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Starting a New Population of *Schwalbea americana* on a Longleaf Pine Restoration Site in South Carolina

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ABSTRACT A new population of federally endangered *Schwalbea americana* (American chaffseed) was initiated at the state of South Carolina Department of Natural Resources Woods Bay Heritage Preserve, near Turbeville, South Carolina, in 2013–14. Based on improved survival over time, growth to maturity, evidence of reproduction, and size structure similar to that of a nearby natural population, we suggest that the new population has met the initial criteria for success. Persistence and growth of the population will depend on appropriate management in the form of prescribed fire or fire surrogates and, if necessary, continued demographic enhancement in the form of additional plantings.

Key words: American chaffseed, federally endangered, longleaf pine flatwoods, population establishment, rare plant, success criteria, survival curve.

INTRODUCTION *Schwalbea americana* L. (American chaffseed) is a federally endangered perennial herbaceous plant (Orobanchaceae) that inhabits frequently burned or otherwise maintained open woodlands and savannas (Peters 1995, Kelly 2006). It is a root hemiparasite, which means that it can attach to the roots of other plant species and benefit from the attachment, although being attached is not absolutely required for growth and survival (Musselman and Mann 1977, Peters 1995, Helton et al. 2000). *Schwalbea americana* has been shown to parasitize a large variety of woody and herbaceous species, including but not limited to, *Aletris farinosa* L., *Chrysopsis mariana* (L.) Elliott, *Carphephorus odoratissimus* (J.F. Gmel.) Herb., *Dichanthelium tenue* (Muhl.) Freckmann & Lelong, *Gaylussacia dumosa* (Andrews.) Torr. & A. Gray., *Ilex glabra* (L.) A. Gray, *Liquidambar styraciflua* L, and *Pityopsis graminifolia* (Michx.) Nutt. (Helton et al. 2000, Kelly 2006). *Pityopsis graminifolia* (grass-leaved goldenaster), a common to dominant ground-layer species within the longleaf pine (*Pinus palustris* Mill.) ecosystem (Jose et al. 2006), may be a preferred host because of compatible nitrogen metabolism (Helton et al. 2000), although Kelly (2006) found that other Asteraceae were equally preferred.

Schwalbea americana is distributed from New Jersey to Florida and west to Louisiana, although it is absent from large portions of its historical range, formerly extending from Massachusetts to Florida to eastern Texas (Peters 1995; see also figure 1 in Kirkman et al. 1998). In 2008, more than one half the total 53 extant known sites were in South Carolina (USFWS 2010), with most of those concentrated in Berkeley and Williamsburg Counties (Townsend 1997). Many

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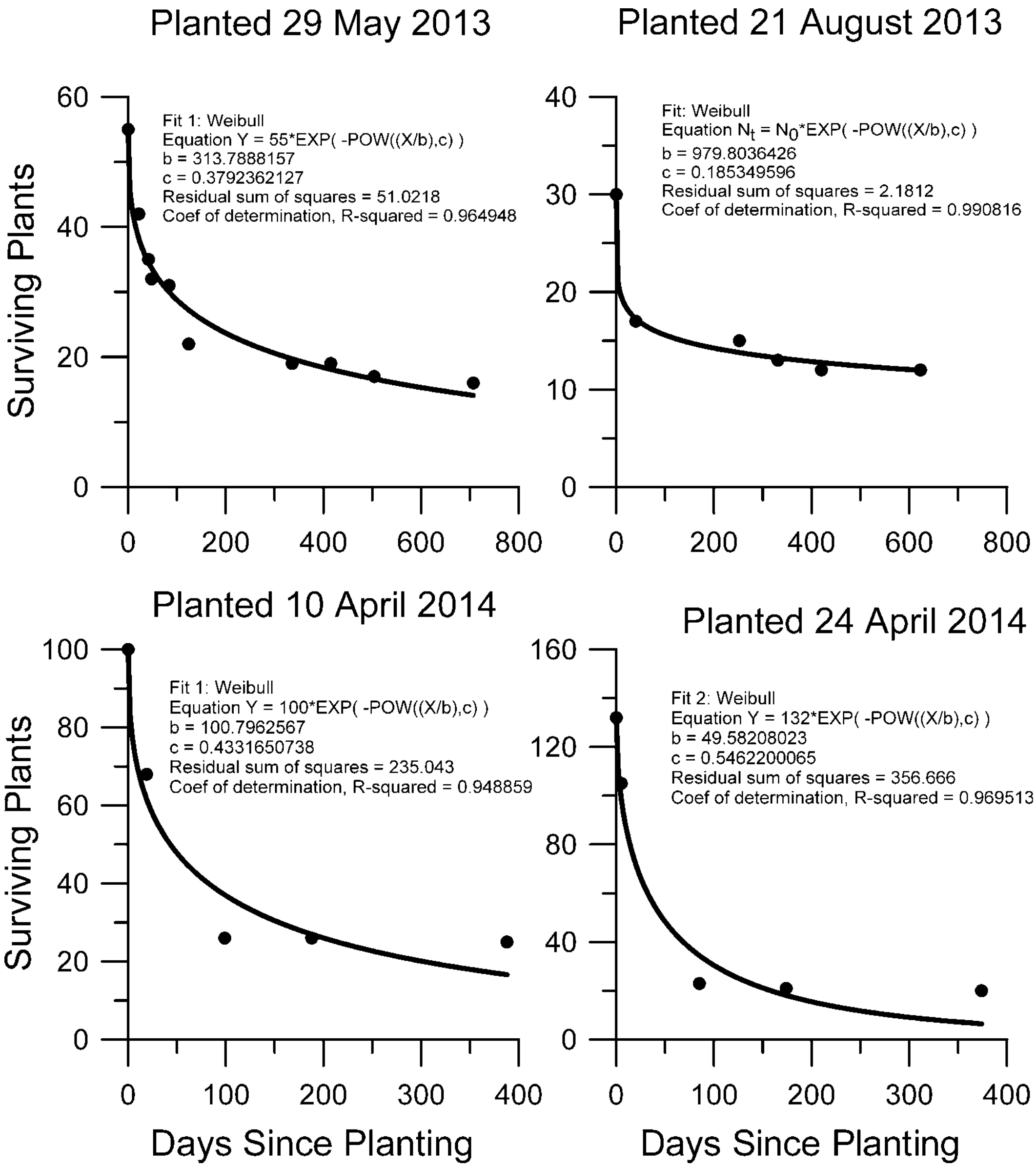

