Restoration of Florida scrub vegetation in an old field through 23 years after planting

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Florida scrub, a fire-maintained, xeromorphic shrubland, hosts many rare and declining species, but most scrub habitat has been lost to development and agriculture. Formerly cultivated sites offer an opportunity to restore Florida scrub. In this 23-year study, we test whether scrub species could be restored to an old field and whether scrub vegetation composition and structure could be reestablished over time. Scrub oaks were planted in a section of an old field in 1992 after the site was cleared and treated with herbicide. Additional oaks and other scrub species were planted in 1993. We determined survival and growth annually of a marked sample of scrub species. We sampled vegetation cover in two height strata annually on 10 permanent line-intercept transects in the old grove and on 20 transects in adjacent, intact scrub. Initial survival of *Quercus geminata* exceeded that of *Quercus chapmanii* or *Quercus myrtifolia*. Cover of scrub oaks greater than 0.5 m increased from 1.3% in 1992 to 65.2% in 2010. However, the vegetation structure of large *Q. geminata* did not resemble that of native scrub. Adaptive management led to cutting large oaks in the fall of 2010, and burning the site in early 2011. Cutting and burning appeared to stimulate sprouting and clonal spread of scrub oaks. Ordination analysis indicated directional change related to increasing scrub oak cover and time since planting but the old field still differed from intact scrub. Vegetation has developed toward scrub composition and structure but exotic grasses persist.

**Implications for Practice**

- Restoration of native species in an old field required site preparation and planting to overcome barriers.
- Adaptive management including cutting and burning was needed to modify vegetation structure. Earlier introduction of prescribed burning should be considered to trigger clonal growth and belowground biomass allocation.
- Initial survival of planted species may benefit from more effective reduction of exotic grasses.

**Introduction**

Former agricultural lands including croplands and pastures have been abandoned at increasing rates worldwide (Hobbs & Cramer 2007). Natural revegetation or active restoration of abandoned agricultural lands (hereafter old fields) could be valuable for conservation of species and communities and for ecosystem services. The dynamics of old fields are more complex and variable than indicated by early models (see Cramer & Hobbs 2007). Cultivation modifies soil properties and these legacies may last decades to millennia (McLauchlan 2006; Walker & Wardle 2014). Past land use has left legacies in vegetation structure and composition, ecosystem processes, and soils (Foster et al. 2003).

Cramer et al. (2008) provided a synthetic framework in which to view the dynamics of old fields contingent on biotic and abiotic legacies of cultivation where recovery of preexisting vegetation becomes increasingly difficult as the biotic and abiotic legacies increase and thresholds are crossed. Where soil modifications are minor, cultivation less intensive, native vegetation is in close proximity, and dispersal of native species can occur or seed banks persist, native species may reestablish and develop toward the historical vegetation with little intervention (Wright & Fridley 2010). With increased scale and duration of agriculture, remnants of native vegetation are reduced, seed banks are lost, and less dispersal of native seed occurs (e.g. Holl 1999; Standish et al. 2007); this may be compounded by introduction of invasive exotic species adapted to the modified conditions resulting from cultivation (e.g. Styinski & Allen 1999; Hooper et al. 2004; Davis et al. 2005; Midoko-Iponga et al. 2005; Kulmatiski 2006; Tognetti & Chaenton 2012; Kubbing et al. 2014). Intensification of cultivation (e.g. nutrient additions) may cross abiotic as well as biotic thresholds such that the recovery of historical vegetation is unlikely without extensive restoration. Such sites may persist in a degraded state.
or develop as novel combinations of native and exotic species (Hobbs et al. 2006).

Substantial areas of Florida scrub have been converted to agriculture, particularly citrus, and subsequently abandoned. With revegetation, these sites could be important in maintaining populations of some rare scrub species (Stephens et al. 2012). Florida scrub is a rare and declining plant community (Myers 1990; Menges 1999) important to a variety of threatened and endangered plant and animal species; at least two-thirds of Florida scrub has been lost to development and agriculture (Christman & Judd 1990; Duncan et al. 2004; Kautz et al. 2007; Weekley et al. 2008). Conservation of remnant scrub vegetation is a matter of state and national concern (Menges 1999).

Scrub vegetation is maintained by periodic, intense fires (Myers 1990; Menges 1999); recovery of dominant species after fire is primarily by sprouting (Abrahamson 1984a, 1984b; Schmalzer & Hinkle 1992a). The dominant species of scrub, Quercus spp. and Serenoa repens (saw palmetto), are rhizomatic and clonal (Menges & Kohfeldt 1995) with much of their biomass belowground (Johnson et al. 1986; Guerin 1993; Langley et al. 2002; Stover et al. 2007). Sandy gaps in the shrub matrix are important for many herbs and subshrubs including rare scrub plant species (Menges & Hawkes 1998; Menges 1999; Menges et al. 2008) and scrub fauna (Greenberg et al. 1994; Hokit et al. 1999; Carrell 2003; Breininger et al. 2014).

Scrub plant species establish poorly in old fields; rather, Sabal palmetto (cabbage palm), woody vines, and exotic grasses often dominate (Schmalzer et al. 1994). Restoring scrub habitat involves not only establishing the appropriate vegetation but also developing a habitat structure that can be managed by prescribed fire (Breininger & Schmalzer 1990). For the Florida Scrub-Jay (Aphelocoma coerulescens), a listed species, a shrub vegetation structure with scrub oaks, vegetation height less than 1.7 m, and open, sandy patches is required (Breininger et al. 2014).

