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Forest Development 44 Years after Fire Exclusion in Formerly Annually Burned Oldfield Pine Woodland, Florida

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ABSTRACT Young mixed hardwood forest communities that colonized abandoned croplands during the late 19th century in northern Florida were typically winter burned annually after pine saplings could survive fire. Hardwood trees persisted as coppice that grew from root crowns within grassy undergrowth. This plant community changed little thereafter, except for the continued growth of pine trees. An 8.64-ha tract of this community was inventoried in 1966, from which fire was permanently excluded thereafter. This tract, called NB66, was reinventoried in 2010 to document maturation of the plant community and to identify the contributing causes that controlled ecological development. Hardwood coppice that was released from fire grew to form a nearly continuous canopy averaging 19.7 m high after 44 years. Many older pines died and disintegrated without causing canopy gaps. Prior to 19th century plantation agriculture, the original vegetation consisted of shortleaf pine-oak-hickory (SPOH) woodland, which intergraded with longleaf pine savanna on sandier soils. These species occur at NB66 but the forest remains dominated by native offsite species, which are aggressively reproducing. These offsite species formerly occurred in less elevated landscape positions in association with magnolia-beech and bottomland hardwood forests. Frequently burned old-field pineland adjacent to NB66 has remained stable indicating that no factors other than fire exclusion caused release of hardwoods from their “fire trap.” There was no trend toward recovery of the original SPOH community, and forest development is postulated on the basis of mesophication processes. Recruitment of new species—both woody and herbaceous—since 1966 was modest; most remain uncommon.

Key words: Coppice, fire trap, mesophication, NB66, novel ecosystem, Tall Timbers, upland pine-oak.

INTRODUCTION Trees of fire-sensitive species growing in pyrogenic savannas and open woodlands are commonly top-killed by recurring fires. They survive between burns from coppice sprouts that arise from the crowns of unharmed roots (Higgins et al. 2007). This process may continue indefinitely, and roots supporting coppice may attain massive size at ground level. Fires are commonly fueled by dense herbaceous ground cover in which grasses predominate and to which low-growing shrubs may contribute.

Trees are said to be caught in a “fire trap” if they normally survive as coppice in a pyrogenic ecosystem rather than attaining normal tree

stature. The notion of fire traps is useful for describing the ecological trajectory of a community that is prone to shifting expressions of biodiversity across time in response to changing environmental influences. For example, the cessation of fire can trigger rapid afforestation as coppice sprouts develop into trees. Gross changes in biotic expression reflect rearrangement of plant community structure and not necessarily altered species composition. Fire traps have been described from different parts of the United States (Keeley and Zedler 1978, Buchholtz 1983, Peterson and Reich 2001, Drewa et al. 2002) and the world (Ojeda et al. 1996, Hoffmann et al. 2009, Werner and Franklin 2010).

Extensive regions of coastal plain in the southeastern United States once contained pine

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savannas and other pyrogenic ecosystems that are identifiable as fire traps, primarily for hardwood tree species (Ellair and Platt 2013). Some of these original ecosystems remain, and more have developed secondarily and are maintained on abandoned, ex-arable lands by anthropogenic fire management. Reduction of hardwood-dominated forests to a fire trap condition was documented at the Santee Experimental Forest, South Carolina, where many larger hardwood trees in a mixed hardwood stand were reduced to coppice on account of frequent burning for 43 years (Waldrop et al. 1992).

Land managers commonly cause trees to escape the fire trap by eliminating fires and allowing coppice sprouts to grow and attain normal arboreal stature. However, this aspect of the fire trap equation has not been unequivocally documented. The 84 permanent, 0.2-ha Stoddard fire demonstration plots, which were established at the Tall Timbers Research Station (TTRS) in northern Florida in 1959, allowed documentation of the initial stages of fire trap evasion. Most plots were placed in annually winter-burned old-field pinelands dominated by *Pinus echinata* (shortleaf pine) and *Pinus taeda* (loblolly pine).¹ Perennially coppicing hardwoods were abundant in the dense, grass-dominated ground cover. Plots were burned over a range of specific fire return intervals, and fire was permanently excluded from some plots. Aspects of fire trap evasion in these plots were recorded by Mehlman (1992) and with considerable thoroughness by Glitzenstein et al. (2012). These investigations revealed a distinct trend for vegetation in plots with fire return intervals of 5 yr or more to shift from dominance by herbaceous to woody plants and for tree coppice to develop normal arboreal stature.

The Stoddard plots were too small to record forest development other than edge effect. Consequently, a much larger, 8.64-ha plot was established at TTRS within the same annually winter-burned old-field pineland. Designated as NB66 ("not burned since the 1966–67 dormant season"), fire and all other anthropomorphic disturbances were subsequently excluded. This paper compares the vegetation of NB66 in 1966 with that occurring in 2010, after 44 years of fire exclusion. In addition, the vegetation that has

remained in adjacent fire-trap environment of old-field pineland was recorded in 2013 and compared to that in 1966 in NB66. If no substantial change in vegetation in the fire trap environment has occurred since 1966, then obvious changes in vegetation that occurred between 1966 and 2010 in NB66 would be attributable to fire exclusion and evasion from the fire trap.

NB66 allows assessment of the degree to which forest development following release from the fire trap fosters recovery of the original vegetation that formerly occupied the loam uplands of TTRS—and most of the Tallahassee Red Hills—prior to 19th century agricultural disturbances. This vegetation consisted of shortleaf pine-oak-hickory woodland (SPOH; *P. echinata*, *Carya tomentosa*, *Quercus stellata*, *Quercus falcata*, *Quercus velutina*, *Nyssa sylvatica*, *Cornus florida*). Shortleaf pine-oak-hickory woodland remains open with a grass-dominated ground cover on account of occasional fires, which keep some but not all hardwood trees in a fire trap and that favor an abundance of the relatively fire-tolerant shortleaf pine. If this community occupies a relatively fire-protected site, it manifests as an oak-hickory forest consisting of the same upland tree species with a much diminished component of pines and grasses. Shortleaf pine-oak-hickory woodland formed broad transition zones with longleaf pine savanna (*Pinus palustris*), which occupied sandier, less fertile soils on hilltops (Clewell 2013).

Another possible outcome of evasion of the fire trap would be development of a novel plant community that lacks historical precedent in species composition. Evidence suggestive of this possibility is that secondary upland forests in the Tallahassee Red Hills are dominated by tree species that are characteristic of pre-agricultural magnolia-beech forests and bottomland hardwood forests, both of which normally occur at distinctly less elevated positions in the landscape (Kurz 1938, Clewell 2011). Among the more common offsite species were *P. taeda*, *Quercus nigra* (water oak), *Liquidambar styraciflua* (sweetgum), *Magnolia grandiflora*, and *Prunus serotina* (Clewell 2013). Most of these offsite species were also well represented by coppice in old-field pinelands that comprised firetraps on annually burned lands, including at NB66.

¹Authorities for scientific names are given in the appendices.

Clewell (2011, 2013) attributed the persistence of offsite species to mesophication (Nowacki and Abrams 2008), which encourages the replacement of upland trees by trees typical of lowlands. The process is widespread in the Southeast (Brose and Van Lear 1998, Brewer 2001, Van Lear 2004). Occasional surface fires characteristically reduce the cover of undergrowth in original upland forests and prevent encroachment by offsite lowland tree species. In the absence of fires, offsite trees become established and the structure of an upland forest is modified in a manner that reduces flammable biomass in the undergrowth and precludes development of microclimatic conditions that are conducive to its ignition. The probability for continued dominance by offsite species is thereby enhanced.

Three questions are addressed in this paper. (1) Is vegetation response at NB66 attributable to release from the fire trap? (2) Is the original, SPOH plant community recovering at NB66 following release from the fire trap? (3) Is a novel forest without historical precedence forming at NB66, due to mesophication?