Figure 1. Survival curves for four successful plantings of *Schwalbea americana* at the State of South Carolina Woods Bay Heritage Preserve restoration area, near Turbeville, South Carolina. The Weibull curve was fit to each planting date separately. Parameter *c* values less than 1.0 indicate improving survival with time after planting.

of the extant sites are small and in decline (Peters 1995, USFWS 2010). *Schwalbea americana* declines are typically attributed to insufficiently frequent fire and loss of open savanna habitat (Peters 1995, Kelly 2006), although some sites are declining even with apparently optimal fire management (Kirkman, pers. comm.). Soil disturbances related to forestry and wildlife management constitute an additional threat, although low-intensity soil disturbance applied infrequently may actually benefit the species (Glitzenstein, pers. obs.).

An important goal for species recovery is to initiate new populations (Peters 1995). Several attempts to initiate new *S. americana* populations have been unsuccessful (Obee and Cartica 1997, Kelly 2006, USFWS 2010), and there is a perception that critical knowledge, (e.g., of genetic, reproductive, habitat, and management requirements) is lacking (Determann et al. 1997). Explanations for prior failures have included improper propagation methods or media, greenhouse disasters including pest, bryophyte, or disease outbreaks; lack of, or inappropriate, fertilizer; failure to grow with proper host plants; inappropriate choice of planting habitat; environmental limitations postplanting; or some combination of these factors (see Kelly 2006 for an exhaustive review of especially the New Jersey efforts; also Determann et al. 1997). Several introduction attempts involved direct-seeding trials in the field, which failed entirely; in most cases, the seeds did not even germinate (Van Clef 2000). In several other instances, greenhouse propagation efforts failed even before plants could be outplanted in the field (Obee 1995, Yurlina 1998, Cartica et al. 1999, Van Clef 2000).

Most attempts at initiating new *S. americana* populations have been reported in the so-called "grey" literature of government documents. In the only previously published, peer-reviewed journal study, to our knowledge, Obee and Cartica (1997) grew and outplanted small *S. americana* seedlings that mostly died within 60 d after planting, and none emerged the following growing season. This failure was attributed to insufficient light in the greenhouse. Perhaps the most critical error, in our opinion, was germinating the seedlings on filter paper before attempting to transplant to pots with hosts. In our experience, this technique cannot be used with this species because of irreversible root damage to the tiny seedlings (Glitzenstein, pers. obs.).

There have been some recent successes in growing *S. americana*. Determann et al. (1997) cite a tissue culture technique developed by R. Gagliardo, which succeeded in producing robust seedlings, although the lack of genetic diversity was a drawback. Helton et al. (2000), Kelly (2006), and Glitzenstein et al. (2015) added seeds to pots with host plants and grew mature *S. americana*. Recently, Gustafson (pers. comm.) demonstrated that, with appropriate choice of artificial soil mixture and fertilizer, robust plants can be grown, even without a host.