Here we report on the long-term changes (23 years after planting) of an old field site where Florida scrub species were planted. We address two overarching questions. Can dominant scrub species be restored to a former agricultural site, and can scrub vegetation composition and structure be reestablished over time? Specifically, we (1) examine the survival and growth of planted scrub species in the old field; (2) determine whether cover of scrub species increases over time in the old field; (3) determine whether cover of exotic grasses decreases over time in the old field; (4) determine whether the height structure of the developing vegetation is similar to that of adjacent intact scrub; and (5) determine whether the composition of the developing vegetation becomes similar to adjacent, intact scrub. The target for this restoration was restoring scrub vegetation that would support the Florida Scrub-Jay. Specifically, the desired vegetation condition would be a shrubland with scrub oaks predominant (≥50% cover), vegetation height of 1.2−1.7 m, minimal exotic species cover, and open, sandy patches present (Breininger & Carter 2003; Breininger et al. 2014). Understanding the complexities of restoring scrub on this old field site will provide valuable insight for future restoration efforts.

**Methods**

**Study Area**

Kennedy Space Center/Merritt Island National Wildlife Refuge (KSC/MINWR) is located on the Cape Canaveral–Merritt Island barrier island complex on the east coast of central Florida (28°38′N, 80°42′W). The climate is warm and humid; precipitation averages 131 cm/year, but year-to-year variability is high (Mailander 1990). The wet season extends from May to October.

Multiple dune ridges occur on the barrier island topography (White 1970) with intervening swales of lower elevation. Scrub vegetation occupies the well-drained ridges, pine flatwoods the more poorly drained flats, and graminoid marshes or woody swamps the lower swales (Schmalzer et al. 1999). Scrub communities on Merritt Island are primarily oak-saw palmetto scrub, a shrubland characterized by three species of oaks (Quercus chapmanii [Chapman oak], Q. geminata [sand live oak], Q. myrtifolia [myrtle oak]) along with Serenoa repens and ericaceous shrubs, and scrubby flatwoods with a similar shrub layer and scattered Pinus elliottii Engelm. var. densa Little & K. W. Dorman (South Florida slash pine) (Schmalzer & Hinkle 1992b; Schmalzer et al. 1999). Nomenclature follows Wunderlin and Hansen (2011) unless otherwise noted.

The northern part of KSC/MINWR was an early center of citrus agriculture (Davison & Bratton 1986). There were about 1,012 ha in citrus cultivation when lands were acquired for KSC in the early 1960s; cultivation continued for decades thereafter but was abandoned subsequently (USDI 2008). Approximately 200 ha were planted to hardwoods (Quercus virginiana [live oak], Q. laurifolia [laurel oak]) or pine in the late 1980s to early 1990s but most have remained fallow (USDI 2008).

Scrub species were planted in a former citrus grove as part of a scrub habitat restoration plan for KSC/MINWR (Schmalzer et al. 1994). Previously, we reported on the early (1992−1999) survival, growth, and vegetation development in this site (Schmalzer et al. 2002). Here we extend the record on the survival and growth of scrub plant species and on changes in community composition and structure through 2015.

This study was conducted in a plot of about 5.6 ha that was part of an abandoned grove circa 20.2 ha in size (Fig. 1). This plot was adjacent to extant scrub vegetation cut and burned in 1993 after greater than 40 years of fire suppression (Schmalzer et al. 1994). This grove was established between 1958 and 1965; it was abandoned after a freeze in 1987, and the citrus trees were cleared and burned in 1988 (Table 1). Both the extant scrub and the former grove are on well-drained, sandy soils (Astatula and Paola series, typic and spodic quartzipsamments, respectively; Huckle et al. 1974) associated with and representative of scrub and scrubby flatwoods in the region (Schmalzer et al. 1999, 2001). Soils of the former grove had higher pH, NO3−−N, available Cu and Zn but lower organic matter, NH4−−N, and available Al and Fe than intact scrub (Schmalzer et al. 2002). A sand road divides the site into a larger northern section and a smaller southern section (Fig. 1).
Figure 1. Location of the former citrus grove in which scrub species were planted in 1992 and 1993. Planting occurred within a 5.6 ha section of a 20.2 ha former grove. Oak survival and growth from the 1992 planting was sampled on 10 sections of oak planting lines. We sampled vegetation cover in the old field on 10 line-intercept transects. We sampled vegetation cover in the adjacent scrub on 20 transects (locations not shown). Background image is from 2015.
Table 1. History of the scrub planting site.

| Date     | Event                                                                 |
|----------|----------------------------------------------------------------------|
| 1958–1965| Grove established in former scrub vegetation.                        |
| 1961–1962| Acquisition for Kennedy Space Center.                                |
| 1987     | Freeze, grove abandoned.                                             |
| 1988     | Citrus trees cleared and burned.                                     |
| 1992     | Sabal palmetto removed, site mowed, herbicide applied twice, scrub oaks (Quercus) planted in August. Transects established in old field and adjacent scrub. |
| 1993     | Planting of other scrub species and second planting of scrub oaks in July–August. Adjacent scrub cut and burned. |
| 2000     | March burn of old field northern section.                             |
| 2002     | March burn of old field both sections.                               |
| 2004     | May burn of northern section of scrub.                               |
| 2005     | May burn of old field southern section and adjacent scrub.           |
| 2007     | March burn of old field.                                             |
| 2008     | May burn of old field and southern section of scrub.                 |
| 2009     | Spotty March burn of old field.                                      |
| 2010     | Large oaks, Sabal palmetto, and some Pinus cut in old field.         |
| 2011     | January burn northern section of old field.                          |
|          | Burn of southern section of old field later in year.                 |
| 2013     | Partial winter (January–February) burn of old field.                |
| 2014     | Partial January burn southern section of old field.                  |

Site Preparation and Planting

Site preparation began with mechanical removal of small Sabal palmetto that had established in the site followed by two applications of glyphosate herbicide (0.5 L/ha, June 1992; 10.0 L/ha, July 1992). Herbicides were applied to reduce cover of exotic species, particularly grasses, to reduce competition with planted, native species. Species chosen to be planted are the dominant plants of scrub on KSC/MINWR including three with planted, native species. Species chosen to be planted are exotic species, particularly grasses, to reduce competition.

We estimated initial planting densities as sufficient to establish the dominant scrub species on this site with the assumption that clonal spread of oaks, Serenoa, and ericaceous shrubs would increase their cover over time.

