the higher, drier ground in areas mostly uninhabitable due to seasonal flooding (Koptur 2006). Light conditions during succession after fire in Everglades rocklands gradually shift from the open, bright conditions in pine forest to dense hardwood hammock vegetation with deep shade (Snyder et al. 1990), providing a situation where a plant species growing in both habitats can produce sun and shade leaves under these different environmental conditions.

A distinctive tropical hardwood species characteristic of the Everglades rocklands, rough-leaved velvetseed (*Guettarda scabra* (L.) Vent.) plants are short in stature and flower profusely when growing in open pine rocklands. Leaves produced in bright sunlight appear smaller and tougher than leaves produced in the shaded hammock environment. Hammock plants appear to exhibit much less sexual reproduction (flowering and fruiting). Our purpose in this study was to quantify these apparent differences, and to compare the reproductive effort of this plant, common in upland rocklands of the Everglades, through the range of habitats in which it occurs in the globally imperiled pine rockland habitat.

METHODS

Study Species

Guettarda scabra (L.) Vent. (Rubiaceae), rough-leaved velvetseed, is a tropical hardwood shrub native to subtropical south Florida and the Caribbean occurring as far south as Brazil. It grows as a shrub in the fire-maintained pine rockland habitat, but persists in succession of the upland rocklands to hardwood hammock, where it grows as an understory or subcanopy treelet (Gunderson 1994). It is dry-season deciduous, with each plant remaining leafless for several weeks to 2 mo. Although its opposite leaves are extremely tough and scabrous, it hosts a wide variety of lepidopteran and other herbivores (Kimball 1965, S. Koptur, unpubl. data). Plants bloom from May through July in southern Florida, and fruits ripen from August to December in long-stalked clusters (Tomlinson 1980). The showy, fragrant flowers are pollinated primarily by hawkmoths (Sphingidae; Richards and Koptur 1993), some of which consume its leaves as larvae (Tuttle 2007, S. Koptur, unpubl. data). Like many Rubiaceae, *Guettarda scabra* exhibits heterostyly (a breeding system with



Figure 1. *Guettarda scabra* (L.) Vert. leaves and fruit. Immature fruits are green, mature fruits are red.

heteromorphic flowers that differ in their relative position of stigma and anthers). This species has an unusual form of distyly in which there is continuous variation in stigma/anther separation, rather than two distinct morphs as is seen in other members of the family (Richards and Koptur 1993). When ripe, the fruits (drupes) are red and velvety (hence the common name) and provide an attractive display for avian and other potential frugivores (Figure 1). A voucher specimen, S. Koptur #643, Long Pine Key, Everglades National Park, is deposited in the ENP museum as per permit requirements.

Sampling Regime

We studied plants growing in pine rockland, hardwood hammock, and the ecotone between (hammock edge). These habitats differ in the density of other species present, light availability due to height of other plants present, and water availability. Hammocks are more crowded, much more shaded, and moister than adjacent pine rockland, and hammock edge is intermediate in these factors. Redd Hammock is an established hardwood hammock in the Long Pine Key region of Everglades National Park, and is approximately 140 m long, with one edge of the hammock bordered by an unpaved fire road that was the hammock-edge site; the open pine rockland site was on the other side of the fire road. At the time of this study (October–November 1987), the pine rockland had been burned 4 yr prior to our sampling.

We located 60 plants in each of both pine rockland and hammock edge habitats and randomly chose 30 for our measurements. Due to scarcity of plants in the inner hammock, we located and measured only 10 individuals. This study was conducted in November and December, long after the plants had flowered and when their fruit were just maturing. Other studies have indicated that *Guettarda scabra* is highly autogamous in Everglades populations, with most flowers setting fruit (Richards and Koptur 1993), so that fruit set is indicative of allocation to sexual reproduction (i.e., not complicated by whether or not the flowers are visited by pollinators).

For each plant, we recorded plant height, numbers of leaves and fruit, and the length and width of the five largest leaves. For plants inside the hammock, we estimated plant height by marking a known length (at the same distance from the viewer as the plant being measured) on a stick, and seeing how many lengths spanned the plant height). We used binoculars to count fruit and leaf numbers of tall individuals, and measured the length and width of five large, fully-expanded leaves collected from each plant. Leaf area was calculated using a regression obtained from measuring length, width, and area (measured using a leaf-area meter) of twenty undamaged leaves spanning the range of sizes. The leaf area regression equation for this species ($r^2 = 0.98$) was determined as

$$\text{Area} = 0 + 0.67 \times \text{Length} + 3.04 \times \text{Width}$$

We tested for a difference among site means for each variable using a Kruskal-Wallis test. Posthoc pairwise comparisons were conducted by Mann-Whitney U tests, with significance levels adjusted using Bonferroni corrections. Analyses were conducted using SPSS 14.0 (IBM Corp. 2014).