Kelly (USFWS 2010 and pers. comm.) planted 42 *S. americana* plants at a reintroduction site in New Jersey during 2006 and 2008. Presently 21 of those plants are still alive, and there have been two new recruits. Glitzenstein (2015) planted several populations in South Carolina that have persisted over many years. In his initial attempts, pots consisting of native soil, *P. graminifolia*, and *S. americana* were outplanted. More recently, he planted plugs (i.e., containerized tubelings). Plugs were grown using the artificial soil mix including slow-release fertilizer, used by Andrews Nursery (Chiefland, Florida) operated by the state of Florida (see the "Materials and Methods" section for further details). This mix has been used to grow a wide variety of longleaf pine ecosystem ground-layer herbs for outplanting on longleaf pine restoration sites (Glitzenstein et al. 2007). Gustafson (pers. comm.) used this same basic soil mix and experimented with different fertilizers and soil additions in a greenhouse study. The Andrews mix, along with organic, hydrolyzed fish fertilizer (2–4–1; N–P–K) produced among the best results, regardless of other additions, including native sands.

Some preliminary results from the Kelly and Glitzenstein efforts have been discussed in government documents (USFWS 2010, Glitzenstein et al. 2015), but there has still not, to our knowledge, been a peer-reviewed journal publication documenting successful establishment of a new *S. americana* population in a natural field habitat. Albrecht et al. (2011) discuss the following four criteria for evaluating the success of rare-plant population introductions: (a) population survival, (b) attaining reproductive maturity, (c) producing a next generation, and (d) attainment of reproductive individuals by the next generation. Herein we document a recent *S. americana* introduction attempt in South Carolina that we suggest meets the first two criteria for success.

MATERIALS AND METHODS

Study Site

The introduction site was located at the South Carolina Department of Natural Resources Woods Bay Heritage Preserve (HP), near Turbeville, Clarendon County, South Carolina. Until 2012, this site was a dense stand of loblolly pine (*Pinus taeda* L.). Except for a few remnant *P. palustris* trees and scattered, large *P. taeda* and *Pinus serotina* Michx. (pond pine) trees, the pine canopy was removed during a timbering

Table 1. Population summary for *Schwalbea americana* planted at Woods Bay Heritage Preserve Restoration Area. Superscript C = plants grown at the Citadel, superscript F = plants grown at a private nursery in Tallahassee, Florida. Mean height is for the final census date on 3 May 2015.

No. Planted	Source	Date Planted	No. Alive	Alive (%)	$\bar{x}$ Height (cm)
63	Longlands^{F}	29 May 2013	16	25.4	13.1
30	Longlands^{F}	21 August 2013	12	40.0	10.9
75	Longlands^{C}	5 March 2014	3	4.0	12.8
100	Scotswood^{C}	10 April 2014	25	25.0	19.3
132	Longlands$^{C–F}$	24 April 2014	20	15.2	10.4
56	Longlands^{F}	15 July 2014	1	1.7	5.0
456	Total		77	16.9	14.0

operation from November 2012 to January 2013. Presently, the site is undergoing restoration for longleaf pine groundcover. *Pityopsis graminifolia*, a favored host of *S. americana*, was among species reappearing following removal of *P. taeda*. Other perennial, herbaceous, and short-shrubby species in the reemerging ground cover, included *Chrysopsis mariana*, *C. paniculatus* (J.F. Gmel.) Herb., *Vaccinium tenellum* Aiton, and *Vernonia angustifolia* Michx., all typical associates of *S. americana* on extant sites in SC (J.S. Glitzenstein, pers. obs.). There was no history of *S. americana* ever having been present on the site. The site was selected because of apparent suitable habitat and because open conditions early in restoration might provide a window for new population establishment. In addition, future management could be anticipated, including prescribed fire. Preferred *S. americana* habitat in South Carolina is mesic longleaf pine flatwoods to subxeric upland, often in proximity to a wetland transition (Townsend 1997, Glitzenstein, pers. obs.). The planting site at Woods Bay HP conformed to these site characteristics. Soils on the site are mapped as Scranton fine sand (siliceous, thermic Humaqueptic Psammaquent) (Web Soil Survey 2015), a soil series of longleaf pine flatwoods (NRCS 2014). As is typical of pine flatwoods soils, this soil is rapidly permeable in the upper horizons but poorly drained because of a seasonally high water table.