Survival and Growth of Planted Species

To determine survival of planted oaks, we tagged 15 oaks in each of 10 selected planted rows (Fig. 1) in late August 1992 (96 Q. geminata, 41 Q. myrtifolia, and 13 Q. chapmanii); rows were selected in a stratified random manner such that samples occurred north to south and west to east (Fig. 1). From the second planting, we tagged 50 scrub oaks, (20 Q. geminata and 30 Q. myrtifolia) and 50 of the additional scrub species (34 Serenoa, 6 Pinus, 4 Vaccinium, and 6 Lyonia) in the early September 1993 to follow survival and growth.

We sampled tagged oaks of the first cohort in April/May 1993 and sampled all tagged individuals from 1994 to 2010. The site did not burn from 1992 to 1999, but burned partially or wholly in prescribed fires six times from 2000 to 2010 (Table 1). These prescribed fires were conducted by USFWS/MINWR staff as part of upland habitat management (USDI 2008); however, many oaks were not top-killed. At each sampling, we determined survival and height of tagged species. In the fall of 2010, large Quercus, Sabal, and some Pinus were cut by chain saw; the site burned in early 2011. This management action was taken because the height structure that had developed was outside the normal range for scrub vegetation and because the oaks (particularly Q. geminata) were growing as single stemmed trees instead of clonal shrubs. We resumed sampling for survival in 2012, but the height of individual scrub oaks was no longer measured because clonal growth made identifying individual stems difficult.

Community Composition and Structure

We established 10 line-intercept transects (15 m length each) (Mueller-Dombois & Ellenberg 1974) in late August 1992 after planting was completed to determine long-term vegetation changes (Fig. 1); transects were located in a stratified random manner. We recorded vegetation cover data by species in two height strata (0–0.5 m and >0.5 m); cover was measured to the nearest 5 cm. We resampled these transects in early fall (late August to early October, typically September) from 1993 to 2015 because the herbaceous vegetation was best developed at that time of year.

Line-intercept cover transects (N = 20, 15 m length each) were established in adjacent scrub in 1992, and vegetation cover sampled as described above. This scrub had never been cleared for agriculture but had been unburned for greater than 40 years. It was cut and burned in 1993 and the transects were sampled from 1994 to 2015.

Data Analysis

We conducted statistical analyses including summary statistics, Chi-square comparisons of survival among oak species, and
Spearman rank order correlations ($r_s$) between selected groups of plants (SPSS ver. 18; IBM, Armonk, NY, U.S.A. www.ibm.com). We used nonmetric multidimensional scaling (NMS) ordination (Kruskal 1964a, 1964b) to examine changes in old field community composition over time (PCORD; version 6, MJM Software Design, Glenden Beach, OR, U.S.A.). NMS is considered the most generally effective method for the ordination of community data (McCune & Grace 2002). We ordinated the greater than 0.5 m strata and 0–0.5 m strata separately, using the Sorenson distance measure. The initial dataset consisted of 237 samples (10 transects sampled 24 times less one transect missing for 3 years). Screening of the greater than 0.5 m data indicated that the 1992 samples ($N = 10$) did not have sufficient cover to be included in the analysis and screening of the 0–0.5 m data indicated that the 1992 samples were an outlier group as most of the cover was dead grass from the recent herbicide application, and these samples were dropped from further analyses. We also dropped species with less than two occurrences in the greater than 0.5 m or 0–0.5 m data set to avoid outliers. The reduced greater than 0.5 m dataset had 227 samples and 51 species and the 0–0.5 m dataset had 227 samples and 64 species. We compared the mean annual stand composition ($>0.5$ m) of the old field site to that of the adjacent scrub using NMS; there were 23 samples of the old field site and 22 of the adjacent scrub. Seventy-five species occurred in the combined scrub and old field data. For some results, we grouped native and introduced species of similar life forms (Table 2) to follow dynamics of the vegetation change over time more readily as there were many species involved.

Results

Survival and Growth of Planned Species

By 8 months after planting, scrub oak survival from the first planting was 54.7% overall; survival differed significantly among species (Fig. 2A; $X^2 = 44.6, p < 0.001$) with Quercus geminata $>$ Q. chapmanii $>$ Q. myrtifolia. Most oaks that survived to 8 months after planting survived to April 2010, 17.6 years after planting (Fig. S1A, Supporting Information). There was some additional loss of Q. geminata $>$ Q. chapmanii $>$ Q. myrtifolia after cutting of large oaks in the fall of 2010 and burning in 2011 and 2013.

Eight months after planting overall scrub oak survival of the second planting was 34.0%; the species differed significantly ($X^2 = 10.5, p = 0.001$) with survival of Q. geminata $>$ Q. myrtifolia survival (Fig. S1A). The survival of the first oak cohort to 8 months after planting was significantly greater than survival of the second cohort ($X^2 = 5.2, p = 0.022$). However, neither the survival of Q. geminata ($X^2 = 1.2, p = 0.266$) nor Q. myrtifolia ($X^2 = 0.35, p = 0.522$) differed between the two cohorts.

Early height growth of Q. geminata exceeded that of Q. chapmanii and Q. myrtifolia (Schmalzer et al. 2002). From 2000 to 2010, six prescribed fires burned all or part of the site (Table 1). All tagged Q. chapmanii and Q. myrtifolia were top-killed at least once in these fires; however, 66% of Q. geminata were not, and their mean height was 8.0 m in 2010, well outside the normal range of scrub height (Fig. S2A). In contrast, height growth in adjacent, intact scrub reached about 2.0 m before being reduced by prescribed fire (Fig. S2B).

Serenoa survival was 100% until April 1995 when it declined to 88.2%; it declined to 61.8% in May 1996 (Fig. S1B). All tagged Serenoa have survived since then. The mortality of Serenoa appeared to be due to rooting of the developing rhizome by feral pigs (Sus scrofa) (Schmalzer et al. 2002). Mean height of Serenoa increased from 19.5 cm (SD = 5.7, N = 34) in 1993 to 154.1 cm (SD = 57.3, N = 21) in 2015. Fire reduced the height of Serenoa but it recovered rapidly.