PROJECT SITE NB66 is located in Leon County, Florida, in northeastern Section 15 of Township 3 North, Range 1 East (30°39'54"N, 84°13'08"W). The northern edge of the tract lies 1.8 km south of the Florida-Georgia state line. NB66 occurs within the Tallahassee Red Hills physiographic region, which served as Florida's most important agricultural district during the 19th century. Prior to the 18th century, the Tallahassee Red Hills had been extensively but not intensively farmed for maize and other crops by Apalachee Indians for several centuries. Many large cotton plantations were established upon the founding of the US Territory of Florida in 1824. The plantation economy began to collapse after the American Civil War ended in 1865, and most were abandoned by 1875. In contrast to offsite vegetation that colonized abandoned plantation lands, no evidence exists of displacement of the original SPOH woodland community by Apalachee agriculture, although *Aristida stricta* Michx. (wiregrass, a keystone species of longleaf pine savannas) may have been depleted Clewell (2013).

NB66 formed part of the Woodlawn Plantation (later renamed as Oaklawn, Hickory Hill, and Tall Timbers), which was established in 1834 on the north shore of Lake Iamonia. In the early 1860s,

the plantation contained 486 improved ha of land that were ready for growing crops and produced 225 bales of cotton and 7,000 bushels of corn in 1859–60 (Paisley 1968). The property was sold in 1871 and again in 1880, and later became a private hunting preserve in 1895 (Bauer 2005). NB66 consisted of a patchwork of former cultivated fields, most of which were abandoned approximately at the end of the great cotton plantation era. Tenant farmers cultivated small fields with mules until mid-20th century, and approximately 150 ha of land at Tall Timbers were cultivated in this manner in 1920 (Bauer 2005).

Former plantations underwent old-field succession (Clewell 2011); however, succession was interrupted early in its development on most abandoned lands by the intentional practice of setting annual grass fires in late winter. The principal grass was *Andropogon virginicus* (broomsedge). Pines that were more than 2 m tall generally survived these fires and formed open woodlands, but young colonizing hardwoods were burned back to their root crowns, and most survived as coppice between fires. Cattle grazed the pinelands for a few weeks each spring during the "greening up" period following late winter fires. Cattle were rounded up when crops were planted and fenced thereafter. Cattle grazing continued until 1949 when state law prohibited open-range foraging.

Beginning in the late 19th century, many abandoned plantations were purchased by wealthy residents of northern US cities who spent winters hunting bobwhite quail (*Colinus virginianus* (L.)) on these lands. Some of these private hunting preserves yet remain in operation. Large quail populations were favored by annual burning of pinelands and by habitat and food resources provided by small fields that were interspersed on which tenant farmers grew subsistence crops. Stoddard (1931) recognized the relationship between quail populations and land use and implemented management practices to foster that landscape (Neel 2010). To encourage additional investigations by Stoddard and colleagues into the ecological uses of fire in land management, plantation owners established TTRS in 1958.

In 1966, Edwin V. Komarek, Sr., who administered TTRS at the time, his brother Roy, and I established NB66. The tract covers part of an elongated, saddle-shaped hill that has a north-south orientation and a rounded ridge top. The

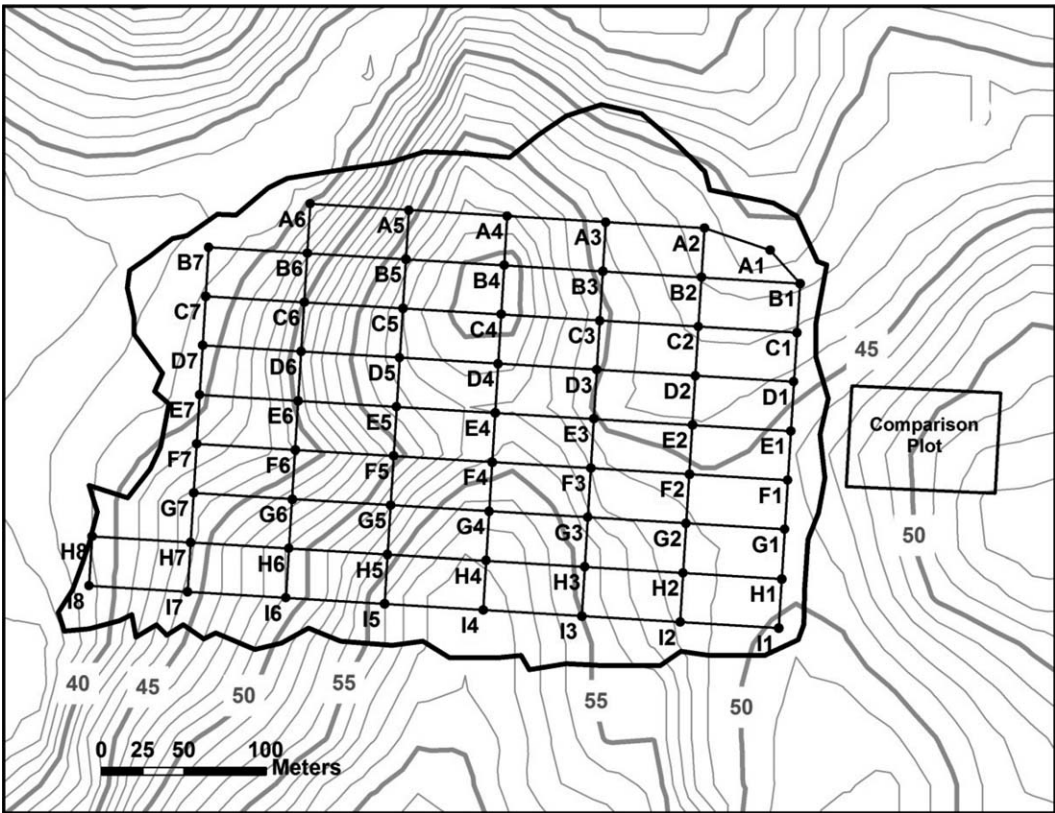


Figure 1. Elevation contours (m above sea level) and plot layout at NB66. The irregular line that surrounds NB66 is the fire break separating unburned land from land to the exterior which is burned frequently, including the comparison plot. NB66 consists of 48 contiguous 60×30 -m plots. Permanent corner posts (dots) for each plot are designated by letter and number. Plots are identified by the posts in their northeastern corners. The post designation that is shown within each plot is also that plot's identification.

tract extends nearly to the base of the hill on its eastern and western sides (Figure 1). In 1966, Roy Komarek and I divided NB66 into 48 contiguous 60×30 -m plots, with each plot marked by concrete corner posts that were individually identified by signage. Plot lines that run north-south are numbered and those running east-west are lettered. Corner posts for each plot are designated by the letter and number of their intersecting plot lines. Each plot is identified by the post that marks its northeastern corner. Plot line 4 generally follows the ridge that divides the tract into its eastern and western slopes.

Elevation gradients west of the ridge are notably steeper than on the eastern slope. Several conspicuous narrow gullies occurred west of plot line 5, primarily in plots C5, D5, E5, D6, and E6. In places, these gullies were approximately 1 m to 5 m deeper than the

original grade (not captured by elevation contours in Figure 1) and undoubtedly formed after fields were cleared for cultivation in the 19th century. Most side slopes and bottoms were vegetated in 1966, and exposed soils were protected from erosion by terrestrial mosses and algae. Carbonate rock fragments were intermixed with exposed soil in deeper gullies.