Propagation

Schwalbea americana seeds were obtained from two private landholdings that are close to each other in Williamsburg County, South Carolina. Seeds were collected on 10 August 2012 (116 capsules) and again on 23 August 2013 (62 capsules), with one capsule removed per plant. Seeds were cold, moist-stratified for 1 mo before initiating propagation, a treatment that consistently yields greater than 70% germination (Vankus, pers. comm.; Gustafson, pers. comm.). *Schwalbea americana* were grown as containerized tubelings (plugs) in hard-plastic, nursery, seedling-production trays (Ropak Multi-Pot, RPP Containers, Cincinnati, Ohio) (96 cells, cell dimensions: 12 cm deep × 3.8 cm top diameter) at an outdoor nursery in Tallahassee, Florida and in 11.4-cm square pots and germination flats in a greenhouse at The Citadel, The Military College of South Carolina, in Charleston. The Florida plug production trays were filled with the standard potting mix ("Andrews Mix") used by state of Florida operated Andrews Nursery, consisting of 50% peat moss, 30% perlite, and 20% vermiculite, along with controlled release fertilizer pellets (17–6–10 [N–P–K] Meister, 9-mo release period, mixing rate 1.8 kg fertilizer/2.67 kg/m^3 potting mix) (Pittman 2002; Gilly, pers. comm.). The Citadel pots and flats were filled either with Andrews Mix or with commercially available Jungle Growth potting media (2:1 Jungle Growth:vermiculite; Jungle Growth Products, Statham, Georgia), as part of a study to determine optimal growing media for *S. americana* (Gustafson, pers. comm.). Florida-grown plants were not additionally fertilized, whereas The Citadel-grown plants were fertilized as needed (Neptune's Harvest organic fish fertilizer, Gloucester, Massachusetts 2–4–1 [N–P–K], diluted according to manufacturer recommendations) based on visual evidence of phosphorus deficiency.

Six plantings were made in 2013–14 totaling 456 plants (Table 1). In 2013, 93 Florida-grown *S. americana* plants were planted into a large patch of existing *P. graminifolia*. However, the 2014 plants were planted in open patches (i.e., "gaps"). The 75 *S. americana* individuals planted on 5 March 2014 were grown in pots with *P.*

graminifolia in The Citadel greenhouse, but the other plantings (Florida plugs and Citadel pots in both years) were grown without host plants before being outplanted.

Statistical Analyses

Survival, stem length, and flowering were recorded on 20 June 2013, 10 July 2013, 16 July 2013, 21 August 2013, 30 September 2013, 30 April 2014, 18 July 2014, 15 October 2014, and 3 May 2015. To analyze survival, we fit the data to a Weibull curve, one of the standard curves for analyzing survival (Ebert 1999). One useful feature of this curve is that the *c* parameter is directly related to temporal changes in survival. Values of *c* less than 1 indicate improving survival with time. Survival data were fit to Weibull curves for each planting using the nonlinear least-squares iterative methods in Grapher 3.02 (Golden Software, Golden, Colorado).

Field observations suggested that variation in weather might explain differences in mortality among plantings. To help interpret mortality, we obtained (a) daily weather data (precipitation and temperature) for the years 2013–15, (b) the Palmer Drought Severity Index (PDSI) calculated monthly for the same time period," and (c) long-term (1948–2015) temperature records for the month of March (Mizzell and Tyler, pers. comm.). Temperature and precipitation data were for Florence (regional airport), South Carolina, the closest, sizeable city, approximately 41 km distant, whereas PDSI data were for US Climate Division SC-4, northeastern South Carolina.

Individual *S. americana* plants commonly consist of multiple stems. Thus, the height of any given stem, even the tallest, is not necessarily the best indicator of plant vigor. In this study, we measured the height of every stem. Herein, we use the "sum of stems"—defined as the summed length in centimeters of all stems of a given plant—as our measure of plant growth and vigor.

One commonly used measure of population structure pertains to age- or size-frequency distribution (Ebert 1999). As a planted population of *S. americana* approaches maturity, the distribution of plant sizes should begin to approach that of natural *S. americana* populations. To make that assessment, we compared the size (i.e., sum of stem lengths) frequency distribution on the final 3 May 2015 census date to the equivalent distribution obtained the previous 1 May 2014 from a nearby (19.5 km) natural population ($n = 288$) at the State of South Carolina Lynchburg Savanna HP, Lee County, South Carolina.

RESULTS

Seventy-seven of the 456 seedlings planted at Woods Bay HP restoration area were still alive on the final census date of 3 May 2015, for an overall survival rate of 16.9% (Table 1). Six different plants and nine stems were in flower on that date. Two of the plantings failed entirely (less than five plants remaining, Table 1), but survival of the four other plantings had stabilized, as indicated by values for the Weibull *c* parameter that were well below 1.0, confirming improved survival with time after planting (Figure 1). Each of the "successful" plantings increased considerably in size after planting (Figure 2; note that this figure includes only plants surviving to the end of the study and, therefore, does not confound growth and survival). By the end of the study period, the size-frequency (i.e., sum of stem length frequency) distribution of the planted population resembled that of the nearby natural population (Figure 3). The planted population incorporated a slightly greater proportion of small plants (0–4 cm), and the largest size classes were somewhat underrepresented. With respect to overall size structure, it appeared that the planted population was close to reaching maturity within 2 yr after the initial planting date.