All Pinus ($N = 6$) survived throughout the initial period (Fig. S1B) and grew rapidly. Mean height increased from 54.5 cm (SD = 9.8, n = 6) in 1994 to 422.0 cm (SD = 92.5, N = 6) in 1999 and 921.7 cm (SD = 102.2, N = 6) in 2008. Subsequently some Pinus were killed by fire or cutting. The remaining Pinus ($N = 2$) had a mean height of 1,040 cm in 2015.

Most of the loss of Lyonia fruticosa occurred soon after planting (Fig. S1B) with no loss since 1999. The sample size of Vaccinium myrsinoides was small ($N = 4$) and all had died by 2000 (data not shown). Some Vaccinium that were not tagged have survived and spread in the site.

| Table 2. Major groups of plants in the scrub planting site. |
|-----------------|-----------------|
| **Group** | **Taxa** |
| Scrub oaks | Quercus chapmanii, Q. geminata, Q. myrtifolia |
| Woody vines | Ampelopsis arborea, Smilax auriculata, Vitis rotundifolia, V. shuttleworthii |
| Native shrubs (not oaks or Serenoa) | Baccharis halimifolia, Callicarpa americana, Ilex ambigua, Lyonia fruticosa, L. ferruginea, Rhus copallinum, Sabal palmetto, Ximenia americana, Zanthoxylum clava-herculis |
| Exotic grasses | Cynodon dactylon, Melinis repens, Panicum maximum, Paspalum notatum, P. urvilleanum, Sorobolus indicus |
| Native grasses | Andropogon spp., Aristida purpurascens var. tenuispaica, Cenchrus echinatus, C. spinifex, Dichanthelium spp., Digitaria ciliaris, Eragrostis hirsuta, Eragrostis spp., Eustachys petrae, Paspalum setaceum, Setaria parviflora, Triplasia purpurea |
| Native forbs | Acalypha gracilens, Ambrosia artemisiafolia, Bidens alba, Chamaecrista fasciculata, C. nictitans, Cnidoscolus stimulosus, Conyza canadensis, Croton glandulosus, Diodia teres, Erechtites hieracifolia, Eupatorium capillifolium, E. compositifolium, E. serotinum, Froelichia florida, Galactia elliotii, G. volubilis, Galium spp., Heterotheca subaxillaris, Lactuca spp., Mikania spp., Monarda punctata, Oenothera humifusa, Opuntia humifusa, Passiflora incarnata, Phytolacca americana, Physalis walteri, Poinsettia cyathophora, Sida spp., Solidago odora var. chapmanii |
Community Composition and Structure

Immediately after planting total cover was low, there was little cover of scrub oaks (Tables S3 & S4), and no cover of *Pinus* or *Serenoa* (Tables S5 & S6). Scrub oaks increased slowly in cover greater than 0.5 m from 1992 through 1999 and then more rapidly to 2010 (Fig. 2A; Table S3). Much of this increase was due to *Q. geminata* reaching large size (Fig. S2A). Cutting in 2010 and burning in 2011 reduced oak cover, but this was followed by increases more related to growth of clonal patches of oaks (Fig. 2A; Table S3).

Cover of *Pinus* greater than 0.5 m increased from zero initially to about 19% in 2015 (Fig. 2B; Table S5) although pine mortality from fire and cutting has occurred. Cover of *Serenoa* greater than 0.5 m remained less than 1% through 2002 but has increased since then (Fig. 2C; Table S5). Fires have reduced *Serenoa* cover in some years, but cover reestablished rapidly after fire.

Cover of native grasses greater than 0.5 m increased for several years after planting (Fig. 2D; Table S3). Native grass cover declined from 2005 to 2010 but increased after cutting of large oaks and burning (Fig. 2D; Table S3). Cover of native forbs greater than 0.5 m increased after planting, decreased from 2003 to 2010, and then increased after the large oaks were cut (Fig. 2E; Table S3). Cover of native forbs declined with increased cover of scrub oaks ($r_s = -0.310, p < 0.001$).

Exotic grasses increased in cover greater than 0.5 m the year after planting, retained substantial cover for several years, declined from 2002 to 2010, but increased after cutting and burning of the large oaks (Fig. 3A; Table S3). Cover of exotic grasses 0–0.5 m increased for several year after herbicide treatment and planting and has fluctuated in a narrow range from 2005 to 2015 (Fig. 3F; Table S6). Increase in cover of scrub oaks was associated with a decline in cover of exotic grasses ($r_s = -0.364, p < 0.001$) but with increases in cover of woody vines ($r_s = 0.475, p < 0.001$) and native shrubs ($r_s = 0.201, p = 0.002$).

Ordination Analysis. Temporal trends in vegetation cover were observed in the NMS ordination. The first axis of the NMS was correlated with time since planting ($r = 0.597, p < 0.001$). Transects sampled in the early years after planting were to the left of the first axis of the old field ordination (Fig. 4A). Subsequent years moved to the right with the transects sampled in 2009 on the extreme right (as were 2010 transects, data not shown). Transects sampled in 2011, after logging and burning, were to the left of the 2009 samples, while 2013 and 2015 transects moved rightward. Cover of native grasses, native forbs, and exotic grasses was greatest in the early years after restoration.
Figure 3. Mean cover of (A) all exotic grasses in the greater than 0.5 m strata, (B) all exotic grasses in the 0–0.5 m strata, (C) the exotic grass Melinis repens in the greater than 0.5 m strata, (D) the exotic grass Panicum maximum in the greater than 0.5 m strata, (E) the exotic grass Cynodon dactylon in the 0–0.5 m strata, and (F) the exotic grass Paspalum notatum in the 0–0.5 m strata. Species groups follow Table 2. Error bars show ± SE.