Figures 2 and 3 are aerial photographs of NB66 taken in 1931 and 2010, respectively, and overlain by NB66 plots. Hunting trails interrupted the pineland in 1931. Tenant fields are evident on the eastern side of what would become NB66 (Figure 2). Most of the western slope consisted of dense forest (Figure 2), which probably predates 1895 and perhaps 1880. A forested buffer that lies within the fire break is evident in Figure 3. Lifelong resident Henry Vickers, (b. ca. 1891; pers. comm., 1967) recalled a narrow field

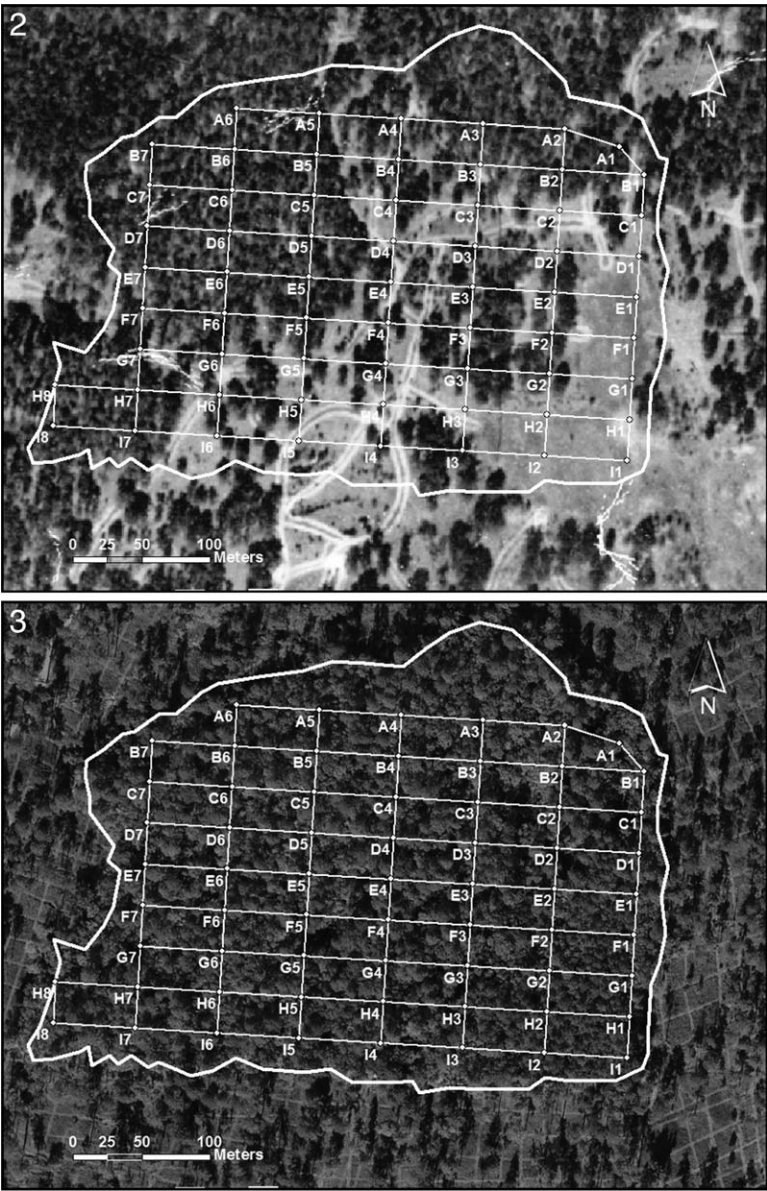


Figure 2. Aerial photograph taken in 1931 shown with the overlay of NB66 plots from Figure 1.
Figure 3. Aerial photograph taken in 2010 shown with the overlay of NB66 plots from Figure 1. The checkered signature of lands surrounding NB66 derives from mowed paths through dense groundcover to facilitate bird census.

extending between posts C1 and D4, which was cultivated until about 1915. The relatively open area seen in Figure 2 between these posts is presumably the outline of that field. Vickers also recalled fields that were cultivated concurrently near plot E6, presumably in the more open areas southeast of E6 as seen in Figure 2. Vickers said that the principal crops were corn and cotton

and that a small amount of manure was applied to fields nearly annually. Silvicultural thinning of larger pines occurred in the early 1940s to supply lumber needed for the war effort during WWII. An ungraded, one-lane road provides vehicular access near the eastern and northern sides of the tract, and the harrowed fire break allows access along the southern and western sides during dry



Figure 4. Open pine woodland of NB66 in 1967, looking southwest through plot A4. Dense, grass-dominated ground cover is evident with brushy hardwood coppice protruding above the grasses.

Figure 5. Closed mixed pine-hardwood forest of NB66 in 2012, looking southwest through plot A4. The view is identical to that in Figure 4.

seasons. The road is hidden beneath trees in Figure 3. The road traverses the middle of what would have been plot A6. Consequently, plot H7 was established as its replacement. The road also traverses the northeastern corner of plot A1 and the northwestern corners of plots A5, and B6. The corner of plot A1 that was isolated by the road was not inventoried and A1 was thereby reduced in size. The area of inventory for plots A5 and B6 were reduced by the area occupied by the road. On account of the road and those portions of plots A5 and B6 that were isolated by

it, the actual area inventoried was 8.60 ha, and all plant density data presented in this paper were calculated on the basis of 8.60 ha.

The last fire was set on March 23, 1967, which thoroughly and evenly consumed leaf litter and aerial shoots of vegetation in the groundcover. Figures 4 and 5 are photos that contrast the vegetation of NB66 in 1967 and 2012. The photos were taken at the same position and in the same direction from near stake A4. I established five extra 60×30 -m plots in spring 1968 in the annually burned pineland adjoining NB66 to the

south. These were intended as annually burned control plots for comparative use in future investigations, but they had to be abandoned due to circumstances that are explained below.

In 1966–68, Clewell and Komarek (1975) developed a comprehensive list of vascular plant species for NB66, including the five extra plots. Subsequent changes in taxonomic interpretation and nomenclature have required modest modifications to this list, which, after revision, now contains 206 species. Species of bryophytes were listed.

We conducted a quantitative census of the vegetation (Clewell and Komarek 1975). Within each 30×60 -m plot we measured the diameters of all trees by species (≥ 5 cm in diameters at breast height [dbh]) and determined their locations visually on a map of each plot. Other than coppice of the year, there were essentially no smaller saplings anywhere on NB66. We determined frequencies of occurrence of potential tree species from annual coppice sprouts growing in 791, 4-m² quadrats (2×2 m). These quadrats were located along lines between posts B1 and B6, C6 and C7, and F2 and I2. We determined frequencies of occurrence of nonarboreal species (herbs, vines, shrubs) in 202, 1-m² quadrats that were located haphazardly in June and November, 1966. Species frequency was determined by dividing the number of plots or quadrats in which one or more plants of a species was rooted by the total number of plots or quadrats.

Soils at NB66 are fine-loamy, siliceous, thermic, typic paleudults. These fine sandy loams are well drained, slightly acid, and have been alternatively identified as belonging to the Orangeburg series with 2–5% slopes on the east side and 8–12% slopes on the west side (USDA, NRCS) and the Ruston series by Julius Sullivan of the USDA, Soil Conservation Service (report on file at Tall Timbers library and summarized in Clewell and Komarek 1975). Sullivan examined soil horizons with an auger to a depth of 1 m, and he recorded the depth of the A1 horizon and the degree of slope near each post. He noted that soils were badly eroded due to agricultural activities, and colluvial deposits occurred at lower elevations. Sullivan discovered a plinthite layer capable of perching a water table at post G6.