RESULTS All traits differed significantly among the three habitats: pineland, hammock, and the hammock edge ecotone (Figure 2 a–2e). Plants inside the hammock were the tallest (Figure 2a), had the lowest mean numbers of leaves (Figure 2b) and the fewest fruits (Figure 2d), and the largest leaves (Figure 2c). Pineland plants were the shortest (Figure 2a) and had the smallest leaves (Figure 2c). Hammock edge plants had the highest mean number of leaves (Figure 2b). The numbers of fruit were almost

equal in the hammock edge and pineland plants (Figure 2d), both substantially more than in hammock plants. The fruit-to-leaf ratio (Figure 2e) was highest in the pineland and lowest in the hammock.

Hammock individuals were substantially taller than hammock edge and pineland individuals. They also differed in their general appearance. Though not precisely measured, they had longer branches, and more of their leaves at the top of the plants than did individuals growing in the more open locations.

DISCUSSION Plants of all species in pine rocklands (except pine trees) are shorter than they are in hammocks, because light availability is much greater (Snyder et al. 1990, Barrios et al. 2016). Consequently, pineland *Guettarda scabra* plants have leaves more evenly distributed on the plant body than do taller plants in hammocks, which have most of their leaves toward their tops. Plants with longer stems are better competitors in shaded situations (Dudley and Schmitt 1996). *Guettarda scabra* plants growing in hammocks are taller than pineland or hammock-edge plants, in part as the result of competition for light (Harper 1977). Because other plants are tall, light available to short plants is low, and plants must grow tall to compete successfully or perish (Weiner 1985).

Fire also has an effect on total plant height. Pine rocklands are maintained as such by either natural fires or controlled burns every 3–10 yr (Snyder et al. 1990), and stems of pineland *Guettarda scabra* are therefore younger than stems of counterparts in the hammock. Burned plants resprout following fire, but stems do not bear flowers the following year (S. Koptur, pers. obs.); plants are taller each subsequent year, and flower and fruit the second year after the fire and annually thereafter, until burned again. Postfire is also the window of opportunity for the establishment of new seedlings of many species (Liu et al. 2005, Barrios et al. 2011, Schneider et al. 2016) including *G. scabra*. The longer the time since fire, the greater the canopy cover because all the plants grow taller (Gunderson 1994, Barrios et al. 2016), and after more than 10 yr without fire, the pineland starts to succeed to a hammock (Alexander 1967). Pineland plants in our study were all less than 1.8 m in height, because they had recovered from fire for only 4 yr.