The north and south sections of the old field differed in vegetation composition in the 0–0.5 m strata. This was shown by the first axis of the NMS of the old field 0–0.5 m strata (Fig. 5A) and was correlated with position ($r = 0.835$, $p < 0.001$). *Paspalum notatum* occurred at the right side of the first axis (Fig. 5B), shown by the right-most exotic grass point, reflecting its abundance in the southern section of the site. It was abundant from the beginning in the section to the south and remained so throughout the study. Although scrub oaks and slash pine increased in cover greater than 0.5 m south of the sand road, *P. notatum* remained abundant 0–0.5 m.

The vegetation cover of the old field has remained distinct from the composition of adjacent scrub. In the ordination of the combined old field and scrub data (Fig. 6), composition of the old field shifted with time since planting toward that of the intact scrub but remained distinct. This reflected the increasing cover of scrub oaks, particularly *Q. geminata*. Variation within the intact scrub was related to time since fire with the most recently burned samples higher on the second axis.

**Discussion**

Reestablishing scrub vegetation requires that the dominant species, particularly scrub oaks and saw palmetto, survive, grow, and develop a vegetation structure that could be maintained by fire. Planted scrub species showed different patterns of survival but survived in sufficient numbers such that composition of the old field changed over time. Changes from cultivation did not pass abiotic thresholds that would have prevented survival and growth of planted scrub species. Cover of scrub species increased over time, and this resulted in a reduction in the cover of exotic grasses as well as that of native grasses and forbs. The structure that developed in the old field differed from that of intact scrub; the dominant oak species grew as large single stem trees instead of clonal shrubs. Additional management was required to transition to a more clonal shrubland.

**Survival and Growth of Scrub Species**

Little is known of the seedling establishment of scrub oaks. In this study, *Quercus geminata* exhibited greater survival than *Quercus chapmanii* and *Quercus myrtifolia* in both planted cohorts; 1-year-old *Q. geminata* were larger than those of the other two oaks, which may have had some effect on survival. Scrub oaks can establish in sandhill vegetation during periods of fire suppression (Guerin 1993; Menges et al. 1993), but exotic grasses may present a more difficult environment for establishment of oak species than the native grasses in sandhills.

We expected clonal spread of scrub oaks to occur after they established. All scrub oaks have extensive underground roots and rhizomes (Guerin 1993), sprout and spread clonally after fire (Menges & Kohfeldt 1995), and reestablish cover quickly (Abrahamson 1984b; Schmalzer 2003). Clonal spread occurred to some extent for *Quercus chapmanii* and *Q. myrtifolia* but most *Q. geminata* grew rapidly in height and became fire resistant more quickly than anticipated. Only after being cut and burned in 2010–2011 did more extensive clonal spread
of *Q. geminata* occur. It may be that *Q. geminata* allocated more biomass to height growth in the old field initially than to belowground biomass. *Quercus geminata* can obtain greater height than the other scrub oaks (Nixon et al. 1997); the more open, and possibly less competitive, conditions of the old field compared to intact scrub may have contributed to the greater height growth.

*Serenoa repens*, a rhizomatous, clonal palm, is an important species in scrub, flatwoods, and other vegetation types in Florida (Abrahamson & Hartnett 1990; Myers 1990). The high initial survival seen here is consistent with observations that seedling and adult mortality is low even after drought and fire (Abrahamson 1995; Abrahamson & Abrahamson 2002, 2009). *Serenoa* grows slowly in intact vegetation (Abrahamson 1995; Abrahamson & Abrahamson 2009), and can reach great age (Takahashi et al. 2011). *Serenoa* exhibited more rapid growth and clonal spread in this old field than in intact scrub except where surrounded by dense *Paspalum notatum* (Foster & Schmalzer 2012).

*Pinus elliottii* var. *densa* is the common canopy tree in flatwoods in central and southern Florida (Abrahamson & Hartnett 1990). It is capable of rapid growth (Lohrey & Kossuth 1990) as demonstrated in this old field site and will establish in old fields (O’Hare & Dalrymple 2006).
Dynamics of Exotic Grasses

As woody cover increased, cover of exotic grasses declined; however, two species, *Panicum maximum* and *Paspalum notatum*, remained common. *Panicum maximum* is a large, perennial clump grass, and this may make it less likely to be shaded out by developing shrub vegetation. *Paspalum notatum* is a perennial, rhizomatous, sod-forming grass known to be persistent in pastures (Hamman & Hawkes 2013) and other upland and drained wetland (Toth & van der Valk 2012) sites where it was planted and limits the establishment of native species (Jenkins et al. 2004; Frances et al. 2010; Tucker et al. 2017).

Dynamics of Native Grasses and Forbs

Increasing cover of woody vegetation resulted in a decline in cover of native grasses and forbs suggesting that they do not constitute a substantial barrier to reestablishing scrub species. These native grasses and forbs are characteristic of open and disturbed habitats including old fields and roadsides (Wunderlin & Hansen 2011). Many of these species (or related congeners) were noted in earlier studies of old field succession in north-central Florida (Laessle 1942), north Florida (Gano 1917; Kurz 1945; Kay et al. 1978; Busing & Clebsch 1983), and more broadly in the southeastern United States (Wright & Fridley 2010).
Changes in Community Composition

Ordination analysis of the greater than 0.5 m strata of the old field data showed directional change with time associated with increasing cover of scrub oaks, *Serenoa*, and *Pinus*, and decreasing cover of native forbs, native grasses, and exotic grasses. When compared to intact scrub, the old field vegetation moved toward scrub in the ordination space but remained distinct. After 23 years the old field vegetation retains exotic and native species absent from intact scrub. Ordination of the 0–0.5 m strata of the old field data further indicated the intermediate character of the current old field vegetation. A persistent but low-growing exotic grass, *P. notatum*, was established in the southern section of the planting site and has retained substantial cover through the initial herbicide treatment and growth of scrub species. Ordination of this stratum reflects its continued abundance rather than directional change with time.