On 7 November 1967, a soil sample was extracted at each post from the A1 horizon (or from the upper 5 cm of soil when an A1 horizon was absent) and sent to the USDA, Coastal Plain

Experiment Station at Tifton, Georgia for mechanical analysis and determination of pH, percent organic matter, and the content of P and K. Values for pH ranged from 5.0 to 6.0. The median value for organic matter was 3.8% and ranged from 1.5% to 10.5%. Potassium content was variable and phosphorus content was generally low. Additional soil samples were taken on 17 May 1967 from near posts A5, B4, C6, and G1 and were sent to the Florida Department of Agriculture at Gainesville, Florida, for analysis of Ca and Mg (both high) and N (low) (Clewell and Komarek 1975).

The warm-temperate climate at NB66 is characterized by mild winters, prolonged growing seasons (normally 238 frost-free days according to the NRCS, *op. cit.*), summer and winter wet seasons with moderate to high humidity, and spring and autumn dry seasons during which time some precipitation occurs. Annual precipitation is approximately 1.5 m and sometimes varies considerably from this norm. Precipitation readily percolates into the deep loam soil which has a high water-holding capacity.

In 1976, Tobi (1977) reinventoried most plots and measured the diameters of trees that were ≥ 5 cm in dbh. Woody thicket prevailed (Figure 6) that largely consisted of the unhindered growth of hardwood coppice into trees. Grassy openings, mostly 5 m to 10 m in diameter, persisted, which had been devoid of hardwood coppice in 1966 (Figure 6). These openings provided opportunities for the successful establishment of trees from seeds shortly after burning ceased.

Engstrom et al. (1984) sampled the vegetation of NB66 in 1981 to document habitat conditions in a study of breeding bird usage. They established 15, 0.04-ha circular plots in a stratified random design. Tree cover was estimated by ocular sightings of trees that were > 4 cm in dbh. The data showed a continuation of hardwood growth recorded by Tobi (1977) and a sharp decline in bird species richness since 1967.

Clewell (2011) described secondary forest that grew on a former 0.2-ha agricultural field in the southeastern corner of NB66 in the eastern portions of plots E1, F1, G1, and H1. This field, called NB66h, was last harrowed in 1968 and can be discerned in Figure 3 from the uniformly smaller crowns of trees than occur elsewhere on NB66. NB66h lacked coppicing hardwoods;



Figure 6. Photo taken in 1977 at nearly the same place as photos in Figures 4 and 5, which shows a thicket of young hardwoods growing from coppice and young pines growing from seeds, with a grassy opening in the foreground. See p. 438 in Engstrom et al. (1984) for a photo with the same view in 1981.

Figure 7. Regrowth of coppice following fire in the previous dormant season from a partially exposed root crown of *Prunus serotina* located in the comparison plot. Photo taken in May 2014.

Figure 8. Three stems of *Prunus serotina* that grew in the absence of fire from a single root crown in NB66. The two larger stems extend into the canopy. Compare to Figure 7. Photo taken in May 2014.

therefore, uninterrupted old-field succession was described rather than a fire trap.

According to foreman Eric Staller (pers. comm., 2013), pineland at TTRS, including that surrounding NB66, was burned annually until 1969 and then switched to a 2- to 5-yr fire return interval. Since 1997, fires have been ignited on a 1- or 2-yr interval. Pineland immediately south of

NB66 became woody thicket owing to longer fire return intervals and the difficulty of burning cleanly around several experimental plots that were installed for other purposes in that area. Consequently, the five extra plots that I established in that area in 1968 could no longer serve as controls for meaningful comparison of vegetation with that in NB66. To replace the extra

plots, I established a 60×90 -m comparison plot east of NB66 in September 2013, shown in Figure 1. The northern and southern borders were extensions of the "D" and "F" lines of the NB66 plots. The western and eastern borders were set 37 m and 127 m east of NB66. The exact position of the western boundary was determined randomly along a short baseline. Although the comparison plot was not investigated quantitatively until 2013, the entrance road into NB66 passed right alongside of it, and it has been a familiar site that has not undergone obvious change, particularly in its groundcover, since 1966. Historical aerial photographs confirm these observations.

METHODS The census of NB66 occurred between 18 October and 11 December 2010. The boundary of each plot was delimited with measuring tapes, and additional tapes subdivided each plot to facilitate accurate inventory. Trees were defined as woody plants, excluding vines, with a stem diameter of at least 5 cm in dbh. All trees were identified to species, counted, and their diameters (dbh) measured in all 48 plots. Density, relative density (RD), and density per ha were calculated from tree tallies. A tree was tallied as a single individual for the calculation of density and RD, even if multiple trunks arose from its base. Diametric data were transformed to basal area (BA), relative basal areas (RBA), and basal area per ha by species. Diameters of all multiple trunks of ≥ 5 cm in dbh from a single tree contributed to calculations of BA. The percent occurrence (out of 48 plots) of a tree species was recorded as its frequency.

Heights of selected trees were measured in February 2011 with an Impulse 200 LR laser ranging instrument (Laser Technology, Inc., Centennial, Colorado) to determine canopy heights for pines and hardwoods. Trees were measured in four areas centered on plot A2-A3, D3-D4, B5-C5, and G5-G6. Trees (27 pines, 24 hardwoods) were selected that visually contributed to the canopy and whose tops were visible in the ranging instrument.

Saplings consisted of juvenile trees with woody stems that were < 5 cm in dbh and > 1 m tall. All saplings were identified to species and counted in each plot. Data are presented as density and RD.

Plants of nonarboreal species and tree seedlings (potential trees that were < 1.0 m tall) were sampled in 1-m^2 quadrats, which were distribut-

ed in clusters of six at each of 34 interior posts (posts B2-H2, B3-H3, B4-H4, B5-H5, and C6-H6). Four of the six 1-m^2 quadrats at each post were located 1 m distant from the post along plot lines. Two additional quadrats were located along the east-west plot lines and spaced 1 m beyond the other two quadrats. One side of each 1-m^2 quadrat consisted of a plot line. The side of a plot line on which a quadrat occurred was selected by random numbers. Cover values were assigned to the nearest 10% except for plants with low percent cover. Values of 1% were assigned if cover was estimated to be less than 3%. Cover values of 5% were assigned if cover was estimated at 3% to 7%. Cover from trees that were > 1 m tall was ignored, because those trees were inventoried as saplings or larger. Cover of vines was recorded for aerial shoots that passed across a quadrat within 1 m of the ground. Total vegetation cover and the collective cover of woody plants, graminoids (grasses and sedges), and forbs were estimated in each quadrat.

Comparative data from 1966 presented herein were taken from Clewell and Komarek (1975). In tabular data, "offsite" species (Appendix 1) are listed separately from "upland" species, which were characteristic of the SPOH woodlands and their ecotones with longleaf pine-wiregrass savannas prior to 19th century agriculture (Clewell 2013).

In September 2013, I established four lines in the comparison plot (Figure 1) for determining species frequencies in the groundcover. Two lines were the western and eastern boundaries of the plot, 37 m and 127 m, respectively, east of NB66. The other two lines were approximately 10 m to the interior of these boundaries; their exact locations were determined randomly along a short base line at 48 m and 116 m east of NB66. I divided each line into 12, 5-m contiguous lengths, each one of which became one side of a 1-m^2 quadrat, each 5×0.2 meters. I recorded every species of vascular plant that was rooted in each quadrat, including coppice of woody plants. The number of quadrats in which a species occurred was converted to frequency for comparison with 1966 data obtained in 202, 1.0-m^2 quadrats in grass-dominated pine woodland and reported by Clewell and Komarek (1975, Table 9). In November 2013 I determined the species of trees represented by coppice sprouts growing from root crowns in 96, 4×4 -m quadrats in the control plot. I sampled along the

Table 1. NB66 plant census data in this paper or archived in the library at Tall Timbers Research Station

1966–1967

Map of locations of all trees by species within each of the 48, 30 × 60-m plots, including:

- dbh of all trees ≥ 5 cm in dbh
- all saplings larger than coppice sprouts that are < 5 cm in dbh

Frequencies by species of trees sprouting as coppice in 791, 4-m² quadrats

Frequencies of nonarboreal species in 171, 1-m² quadrats

List of all species

2010

List of all trees by species in each of the 48, 30 × 60-m plots, including:

- dbh of all trees ≥ 5 cm in dbh
- all saplings < 5 cm in dbh and ≥ 1.0 m tall

Frequencies by species of tree seedlings < 1 m tall and of nonarboreal species, both in 204, 1-m² quadrats, with 6 quadrats located near each of 34 permanent interior plot posts

List of all species

2013, comparison plot east of NB66

Frequencies of all species in 48, 1-m² quadrats

Frequencies of all tree species sprouting as coppice in 96, 4-m² quadrats

same four lines that I had used for sampling nonarboreal species and established 24 contiguous quadrats beginning at the northern end of each line. I counted all trees in the entire plot that were larger than coppice sprouts.