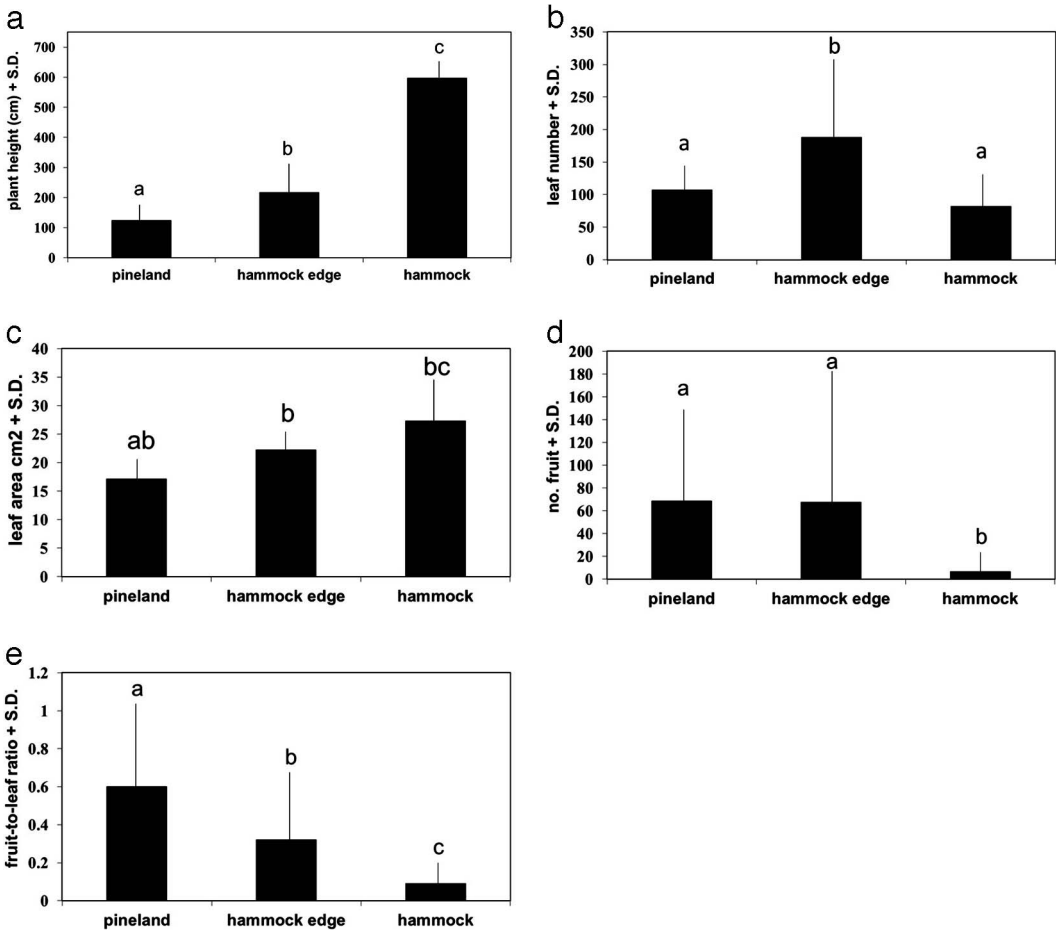


Figure 2. Comparisons of characters of *Guettarda scabra* (L.) Vent. plants from three habitat locations in Long Pine Key, Everglades National Park. In each graph, different letters over bars indicate significant differences with Kruskal-Wallis with posthoc Mann-Whitney for each pair of groups, alpha adjusted for each using a Bonferroni multiple comparison. (a) Mean plant height (cm) + standard deviation (SD) for individuals from pineland (N = 30), outer hammock (N = 30), and inner hammock (N = 10); (b) mean number of leaves + SD for individuals from the three locations; (c) Leaf area of the five largest leaves of each individual averaged across individuals from the three locations; (d) Mean number of fruit per individual + SD; (e) Fruit-to-leaf ratios (means of the number of fruit divided by the number of leaves for each individual) for plants from the three locations.

In addition to height differences, individuals of *Guettarda scabra* differ in morphology between pine rockland and hammock habitats. As in many pine rockland plant species (Olmsted et al. 1983, Gunderson 1994), *G. scabra* plants resprout after fire from underground parts, and can have several to many stems arising from the same top-killed rootstock. Individuals of this species persisting in hammocks have fewer stems, and normally only a single stem persists.

Leaf morphology is influenced by the conditions in which they are produced (Richards and

Lee 1986, Jones 2001). *Guettarda scabra* leaves are largest in hammocks, and smallest in pineland, as seen in many species that have different-sized leaves in shade vs. sun habitats. When light levels are very low, leaves require a greater surface area to absorb enough light for photosynthesis. *Carica papaya* plants produce larger, thinner leaves in the shade (Buisson and Lee 1993). For example, *Melaleuca* seedling leaves look entirely different when they grow under wet or dry conditions (Kaufman and Smouse 2001).

Hammock plants had the lowest fruit numbers, and the lowest fruit set relative to the number of leaves. These phenomena might be explained by both differential energy allocation patterns (Aarsen 2005) and effects of shading (Pate et al. 1980, Willson and Price 1980). Hammock plants competing for light allocate more energy toward vegetative growth rather than sexual reproduction. Mean fruit numbers were almost equal in the hammock edge and pineland plants, but hammock edge trees had more leaves, larger leaves, and were taller. Hammock edge plants therefore invested more energy into vegetative growth than pineland plants, and their fruit-to-leaf ratio was lower than pineland plants.

The shrub layer of Miami Rock Ridge pine-lands is very diverse and includes many species also found in adjacent hammocks (Snyder et al. 1990). Our difficulty in locating thirty individuals to measure inside the hammock indicates that this species is less common in hammock interiors than on hammock edges or in pine-lands. *G. scabra* appears to be a pineland plant that can survive in hammocks, in contrast to a tree species such as *Lysiloma bahamensis* (wild tamarind, Fabaceae) that occurs occasionally in pineland, but is more truly a hammock species (Olmsted et al. 1983). The issue of fire tolerance is important, as well as light environment. *Guettarda scabra* is shade-tolerant enough to persist in hammocks, but not with the abundance or reproductive success the plants display in the more open habitat with less competition for light. Additionally, this species is able to thrive in drier conditions than many species typical of hardwood hammocks, and is especially abundant at particular pine rockland sites where drought stress is acute (e.g., Navy Wells, a site near Everglades National Park from which water is drained for use in the Florida Keys). It might be better at competing for belowground than aboveground resources (Ryser and Eek 2000).

Our preliminary investigation documents the differences in leaf size and reproductive allocation of *Guettarda scabra* in pine rockland and rockland hammock habitats of Everglades National Park. These data, limited as they are from a single study site, can serve as a basis for further investigation into structural differences in sun and shade leaves of this distinctive and resilient species.

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