Scrub vegetation does not develop spontaneously on former agricultural sites. Scrub oaks and *Serenoa* have relatively large seeds dispersed by animals; therefore, limited dispersal would be expected to be a factor in the lack of natural establishment in cleared areas. Establishment of seedlings in sandy soils, low in nutrients and organic matter, and subject to periodic droughts, may be infrequent. Competition with exotic grasses may further limit establishment in these old fields as found in other systems (Davis et al. 2005; Midoko-Iponga et al. 2005; Kulmatiski 2006; Standish et al. 2007; Tognetti & Chaenton 2012). Limited dispersal of native species and established populations of exotic grasses could be considered a biotic threshold.

Planting and initial reduction in exotic grasses helped overcome that biotic threshold. There has been a clear increase in woody cover of native scrub species along with a reduction in exotic grasses, native grasses, and forbs over time. These changes occurred despite relatively high initial mortality of planted oaks and the unexpected growth of *Q. geminata* to large trees. A second round of management intervention in 2010–2011 was required to stimulate the sprouting and clonal spread of *Q. geminata*. The current community composition retains substantial cover of two exotic grasses (*P. maximum, P. notatum*) and remains distinct from scrub that was never cultivated.

Soils of this old field differed in several parameters from adjacent scrub soils (Schmalzer et al. 2002). These soil legacies did not prevent the survival and growth of planted scrub species, indicating that the site had not passed an abiotic threshold as described by Cramer et al. (2008). Modified soils may have favored invasive exotic grasses (Greenberg et al. 1997; David & Menges 2011) that competed with scrub species. Soil treatments without planting of scrub species affected soil properties but not vegetation on similar sites (Weiler et al. 2013). Persistent soil legacies even after removal of exotic
grasses may limit germination of scrub herbs (Hamman & Hawkes 2013).

The future composition and structure of this site is not certain, but the current trajectory is toward greater abundance of scrub species. The clonal growth patterns of oaks and *Serenoa* should allow them to continue to expand. Shade from oak clones and needle drop from pines are expected to reduce grasses over time. Meiners et al. (2002) noted a decline of exotics over 40 years of succession in a New Jersey old field but found that shade-tolerant exotics remained.

This study illustrates the importance of long-term monitoring in restoration practice. Little was known about reestablishing scrub vegetation at the beginning of this project (Schmalzer et al. 1994). Future restoration should benefit from this experience. We recommend greater initial effort to reduce established populations of exotic grasses, in particular the dense sod formed by *P. notatum* and the large clumps of *P. maximum*. Approaches combining tilling to break up the dense rhizomes of *P. notatum* and repeated herbicide applications have shown some success on other sites (Jenkins et al. 2004; Freeman et al. 2017). Planting larger stock of scrub oaks might reduce initial mortality. Triggering the clonal growth of *Q. geminata* appears to require coppicing either by fire or cutting. We recommend burning earlier in the vegetation development before *Q. geminata* becomes fire resistant. A limitation of this study was that it involved only one site. Future studies would benefit from replication; multiple sites could allow testing burning at different intervals after planting.

**Acknowledgments**

This work was conducted under NASA Contracts NAS10-11624, NAS10-12180, NAS10-02001, NKK080Q01C, and NKK160B01C. We thank F. Adrian, S. Turek, and C. Dunley for their assistance during early years of the project. The authors declare no conflict of interest. We thank several reviewers and editors for their constructive comments.

**LITERATURE CITED**

Abrahamson WG (1984a) Post-fire recovery of Florida Lake Wales ridge vegetation. American Journal of Botany 71:9–21

Abrahamson WG (1984b) Species responses to fire on the Florida Lake Wales ridge. American Journal of Botany 71:35–43

Abrahamson WG (1995) Habitat distribution and competitive neighborhoods of two Florida palmettos. Bulletin of the Torrey Botanical Club 122: 1–14

Abrahamson WG, Abrahamson CR (2002) Persistent palmettos: effects of the 2000-2001 drought on *Serenoa repens* and *Sabal etonia*. Florida Scientist 65:281–292

Abrahamson WG, Abrahamson CR (2009) Life in the slow lane; palmetto seedlings exhibit remarkable survival but slow growth in Florida’s nutrient-poor uplands. Castanea 74:123–132

Abrahamson WG, Hartnett DC (1990) Pine flatwoods and dry prairies. Pages 103–149. In: Myers RL, Ewel JJ (eds) Ecosystems of Florida. University of Central Florida Press, Orlando

Breininger DR, Carter GM (2003) Territory quality transitions and source-sink dynamics in a Florida Scrub-Jay population. Ecological Applications 13:516–529

Breininger DR, Schmalzer PA (1990) Effects of fire and disturbance on plants and animals in a Florida oak/palmetto scrub. American Midland Naturalist 123:64–74

Breininger DR, Stolen ED, Carter GM, Oddy DM, Legare SA (2014) Quantifying how territory quality and sociobiology affect recruitment to inform fire management. Animal Conservation 17:72–79

Busing RT, Clebsch EEC (1983) Species composition and species richness in first year old fields: responses to season of soil disturbance. Bulletin of the Torrey Botanical Club 110:304–310

Carrell JE (2003) Burrowing wolf spiders, *Geolycosa* spp. (*Araneae: Lycosidae*): gap specialists in fire-maintained Florida scrub. Journal of the Kansas Entomological Society 76:557–566

Christian SP, Judd WS (1990) Notes on plants endemic to Florida scrub. Florida Scientist 53:52–73

Cramer VA, Hobbs RJ (eds) (2007) Old fields: dynamics and restoration of abandoned farmland. Island Press, Washington D.C.