Table 1 summarizes the kinds of plant census information available from studies conducted when the NB66 project was initiated in 1966–68 (Clewett and Komarek 1975) and from current investigations conducted in 2010–2013.

RESULTS

Species Composition

Vascular plant species occurring at NB66 in 2010 (entire tract) are listed in Appendix 1 and for the comparison plot in 2013 (quadrats only) in Appendix 2. The vascular flora of NB66 consisted of 127 species: 37 trees, 16 shrubs, 12 woody vines, 14 grasses and sedges, and 48 forbs. Two species were epiphytic. Only five species were alien, none of them invasive. Forty-one species had not been recorded in 1966–68. I recognized 39 species as growing offsite, including 22 tree species. Of the tree species that were represented by individuals that were ≥ 5 cm in dbh (Table 2), 14 were offsite species and 13 were upland species. NB66 gained 14 tree species in 2010 that were unrecorded in 1966. One of them (*Celtis*

occidentalis) was an upland species and the others were offsite species (Appendix 1).

Several of the 14 additional trees were typical of magnolia-beech forest, including *M. grandiflora*, which was represented in 11 plots, usually by a single seedling. The largest *M. grandiflora* was 4 cm in dbh. Saplings of *Ilex opaca* occurred in nearly every plot (Table 3), and some were small trees (Table 2). Tobi (1977) recorded *M. grandiflora* and *I. opaca* in 1976. *Fagus grandifolia* was represented by one sapling 2.3 m tall in plot G6 in 2010. Other typical trees of magnolia-beech forest that were absent in 1966 were *Acer saccharum*, *Morus rubra*, *Osmanthus americanus*, *Ostrya virginiana*, *Fraxinus americanus*, *Quercus laurifolia*, and *Quercus michauxii*. The latter three species tend to be more characteristic on flood plains than in magnolia-beech forest with better-drained soils. *Quercus michauxii* was represented by one sapling 0.8 m tall in plot C2.

Several post-1968 species additions that are listed in Appendix 1 were native shrubs and woody vines, including *Ilex vomitoria*, *Smilax tamnoides*, and the arborescent *Aralia spinosa*. Three alien shrubs grew as one or few individuals (*Elaeagnus pungens*, *Ligustrum sinense*, *Nandina domestica*) all of which are invasive elsewhere in the Tallahassee Red Hills (Clewett and Tobe 2011). Among the herbaceous species listed in Appendix 1, most flourished under open conditions in 1966 and were now represented by only a few individuals that had not yet succumbed to hardwood competition, e.g., *Lespedeza* spp. Several common post-1966 additions were typical forest herbs, particularly *Chasmanthium sessiliflorum*, *Dichanthelium boscii*, *Oplismenus hirtellus*, *Galium hispidulum*, and *Mitchella repens*. Less common herbaceous additions were *Aristolochia serpentaria*, *Asplenium platyneuron*, *Botrychium biternatum*, *Desmodium glabellum*, *D. nudiflorum*, *Matalea gonocarpos*, *Symphytotrichum lateriflorum*, and a few others that may be candidates for potential demographic increase.

Community Structure

The number of trees on NB66 increased from 914 in 1996 to 6,224 in 2010 (Table 2). Basal area nearly doubled from 14.6 m² per ha in 1996 to 28.2 m² per ha in 2010. Pines decreased in both density and basal area relative to hardwoods. In 1996, pines contributed 68% of the trees and 85%

Table 2. Tree (>5 cm in dbh) densities, basal areas, and frequencies (percent occurrence), in 1966 and 2010

	Number of Trees		Basal Area (cm ²)		% Frequency	
	1966	2010	1966	2010	1966	2010
Offsite trees						
<i>Pinus taeda</i>	184	334	452,524	485,696	78	94
<i>Pinus elliotii</i>	21	14	68,997	42,112	19	15
<i>Quercus nigra</i>	93	2,181	37,327	587,092	54	100
<i>Liquidambar styraciflua</i>	48	945	21,106	129,185	23	96
<i>Prunus serotina</i>	17	934	8,574	236,436	23	100
<i>Quercus virginiana</i>	45	128	80,794	60,433	19	75
<i>Ilex opaca</i>	0	24	0	1,040	0	42
<i>Diospyros virginiana</i>	6	11	1,768	661	4	13
<i>Acer rubrum</i>	0	9	0	1,346	0	15
<i>Ostrya virginiana</i>	0	5	0	289	0	4
<i>Quercus laurifolia</i>	0	4	0	436	0	6
<i>Osmanthus americanus</i>	0	1	0	65	0	2
<i>Morus rubra</i>	0	1	0	53	0	2
<i>Prunus americana</i>	0	1	0	20	0	2
Total	414	4,592	671,090	1,544,864		
Trees per ha	48	534				
Basal area (m ² /ha)			7.8	18		
Upland trees						
<i>Pinus echinata</i>	383	427	476,265	630,997	96	100
<i>Pinus palustris</i>	31	20	73,946	56,101	42	35
<i>Cornus florida</i>	35	553	7,673	55,190	25	100
<i>Quercus hemisphaerica</i>	15	260	11,016	50,084	19	94
<i>Quercus falcata</i>	26	72	9,384	36,230	27	73
<i>Malus angustifolius</i>	0	72	0	2,732	0	38
<i>Nyssa sylvatica</i>	4	53	3,807	8,470	4	42
<i>Sassafras albidum</i>	0	50	0	4,313	0	33
<i>Quercus alba</i>	1	47	74	16,161	2	50
<i>Carya tomentosa</i>	2	32	0	4,543	4	35
<i>Vaccinium arboreum</i>	0	18	0	673	0	27
<i>Quercus stellata</i>	3	15	5,590	7,326	4	21
<i>Carya glabra</i>	0	13	102	550	0	23
Total	500	1,632	587,857	873,370		
Trees per ha	58	190				
Basal area (m ² /ha)			6.8	10.2		
All trees						
Total	914	6,224	1,258,947	2,418,234		
Trees per ha	106	724				
Basal area (m ² /ha)			14.6	28.2		

of the basal area. In 2010, pines contributed 13% of the trees and 50% of the basal area. *Pinus taeda* and *P. echinata* remained the most abundant pines in 2010. *Quercus nigra*, *P. serotina*, and *L. styraciflua* were the most abundant overstory hardwoods in 2010, and *Q. hemisphaerica* and *Q. virginiana* were common. The number of offsite trees relative to upland trees was 45% in 1966 and rose to 74% in 2010. The collective basal area of offsite trees also rose from 53% of all trees in 1996 to 64% in 2010. Species frequencies in 2010 generally reflected values for species density.