Examining the individual plantings more closely, the importance of weather can, perhaps, be inferred in determining the success of the plantings. Survival was greatest in 2013 (Table 1), when precipitation was abundant (Figure 4) and conditions were wet (Figure 5). The planting on 5 March 2014, consisting of plants grown in The Citadel greenhouse, failed, with only 3 of 75 plants surviving. The most likely explanation is that the greenhouse-grown plants lacked cold hardiness, which was combined with unusually low temperatures. According to the National Weather Service (2014), March 2014 "was a very cold month; average temperatures were 3–6 degrees [1.8–3.6°C] below normal," including 6 d with low temperatures below freezing (0°C). The greatest survival in 2014 was obtained for the 10 April planting, which was accomplished after frost but well in advance of the dry weather that developed later in the season. The planting on 15 July 2014 failed (only a single survivor).

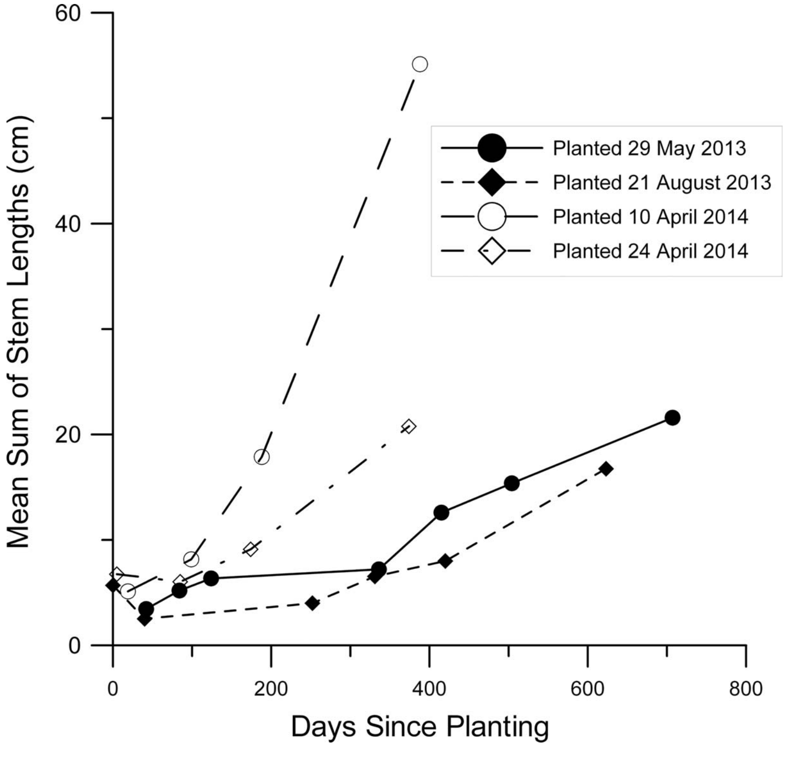

Figure 2. *Schwalbea americana* growth at state of the South Carolina Woods Bay Heritage Preserve restoration area, near Turbeville, South Carolina, as determined by the mean sum of stem lengths. Results are plotted separately for each of the four successful plantings. Only plants surviving the duration of the study period are included.

Although it rained on the planting date (1.96 cm) and 5 d previously (5.05 cm), there had been little rain since mid May (Figure 4), and incipient drought (PDSI –0.5 to –1.0) had developed (Figure 5). Furthermore, the adjacent wetland was dry, and the plantings may have derived some moisture from that source (Glitzenstein, pers. obs.). Dry conditions persisted until a major rain event, and cooler temperatures in mid September (Figures 4–5). The July 2014 planting likely succumbed to insufficient soil moisture.

Growth curves for the four successful plantings are shown in Figure 2. All plantings increased in mean plant size (i.e., sum of stem lengths), but the rate of increase was markedly greater for the 2014 plantings and, in particular, for the planting of 10 April 2014 (Figure 4). Two explanations can be suggested. The 2014 plantings included a preponderance of Citadel-grown plants, which were larger at the time of outplanting, and that initial advantage appears to have translated into more rapid growth after outplanting. The most legitimate comparison is on 24 April 2014 when both Citadel- and Florida-grown plants were planted on the same date (Figure 6). Florida plants had somewhat greater initial survival (Figure 6a) but Citadel plants, which were larger to begin with, increased in size more rapidly (Figure 6b). Greater initial survival of Florida plants may be due to the type of planting; Florida plantings were plugs and were, perhaps, less prone to desiccation than the bare-root Citadel plants.

A second possible explanation for improved growth in 2014 is that 2014 plantings were into gaps—open spaces in the ground cover, rather than into an intact, dense *Pityopsis* population, as was done in 2013. Given that we did not investigate nursery treatments or gaps experimentally, our observations on these potential influences should be treated as suggestions for future research, rather than as firm conclusions.