Cramer VA, Hobbs RJ, Standish RJ (2006) What’s new about old fields? Land abandonment and ecosystem assembly. Trends in Ecology and Evolution 23:104–112

David AS, Menges ES (2011) Microhabitat preference constrains invasive spread of non-native natal grass (*Melinis repens*). Biological Invasions 13:2309–2322

Davis MA, Bier L, Bushelle E, Diegel C, Johnson A, Kujala B (2005) Non-indigenous grasses impede woody succession. Plant Ecology 178:249–264

Davison KL, Bratton SP (1986) The vegetation history of Canaveral National Seashore, Florida. National Park Service Cooperative Park Studies Unit Technical Report 22. Institute of Ecology, University of Georgia, Athens

Duncan BW, Larson VL, Schmalzer PA (2004) Historic landcover and recent landscape change in the North Indian River Lagoon Watershed, Florida. Natural Areas Journal 24:198–215

Foster TE, Schmalzer PA (2012) Growth of *Serenoa repens* planted in a former agricultural site. Southeastern Naturalist 11:331–336

Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A (2003) The importance of land-use legacies to ecology and conservation. Bioscience 53:77–88

Frances AL, Adams CR, Norcini JG (2010) Importance of seed and microsite limitation: native wildflower establishment in non-native pasture. Restoration Ecology 18:944–953

Freeman JE, Williges K, Gardner AG, Leone EH (2017) Plant functional group composition on restored longleaf pine-wiregrass (*Pinus palustris-Aristida stricta*) savannas with a history of intensive agriculture. Natural Areas Journal 37:434–456

Gano L (1917) A study in physiographic ecology in northern Florida. Botanical Gazette 128:249–264

Greenberg CH, Neary DG, Harris LD (1994) Effects of high-intensity wildfire and silvicultural treatments on reptile communities in sand pine scrub. Conservation Biology 8:1047–1057

Greenberg CH, Crownover SH, Schmalzer PA (1997) Roadside soils: a corridor for invasion of xeric scrub by nonindigenous plants. Natural Areas Journal 17:99–109

Guerin DN (1993) Oak dome clonal structure and fire ecology in a Florida longleaf pine dominated community. Bulletin of the Torrey Botanical Club 120:107–114

Hamman ST, Hawkes CV (2013) Biogeochemical and microbial legacies of non-native grasses can affect restoration success. Restoration Ecology 21:58–66

Hobbs RJ, Cramer VA (2007) Why old fields? Socioeconomic and ecological causes and consequences of land abandonment. Pages 1–14. In: Cramer VA, Hobbs RJ (eds) Old fields: dynamics and restoration of abandoned farmland. Island Press, Washington D.C.

Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, et al. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15:1–7
Hokit DG, Stith BM, Branch LC (1999) Effects of landscape structure in Florida scrub: a population perspective. Ecological Applications 9: 124–134

Holl KD (1999) Factors limiting tropical forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31:229–242

Hooper ER, Legendre P, Condit R (2004) Factors affecting community composition of forest regeneration in deforested, abandoned land in Panama. Ecology 85:3313–3326

Hackle HF, Dollar HD, Pendleton RF (1974) Soil survey of Brevard County, Florida. USDA Soil Conservation Service, Washington D.C.

Jenkins AM, Gordon DR, Renda MT (2004) Native alternatives for non-native turfgrasses in Central Florida: germination and responses to cultural treatments. Restoration Ecology 12:190–199

Johnson AF, Abrahamson WG, McCrea KD (1986) Comparison of biomass recovery after fire of a seeder (Ceratiola ericoides) and a sprouter (Quercus imbricaria) species from south-central Florida. American Midland Naturalist 116:423–428

Kautz R, Stys B, Kawula R (2007) Florida vegetation 2003 and land use change between 1985-89 and 2003. Florida Scientist 70:12–23

Ker CAR, Clewelling AF, Ashler EW (1978) Vegetative cover in a fallow field: responses to season of soil disturbance. Bulletin of the Torrey Botanical Club 105:143–147

Kruskal JB (1964a) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29:115–129

Kruskal JB (1964b) Nonmetric multidimensional scaling: a numerical method. Psychometrika 29:1–27

Kuebbing SA, Souza L, Sanders NJ (2014) Effects of co-occurring non-native invasive plant species on old-field succession. Forest Ecology and Management 324:196–204

Kulmatiski A (2006) Exotic plants establish persistent communities. Plant Ecology 187:261–275

Kurz H (1945) Secondary forest succession in the Tallahassee Red Hills. Proceedings of the Florida Academy of Sciences 7:1–42

Laessle AM (1942) The plant communities of the Welaka area. University of Florida Publications: Biology Science Series 4:1–143

Langley JA, Hungate BA, Drake BG (2002) Extensive belowground carbon storage supports roots and mycorrhizae in regenerating scrub oaks. Oecologia 131:542–548

Lohrey RE, Kosuth SV (1990) Pinus elliottii Engelm: Slash pine. Pages 338–347. In: Burns RM, Honkala BH (eds) Silvics of North America: conifers. Vol I. U.S. Department of Agriculture, Forest Service, Kennedy Space Center, Washington D.C.

Mailander JL (1990) Climate of the Kennedy Space Center and vicinity. NASA Technical Memorandum 103,498. Kennedy Space Center, Florida

McCune B, Grace JB (2002) Analysis of ecological communities. MJM Software Design, Gleneden Beach, Oregon

McLachlan K (2006) The nature and longevity of agricultural impacts on soil carbon and nutrients: a review. Ecosystems 9:1364–1382

Meiners SJ, Pickett STA, Cadenasso ML (2002) Exotic plant invasions over 40 years of old field succession: community patterns and associations. Ecography 25:215–223

Menges ES (1999) Ecology and conservation of Florida scrub. Pages 7–22. In: Anderson RC, Fralish JS, Baskin JM (eds) Savannas, barrens and rock outcrop plant communities of North America. Cambridge University Press, New York

Menges ES, Hawkes CV (1998) Interactive effects of fire and microhabitat on plants of Florida scrub. Ecological Applications 8:935–946

Menges ES, Kohlfeldt N (1995) Life history strategies of Florida scrub plants in relation to fire. Bulletin of the Torrey Botanical Club 122: 282–297

Menges ES, Abrahamson WG, Givens KT, Gallo NP, Layne JN (1993) Twenty years of vegetation change in five long-unburned Florida plant communities. Journal of Vegetation Science 4:375–386

Menges ES, Craddock A, Salo J, Zinthofer R, Weekley CW (2008) Gap ecology in Florida scrub: species occurrence, diversity, and gap properties. Journal of Vegetation Science 19:503–514