Trees with multiple stems from the base were common, and all or nearly all arose from

multiple coppice sprouts growing from root-crowns. There were 424 trees recorded in 2010 with two or more basal stems, each of which were ≥5 cm in dbh. Figure 7 shows new coppice sprouts developing from a root crown of *P. serotina* in the recently burned comparison plot. Figure 8 shows a tree of *P. serotina* with multiple trunks that arose initially as coppice sprouts from a single root crown. Those sprouts grew and attained normal tree stature subsequent to the cessation of burning at NB66.

The tree canopy consisted of two strata. The taller stratum was discontinuous and consisted of pines that were already present in 1966. The lower stratum was nearly continuous and was

Table 3. Number of tree saplings by species (all 48 plots) and their frequencies in 2010

	Number of Stems	% Frequency
Offsite species		
<i>Pinus taeda</i>	75	29
<i>Liquidambar styraciflua</i>	1,405	98
<i>Quercus nigra</i>	491	92
<i>Quercus virginiana</i>	385	94
<i>Ilex opaca</i>	243	96
<i>Prunus serotina</i>	142	79
<i>Ostrya virginiana</i>	127	13
<i>Diospyros virginiana</i>	51	52
<i>Acer rubrum</i>	11	17
<i>Osmanthus americanus</i>	7	13
<i>Fraxinus americana</i>	4	8
<i>Aralia spinosa</i>	4	2
<i>Prunus caroliniana</i>	3	4
<i>Magnolia grandiflora</i>	2	4
<i>Morus rubra</i>	1	2
<i>Carpinus carolinia</i>	1	2
<i>Fagus grandifolia</i>	1	2
Total	2,953	
Upland species		
<i>Pinus echinata</i>	4	8
<i>Vaccinium arboreum</i>	383	92
<i>Malus angustifolius</i>	294	54
<i>Cornus florida</i>	161	79
<i>Quercus hemisphaerica</i>	130	60
<i>Carya tomentosa</i>	63	60
<i>Carya glabra</i>	28	27
<i>Quercus falcata</i>	22	29
<i>Nyssa sylvatica</i>	22	21
<i>Quercus alba</i>	14	19
<i>Celtis occidentalis</i>	1	2
<i>Crataegus pulcherrima</i>	5	6
<i>Viburnum rufidulum</i>	4	8
<i>Sassafras albidum</i>	4	4
<i>Quercus stellata</i>	3	4
<i>Crataegus uniflora</i>	2	4
Total	1,140	
Total	4,093	

comprised mainly of hardwoods with occasional pines interspersed. Trees in the lower stratum grew either from coppice sprouts that were present in 1966 or from seeds that germinated after 1966. In 1966, hardwoods were absent and pines were approximately 28 m tall; the tallest tree was *Pinus elliotii* 34 m tall, 77 cm in dbh, containing 106 annual rings. In 2010, the pine stratum averaged 33.6 m in height. Trees of *Pinus palustris* were tallest (38.9 m, n = 6 trees), followed by *P. taeda* (34.3 m, n = 12) and *P. echinata* (29.1 m, n = 9). The tallest pine was 48.7 m (*P. palustris*). Many taller pines had died recently. Most dead pines remained standing as snags that disintegrated in situ by the loss of larger limbs over a period of several years before

their trunks were wind-thrown. Pine reproduction was low (79 saplings, Table 3), and most of these were etiolated with little chance for survival. The lower stratum averaged 19.7 m tall. Trees of *Q. nigra* were tallest (22.0 m tall, n = 11), followed by *P. serotina* (18.8 m, n = 6), *L. styraciflua* (16.8 m, n = 5), and *N. sylvatica* (16.5 m, n = 1). The tallest hardwood was 30.5 m tall (*Q. nigra*).

Several large live oaks (*Quercus virginiana*) were recorded in plots E2, F2, and G3 in 1966 and were rediscovered in 2010, although most were senescent or dead snags. These oaks occurred in two rows at right angles to each other. Crowns of those trees provided most of the canopy cover in those plots as seen in the 1931 aerial photograph (Figure 2). These trees became established in fencerows between cultivated fields early in the 20th century (Clewell and Komarek 1975).

Tree saplings, which were essentially absent from NB66 in 1996, were common in 2010 (Table 3); 4,093 saplings (476 per ha) consisting of 33 species were tallied. Offsite species were represented by 72% of the saplings. *Ostrya virginiana* occurred in only six plots but was represented by 127 saplings, all of them surrounding a single tree (12 cm in dbh, 12 m tall) that probably produced the seeds from which they grew. *Liquidambar styraciflua*, *Q. nigra*, *Q. virginiana*, *P. serotina*, and *Q. hemisphaerica* were the most abundant saplings of hardwood tree species with the potential to contribute to the overstory. All were offsite species except *Q. hemisphaerica*, and all were native.

Most of these same species were among the more frequently represented by coppice from root crowns in 1966 (Table 4). Coppice in the comparison plot in 2013 consisted essentially of the same species of trees with mostly the same relative abundance as occurred at NB66 in 1966 (Table 4). There was a similarly close correspondence in nonarboreal species composition and abundance between NB66 in 1966 and the comparison plot in 2013 (Table 5), particularly among grasses. Twenty-four of 27 species with frequency values of at least 20 in 1966 were sampled in 2013, and 18 of those same species exceeded frequency values of 20. Relative to 1966, the two most notable differences in the nonarboreal community in 2013 were increases in the numbers of species sampled (Appendix 2) and increases in overall species frequency

Table 4. Frequencies (percentage of quadrats) in which coppice of arboreal species occurred in 4-m² quadrats in 1966 (NB66) and 2013 (comparison plot)

	1966	2013
Offsite trees		
<i>Quercus nigra</i>	34	84.4
<i>Diospyros virginiana</i>	18.8	20.8
<i>Liquidambar styraciflua</i>	14.2	37.5
<i>Prunus serotina</i>	6.3	1
<i>Quercus virginiana</i>	4.3	17.7
<i>Acer rubrum</i>	0.4	0
<i>Pinus taeda</i>	0	9.4
Upland trees		
<i>Sassafras albidum</i>	20.8	1
<i>Quercus hemisphaerica</i>	12.1	4.2
<i>Quercus falcata</i>	4	2.1
<i>Pinus echinata</i>	2.2	0
<i>Cornus florida</i>	2	0
<i>Nyssa sylvatica</i>	1.6	2.1
<i>Carya tomentosa</i>	1	2.1
<i>Quercus stellata</i>	0.6	2.1
<i>Quercus alba</i>	0.3	0
<i>Vaccinium arboreum</i>	0	1
<i>Malus angustifolius</i>	0	3.1

values. In other words, the number of species and their overall abundance has increased with time.

Until NB66 was established, all leaf litter was consumed by annual fires, and ground cover vegetation consisted largely of herbaceous plants with a collective cover of essentially 100% (Figure 4). No tree seedlings occurred among the 27 taxa with percent occurrence frequency values of at least 20 in the ground cover in 1966 (Table 5), and only four of those species were woody. In 2010, hardwood leaf litter covered the soil (Figure 5). Groundcover vegetation averaged only 28.6% cover and consisted almost entirely of woody species (27.7% cover). Of the 64 species recorded in quadrats in 2010, 38 were woody, and percent occurrence frequency values of 12 of them exceeded 10% (Table 6). Tree seedlings were prominent, and the most frequent were *Q. nigra*, *Q. virginiana*, *P. serotina*, *Q. hemisphaerica*, and *L. styraciflua*, all except *Q. hemisphaerica* being offsite species. Pine seedlings were poorly represented. Woody vines were prominent, particularly species of *Smilax*, *Vitis*, and *Gelsemium*. *Vaccinium stamineum* and *Callicarpa americana* were the most frequently occurring shrubs (Table 6). *Myrica cerifera* was also common and grew colonially in small, mostly