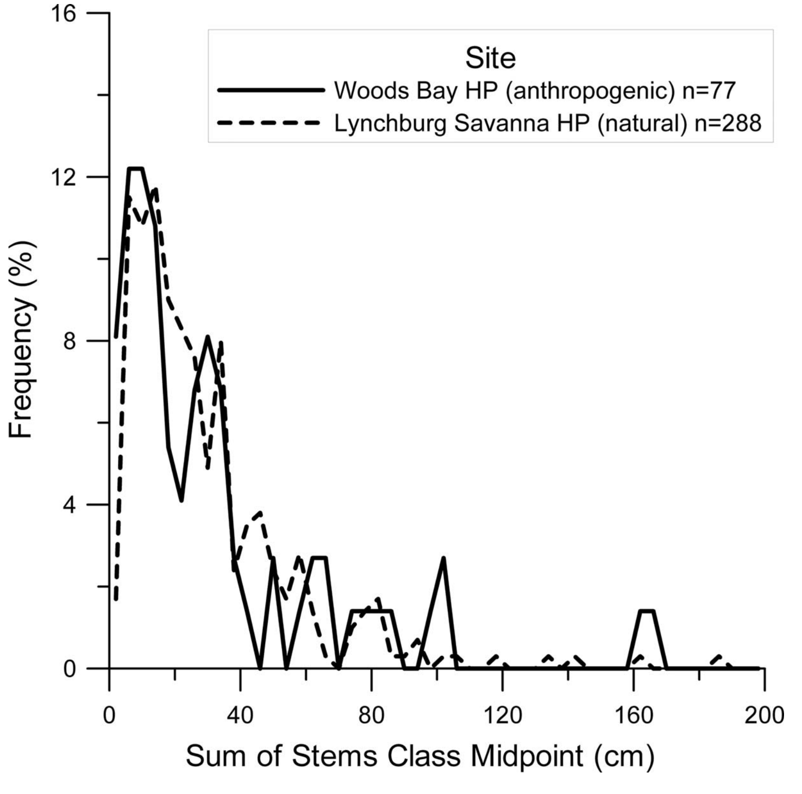

Figure 3. Size structure (sum of stem lengths) for the planted *Schwalbea americana* population at State of South Carolina Woods Bay Heritage Preserve (HP) on 3 May 2015 (last census date) and a nearby natural population (State of South Carolina Lynchburg Savanna HP), on 1 May 2014. Size classes are 4 cm, and the midpoint of each size class is plotted.

DISCUSSION Obee and Cartica (1997), in the only previous, peer-reviewed journal publication on this topic, to our knowledge, attempted to initiate a new field population of *S. americana* in New Jersey. They grew small plants, which mostly died soon after outplanting, and none reemerged the following year. We also had low overall outplant survival. However, in our study, survival improved with time since planting, the surviving plants exhibited meaningful growth, many reached mature size, and some flowered. Thus, we consider that our attempt represents significant improvement, at least in comparison to the results in Obee and Cartica (1997).

Albrecht et al. (2011) discussed the following four criteria for evaluating rare plant reintroduction attempts: (a) population survival, (b) attaining reproductive maturity, (c) producing a next generation, and (d) attainment of reproductive individuals by the next generation. We consider that our planted *S. americana* population at the Woods Bay HP restoration site attained the first two criteria. Evaluating population survival is somewhat challenging, because no population survives indefinitely. Admittedly, our population has not yet confronted extreme drought or other natural or anthropogenic events that might pose a serious threat to its survival. However, the large number of established plants and a size structure similar to that of a natural population bode well for the future.

As a basis for comparison, our planted population of 77 *S. americana* individuals exceeds 20 (out of 53) extant, natural populations according to 2008 data (USFWS 2010). One of those populations was the Halfway Creek Road population in Francis Marion National Forest, north of Charleston, South Carolina. In 2008, that population was listed as 42 plants (USFWS 2010). However, recent data from spring 2016 indicates a substantial increase to