Milodko-Ipanga D, Krug CB, Milton SJ (2005) Competition and herbivory influence growth and survival of shrubs on old fields: implications for restoration of renosterveld shrubland. Journal of Vegetation Science 16: 685–692

Mueller-Dombois D, Ellenberg H (1974) Aims and methods of vegetation ecology. John Wiley & Sons, New York

Myers RL (1990) Scrub and high pine. Pages 150–193. In: Myers RL, Ewel J (eds) Ecosystems of Florida. University of Central Florida Press, Orlando

Nixon KC, Jensen RJ, Manos PS, Muller CH (1997) Quercus. Pages 445–506. In: Flora of North America Editorial Committee (ed) Flora of North America north of Mexico. Vol III. Oxford University Press, New York

O’Hare NK, Dalymple GH (2006) Growth and survival of South Florida slash pine (Pinus elliottii var. densa) on restored farmlands in Everglades National Park. Ecological Restoration 24:242–249

Schmalzer PA (2003) Growth and recovery of oak-saw palmetto through ten years after fire. Natural Areas Journal 23:5–13

Schmalzer PA, Hinkle CR (1992a) Recovery of oak-saw palmetto after fire. Castanea 57:158–173

Schmalzer PA, Hinkle CR (1992b) Species composition and structure of oak-saw palmetto scrub vegetation. Castanea 57:220–251

Schmalzer PA, Brenninger DR, Adrian F, Schaub R, Duncan BW (1994) Development and implementation of a scrub habitat compensation plan for Kennedy Space Center. NASA Technical Memorandum 109202. Kennedy Space Center, Florida

Schmalzer PA, Boyle SR, Swain HM (1999) Scrub ecosystems of Brevard County, Florida: a regional characterization. Florida Scientist 62:13–47

Schmalzer PA, Hensley MA, Dunlevy CA (2001) Background characteristics of soils of Kennedy Space Center, Merritt Island, Florida: selected elements and physical properties. Florida Scientist 64:161–190

Schmalzer PA, Turek SR, Foster TE, Dunlevy CA, Adrian FW (2002) Reestablishing Florida scrub in a former agricultural site: survival and growth of planted species and changes in community composition. Castanea 67:146–160

Standish RJ, Cramer VA, Wild SL, Hobbs RJ (2007) Seed dispersal and recruitment limitation are barriers to native reclamation of old-fields in western Australia. Journal of Applied Ecology 44:435–445

Stephens EL, Castro-Morales L, Quintana-Ascencio PF (2012) Post-dispersal seed predation, germination, and seedling survival of five rare Florida scrub species in intact and degraded habitats. American Midland Naturalist 167:223–239

Stover DB, Day FP, Butnor JR, Drake BG (2007) Effect of elevated CO2 on coarse-root biomass in Florida scrub detected by ground-penetrating radar. Ecology 88:1328–1334

Styinski CD, Allen EB (1999) Lack of native species recovery following severe exotic disturbance in southern California shrublands. Journal of Applied Ecology 36:544–554

Takahashi MK, Horner LM, Kubota T, Keller NA, Abrahamson WG (2011) Extensive clonal spread and extreme longevity in saw palmetto, a founntion species of a pine flatland. Molecular Ecology 20:3730–3742

Tognetti PM, Chaenton EJ (2012) Invasive exotic grasses and seed arrival limit native species establishment in an old-field grassland succession. Biological Invasions 14:2531–2544

Toth LA, van der Valk A (2012) Predictability of flood pulse driven assembly rules for restoration of a floodplain plant community. Wetlands Ecology and Management 20:59–75

Tucker RC, Rothermel BB, Daskin JH (2017) Preparing Florida pasture for restoration of Florida scrub vegetation. Castanea 82:245–254

USDI (U. S. Department of the Interior, Fish and Wildlife Service) (2008) Merritt Island National Wildlife Refuge comprehensive conservation plan. U.S. Department of the Interior, Fish and Wildlife Service, Southeast Region, Atlanta, Georgia
Walker LR, Wardle DA (2014) Plant succession as an integrator of contrasting ecological time scales. Trends in Ecology & Evolution 29:504–510
Weekley CW, Menges ES, Pickert RL (2008) An ecological map of Florida’s Lake Wales Ridge: a new boundary delineation and an assessment of post-Columbian habitat loss. Florida Scientist 71:45–64
Weiler A, Von Holle B, Nickerson DM (2013) Reducing biotic and abiotic land-use legacies to restore invaded, abandoned citrus groves. Restoration Ecology 21:755–762
White WA (1970) The geomorphology of the Florida peninsula. Geological Bulletin No. 51. Bureau of Geology, Florida Department of Natural Resources, Tallahassee
Wright JP, Fridley JD (2010) Biogeographic synthesis of secondary succession rates in eastern North America. Journal of Biogeography 37:1584–1596
Wunderlin RP, Hansen BF (2011) Guide to the vascular plants of Florida. 3rd edition. University Presses of Florida, Gainesville

Supporting Information
The following information may be found in the online version of this article:

**Figure S1.** (A) Survival of scrub oaks planted in 1992 and 1993. (B) Survival of other scrub species planted in 1993.

**Figure S2.** (A) Height growth of *Quercus geminata* planted in 1992 and measured annually from 1993 through 2010. (B) Height growth of intact scrub vegetation adjacent to the scrub planting site.

**Table S1.** Mean cover (%) greater than 0.5 m of species groups at the scrub planting site from 1992 through 2015.

**Table S2.** Mean cover (%) 0–0.5 m of species groups at the scrub planting site from 1992 through 2015.

**Table S3.** Mean cover (%) greater than 0.5 m of species at the scrub planting site from 1992 through 2015.

**Table S4.** Mean cover (%) 0–0.5 m of species at the scrub planting site from 1992 through 2015.

Coordinating Editor: Stephen Murphy

Received: 19 March, 2018; First decision: 23 April, 2018; Revised: 18 July, 2018; Accepted: 18 July, 2018; First published online: 29 August, 2018