Table 5. Frequencies of nonarboreal species in 1-m² quadrats at NB66 in 1966 and the comparison plot in 2013

	1966	2013
Graminoids		
<i>Andropogon virginicus</i>	60	63
<i>Aristida purpurascens</i> var. <i>virgata</i>	40	29
<i>Dichanthelium</i> spp.	65	
<i>D. ovale</i>		90
<i>Gymnopogon ambiguus</i>	30	13
<i>Saccharum brevibarbe</i> var. <i>contortum</i>	30	54
<i>Schizachyrium tenerum</i>	20	17
<i>Scleria ciliata</i>	45	27
<i>Sorghastrum nutans</i>	45	75
Forbs		
<i>Acalypha gracilens</i>		23
<i>Ambrosia artemisiifolia</i>	20	52
<i>Centrocema virginianum</i>	50	17
<i>Chamaecrista fasciculata</i>	100	98
<i>Chamaesyce hysopifolia</i>		25
<i>Conoclinium coelestinum</i>		42
<i>Desmodium ciliare</i>		38
<i>Desmodium obtusum</i>	25	8
<i>Elephantopus elatus</i>	20	79
<i>Erigeron strigosus</i>		23
<i>Galium pilosum</i>	30	35
<i>Helianthus angustifolius</i>	20	69
<i>Helianthus hirsutus</i>		35
<i>Lespedeza procumbens</i>	20	2
<i>Lespedeza repens</i>	25	4
<i>Lespedeza stuevei</i>	20	0
<i>Pityopsis aspera</i>	40	75
<i>Solidago nemoralis</i>	20	0
<i>Solidago odora</i>	25	35
<i>Strophostyles umbellata</i>		33
<i>Symphyotrichum dumosum</i>		31
<i>Tephrosia spicata</i>	40	31
<i>Tragia smallii</i>		25
<i>Trichostema dichotomum</i>	25	63
Shrubs and woody vines		
<i>Ceanothus americanus</i>	20	0
<i>Rhus copallinum</i>	40	69
<i>Smilax bona-nox</i>	30	31
<i>Rubus cuneifolius</i>	80	69
<i>Vaccinium corymbosum</i>		21
21 additional species	5 to <20	
55 additional species		5 to 19
Number of 1.0 m ² quadrats in sample	171	48

4-m² to 8-m² patches in which other species were rare or absent.

There were 30 pine trees of approximately merchantable size in the comparison plot in 2013, all *P. echinata*. Trees of *P. taeda* and *Q. virginiana* grew nearby. In addition, there were 18 small trees of *P. echinata* that were 2–4 m tall. All other woody plants occurred as coppice, including shrubs and vines. Several stumps indicated recent tree removal in the comparison plot, dating to a sale of hardwood saw timber of

Table 6. Ground cover species frequencies in 204, 1-m² quadrats in 2010

	% Frequency
Trees	
<i>Acer rubrum</i>	1
<i>Carya glabra</i>	1
<i>Carya tomentosa</i>	1
<i>Celtis occidentalis</i>	<1
<i>Cornus florida</i>	1
<i>Diospyros virginiana</i>	4
<i>Ilex opaca</i>	1
<i>Liquidambar styraciflua</i>	9
<i>Magnolia grandiflora</i>	<1
<i>Malus angustifolius</i>	4
<i>Nyssa sylvatica</i>	1
<i>Pinus echinata</i>	<1
<i>Pinus taeda</i>	2
<i>Prunus serotina</i>	18
<i>Quercus alba</i>	<1
<i>Quercus falcata</i>	1
<i>Quercus hemisphaerica</i>	11
<i>Quercus nigra</i>	75
<i>Quercus stellata</i>	1
<i>Quercus virginiana</i>	20
<i>Sassafras albidum</i>	<1
<i>Vaccinium arboretum</i>	1
Shrubs	
<i>Callicarpa americana</i>	23
<i>Ilex vomitoria</i>	<1
<i>Myrica cerifera</i>	13
<i>Rhus coppallinum</i>	1
<i>Rubus trivialis</i>	12
<i>Vaccinium elliotii</i>	1
<i>Vaccinium stamineum</i>	30
Woody vines	
<i>Campsis radicans</i>	2
<i>Gelsemium sempervirens</i>	26
<i>Parthenocissus quinquefolia</i>	2
<i>Toxicodendron radicans</i>	8
<i>Smilax bona-nox</i>	14
<i>Smilax galuca</i>	3
<i>Smilax pumila</i>	<1
<i>Smilax tamnoides</i>	70
<i>Vitis rotundifolia</i>	46
Grasses & sedges	
<i>Andropogon virginicus</i>	<1
<i>Chasmanthium sessiliflorum</i>	5
<i>Dichanthelium acuminatum</i>	2
<i>Dichanthelium boscii</i>	5
<i>Gymnopogon ambiguus</i>	<1
<i>Optismenus hirtellus</i>	11
<i>Rhynchospora harveyi</i>	2
<i>Scleria ciliata</i>	1
<i>Sorghastrum nutans</i>	1
Forbs	
<i>Acalypha gracilens</i>	1
<i>Ageratina aromatica</i>	<1
<i>Aristolochia serpentaria</i>	<1
<i>Asplenium platyneuron</i>	<1
<i>Botrychium biternatum</i>	3
<i>Cassia fasciculata</i>	<1
<i>Desmodium laevigatum</i>	1
<i>Desmodium floridanum</i>	<1

Table 6. Continued

	% Frequency
<i>Euphorbia pubentissima</i>	<1
<i>Galactia macreei</i>	5
<i>Galium hispidulum</i>	4
<i>Lespedeza procumbens</i>	<1
<i>Mitchella repens</i>	12
<i>Sanicula canadensis</i>	1
<i>Solidago odora</i>	2
<i>Tragia urens</i>	<1
<i>Trichostema dichotomum</i>	<1

merchantable size (≥ 30 cm in diameter) about a decade ago. Most hardwoods were *Q. virginiana*, as identified from stumps.

DISCUSSION

Release from Fire Trap

The first question addressed in this paper asks if vegetation response at NB66 is attributable to release from the fire trap? To answer this question, we must ensure that there were no other contributing factors besides fire exclusion. Frequent reconnaissance by research personnel and the TTRS land management staff assures that NB66 has been well protected from intentional disturbances of all sorts. The only acute natural disturbance of consequence occurred 21 November 1985, when Hurricane Kate passed within 50 km to the west of NB66 with 100 km winds. William J. Platt (pers. comm., 2013) inspected NB66 shortly thereafter. He noted that many large pines and hardwoods were damaged; numerous downed branches and boles from snaps and tip-ups made it almost impossible to walk through NB66 without climbing through and over fallen debris. By 2010, these consequences of storm damage were no longer evident. Larger pines in frequently burned pinelands were also downed by Kate, demonstrating that natural disturbance was widespread and not confined to NB66. No evidence exists that that NB66 has suffered unique natural disturbance that did not also impact the surrounding landscape.

Fire suppression remains the viable explanation for release as long as the plant community in adjacent, frequently burned pinelands has remained stable since NB66 was established. If substantial change has occurred in that adjacent community, then previously undetected factors other than fire may be influencing local vegetation, including forest development at NB66. The

plant community in the comparison plot (Figure 1) in 2013 was remarkably similar to that on NB66 in 1966 in terms of hardwood coppice (Table 4), species composition (Appendix 2), and species frequencies (Table 5). Hardwood coppice was more abundant in 2013 than in 1966, particularly *Q. nigra* and *L. styraciflua*. That increase would be expected from the change from annual to biennial burning, which allowed a longer opportunity for coppice to establish. Coppice abundance for two other important species, *P. serotina* and *Q. hemisphaerica*, did not increase, presumably because of their greater fire sensitivity.