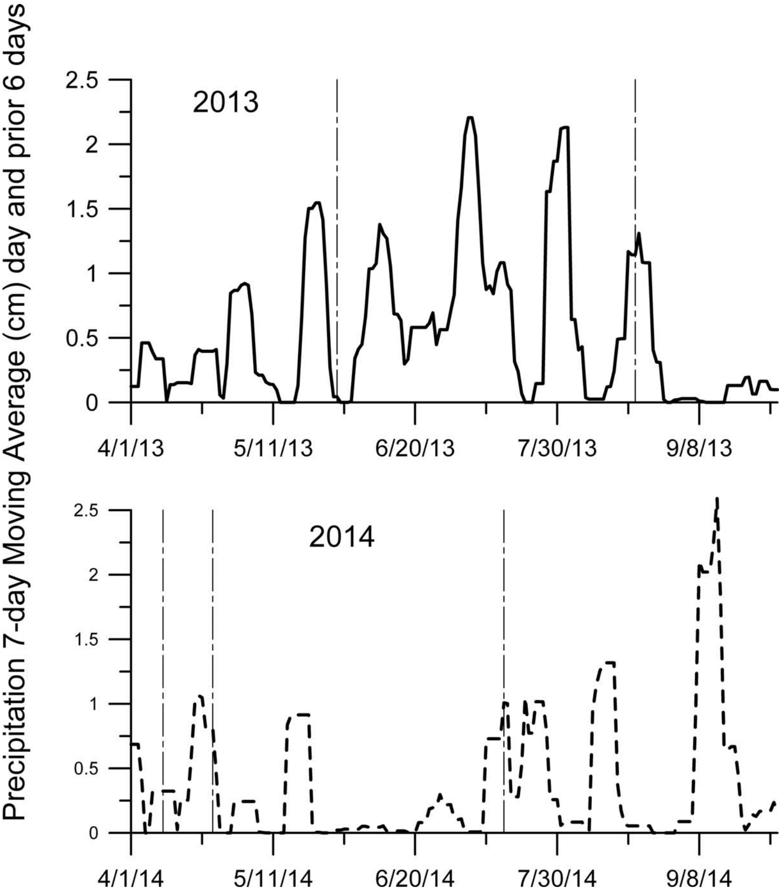

Figure 4. Precipitation data for growing seasons 2013–14 (April–September) obtained for Florence, South Carolina, approximately 40 km distant from the *Schwalbea americana* planting site at state of SC Woods Bay Heritage Preserve. Data are presented as a 7-d moving average, including the date in question and the 6 d before. Thus, a low value for any given date indicates little rain during the prior week. Vertical, interrupted lines indicate planting dates. The 5 March 2014 planting date is not shown because it was outside the range of dates on the x axis. The limiting factor for that planting was likely freezing temperatures rather than precipitation.

354 plants (Glitzenstein, pers. comm.). Another example is the natural New Jersey Whites Bog population (i.e., the only remaining original *S. americana* population north of North Carolina), which was listed as less than 100 individuals in 2008 (USFWS 2010) but now numbers more than 700 plants (Kelly, pers. comm.). Given appropriate conditions, *S. americana* is evidently capable of rapid increase in a relatively short period. Thus, an additional approximately 10 yr of monitoring may be sufficient to fully evaluate all Albrecht et al. (2011) criteria for our new population.

Although we are optimistic that we have successfully initiated a new *S. americana* population, the low survival of our outplants is still a concern. In previous outplanting studies, with perennial herbs of longleaf pine groundcover, variation in rainfall and attendant drought was the single most critical factor in survival (Glitzenstein et al. 2001). This generalization appears true for *S. americana*, as well. If field irrigation can be arranged, that should improve survival substantially. In addition, greenhouse-grown plants should not be outplanted until well after the danger of freezing has passed. Although we demonstrated that *S. americana* can survive and grow to maturity if outplanted without a host, outplanting along with a host evidently does improve survival (Kelly, pers. comm.).

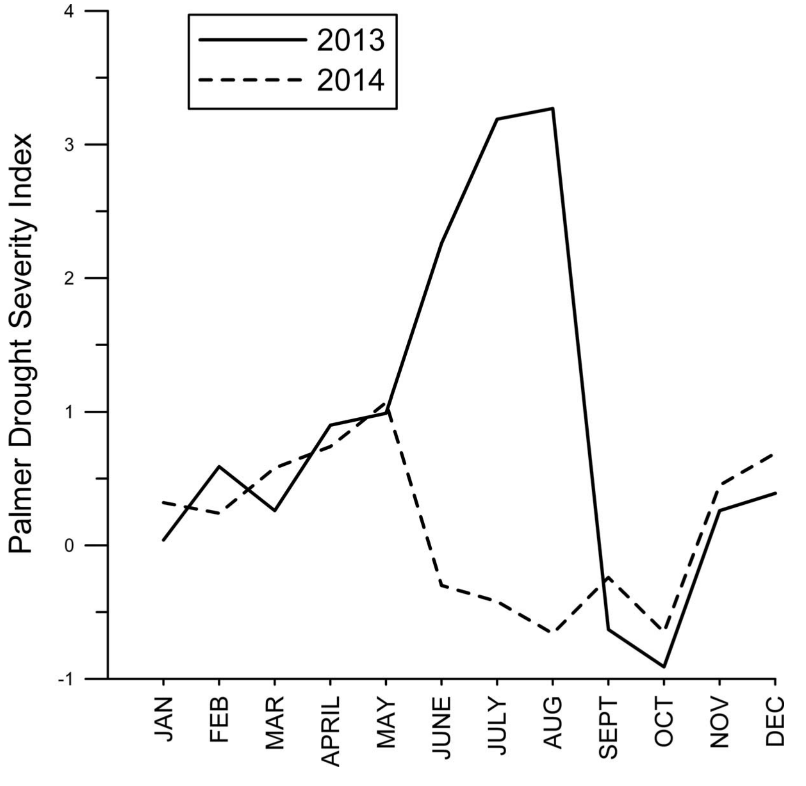

Figure 5. Palmer Drought Severity Index Data, US Climate Division South Carolina-4, northeastern South Carolina, calculated monthly for 2013 and 2014. Values less than 0 indicate dry conditions. Values between –0.5 and –1.0 indicate incipient drought. Values > 2.0 indicate very wet conditions.

Kelly (2006, and pers. comm.) also suggests that further studies to target the appropriate microhabitat and associated plant community carefully might be productive. This may well be the case, although in the southern part of its range, *S. americana* can be found in a rather broad range of longleaf pine type associations, ranging from wet pine savanna through subxeric sandhills (Glitzenstein, pers. obs.).

Gustafson (pers. comm.) investigated growth media and fertilization regimes experimentally for growing robust *S. americana* in the Citadel greenhouse. Our results indicated that the initially larger Citadel plants outpaced the Florida nursery-grown plants, when planted in the field on the same date and under the same conditions. We consider that there is very likely to be a causal effect between growth in the greenhouse and subsequent performance in the field. However, further experimentation is needed before reaching a firm conclusion.

Most efforts to plant federally endangered plants have selected reintroduction sites (Albrecht et al. 2011) presuming that (a) such sites are known to be suitable because they historically supported the plant in question, and (b) we lack sufficient understanding of habitat factors to risk planting on sites not known to have previously supported populations. Both of these presumptions are doubtful with respect to longleaf pine ground-layer plants generally and *S. americana* in particular. Historical sites may no longer be suitable because of fire exclusion, manipulations from silviculture, hydrological alteration of nearby wetlands, or conversion to other land uses. For *S. americana*, we now have a large body of observations on the types of habitats in which the plant can thrive, and such potential habitats are more abundant than are known historical sites. Our results suggest that attempts to initiate new *S. americana* populations need not be limited to known historical sites but should also focus on existing high-

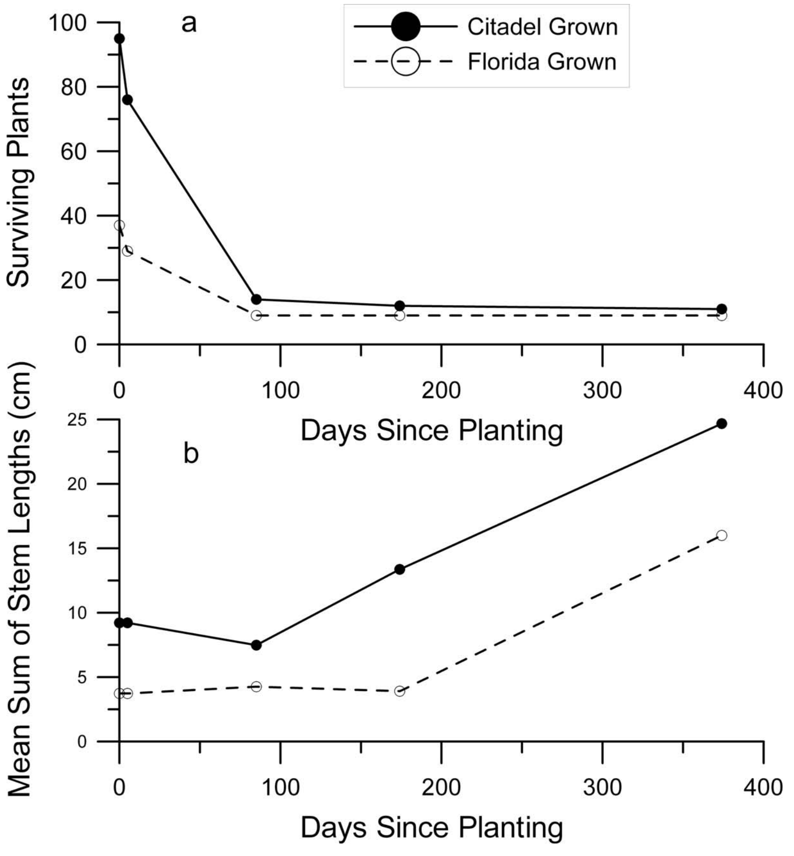

Figure 6. Mortality (a) and growth (b) of Citadel-grown and Florida-grown *Schwalbea americana* planted on 24 April 2014. Citadel plants were bare root from germination trays, whereas Florida plants were plugs (tubelings) from propagation trays. Only plants surviving the duration of the study period were included in the growth plots.

quality habitat and/or restoration opportunities within the range of the species. A critical factor is the future likelihood of appropriate management, particularly prescribed fire (Kirkman et al. 1998, Norden and Kirkman 2004, Kelly 2006).

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