There was also a notable increase in the number of species encountered in sampling of the comparison plot during 2013 relative to 1966 (Table 5). In 1966, 48 species were recorded at least once in 171 quadrats. In 2013, 89 species were recorded at least once in only 48 quadrats. The most obvious explanation for this discrepancy is the greater length of time since agricultural abandonment for natural dispersal of plant species. The slightly lengthened fire return interval likely facilitated establishment. Increases in the abundance of coppice and numbers of species do not detract from the overall similarities in plant species composition and community structure that has persisted since 1966. Community stability firmly supports the contention that fire suppression was the only factor that triggered hardwood escape from the fire trap. Mehlman (1992) and Glitzenstein et al. (2012) came to the same conclusion from studies at the numerous but much smaller Stoddard plots, and the rearrangement of community structure at NB66 verifies their assumptions.

When fire was excluded after 1966, coppice of hardwood trees responded with rapid aerial growth from well-developed root systems (Tobi 1977). After 10 years of fire exclusion, the thicket of hardwoods was 5 m tall. The pine canopy was approximately 30 m tall in 1981 (Engstrom et al. 1984). Tobi (1977) reported a flush of pine saplings (*P. echinata*, *P. taeda*) that became established from seeds within the first few years of fire exclusion (Figure 6). These pines augmented densities for these species (Table 2). Pine tree establishment thereafter has been negligible (Table 4); however, their prevalence in smaller size categories (Table 3) suggests a potential for pine recovery after a major storm event. Woody shrubs and vines

were prominent in 2010 (Table 6), and most were already established before fire exclusion began (Clewell and Komarek 1975).

Relationship to Original Vegetation

The second question that is addressed by this paper is whether or not the original SPOH plant community is recovering at NB66 following release from the fire trap. Tree species commonly identifiable with the SPOH community have been growing at NB66 ever since that plot was established (*Q. velutina* excepted). The presence of *P. palustris* suggests that the original vegetation may have included longleaf pine savanna on the ridge; however, the soil there does not seem sufficiently coarse textured to support that community. Therefore, the ridge community may have been an ecotone between SPOH and longleaf pine savanna. However, deep gullies on the western slope betray considerable erosion. Sandy soils on the ridge could have eroded during the several decades of 19th century plantation agriculture, exposing loam subsoil. If so, the ridge may have once supported longleaf pine savanna.

Agricultural practices in the cotton plantation era were far different from modern mechanized farming. Power was supplied by draught animals. Roads were placed where animal-drawn carts could traverse the landscape in wet seasons. Figure 2 reveals segments of a possible 19th century farm road along the ridge. Some roadside areas were likely spared from cultivation to provide shade and shelter for both farm animals and laborers—mainly African slaves—and as staging areas for transport of harvested crops. In short, there were likely broad roadsides, fence rows, and staging areas that escaped cultivation. Although disturbed by agricultural activities, these were places where the original SPOH vegetation could have persisted, including trees and groundcover species such as *Schizachyrium tenerum*, which is usually absent on soils that have suffered mechanical disturbance. Other areas on NB66 probably escaped cultivation because of gradients that were too steep to cultivate. These occurred in the western half of plot H2 and adjacent plot H3. Some of the largest upland trees grew there, including *P. palustris* (78 cm in dbh), *N. sylvatica* (55 cm), and *Q. stellata* (67 cm). P and K levels were particularly high there in 1966 (Clewell and Komarek 1975), which suggested that these nutrients had not been depleted by harvested crops.

The persistence of SPOH and longleaf savanna elements from the original flora is the likely explanation for the presence of SPOH upland species at NB66 (Table 2), rather than subsequent recruitment. Most are midstory trees such as *C. florida*. The only common upland overstory trees are *P. echinata* and *Q. hemisphaerica* (Table 2). The latter may not have been an important species in original SPOH woodlands on account of its sensitivity to occasional fires and may have been restricted mainly to ravines and bluffs prior to 19th century agriculture (Clewell 2013). One reason that most SPOH hardwoods are uncommon at NB66 may be that they tend to be large-fruited and produce mast irregularly. After agricultural fields were abandoned in the late 19th century, seed production and dispersal may have been insufficient for their widespread establishment. Trees of offsite species (Tables 2–3) reproduce copiously to the detriment of upland hardwood species at NB66.

Canopy gap formation could provide future opportunities for upland tree species establishment; however, only a few canopy gaps have formed. Tall dead pines that could cause gaps tend to disintegrate before they fall. Smaller trees in the path of fall are little damaged, and their continued growth recloses the canopy before juveniles of other species can attain canopy height. With the possible exception of climate change towards warmer, drier conditions, I foresee little opportunity for the recovery of the original upland vegetation in the continued absence of fire. Hurricane-force winds could contribute to the demise of offsite hardwoods, particularly since many trees arising from coppice are infected by basal heart-rot which may increase their susceptibility to wind-throw. However, the prevalence of these species in smaller size classes (Table 3, Table 6) suggests that downed trees will be replaced by offsite species, which will perpetuate their dominance. No trend towards recovery of original vegetation is occurring, and none is likely in the near term.

Novel Trajectory

The third question addressed in this paper asks if a novel forest without historical precedence in species composition is forming at NB66, due to mesophication. In the late 19th century, when croplands were abandoned, the principal sources of tree seeds were streamside forests. Magnolia-beech forest and bottomland hardwood forest grew along one such stream 180 m

west of NB66. The forest harbors most offsite tree species listed in Appendix 1, including *P. taeda*, and it may have been a significant source of seeds that populated NB66. At the end of the plantation era, nearly all upland forests in that vicinity had been cleared for agriculture (Clewell 2011). Consequently, only seeds from species in those stream bottoms would have been available in abundance to repopulate uplands. Annual burning began at an early stage of old-field succession, as evidenced by the number of annual rings on larger pines (Clewell and Komarek 1975). Those fires prevented subsequent colonization by trees belonging to species that had not previously become established. Grasses and forbs were favored by annual burning, including additional groundcover species that colonized after the burning regime began.

The existing plant community consisting of offsite species has no historical precedent on upland sites in the Tallahassee Red Hills (Clewell 2013), and it qualifies as a novel ecosystem (Hobbs et al. 2006). Indicators of mesophication exist at NB66. These include a paucity of undergrowth biomass that could carry a surface fire, development of flattened hardwood leaf litter that is not especially flammable, and a microclimatic trend towards increased humidity and lower wind speeds. All evidence points to the conclusion that the forest at NB66 represents a novel plant community dominated by lowland species that are persisting on an upland site on account of processes of mesophication.

If windstorm events damage the existing hardwood-dominated forest, *P. echinata* establishment may be favored to form a pine-hardwood forest. *Pinus taeda* saplings, should they become established, would be much less likely to survive forested competition under upland site conditions (Clewell 2011). Much more likely will be an eventual colonization of *Pinus glabra* Walter (spruce pine) to the detriment of both *P. echinata* and *P. taeda*. *Pinus glabra* occurs in forests within 2 km of NB66 and is known to aggressively colonize forest gaps in the absence of fire.

Carya tomentosa and *Q. hemisphaerica* are the only upland hardwoods that are likely to contribute significantly to the next forest generation at NB66. *Quercus hemisphaerica* is an invasive native tree throughout the Florida

panhandle on sites that have experienced fire suppression or mechanical disturbance; however, it may encounter competitive resistance at NB66 from trees of *Q. nigra*, *L. styraciflua*, and other offsite species that are already established. Juveniles of *M. grandiflora* have been present at NB66 for more than 30 years but have not yet become established as young trees. They are apparently incapable of surviving forested competition (Platt and Hermann 1986) and may not contribute substantially in the next forest generation unless larger canopy gaps develop, which seems unlikely. *Ilex opaca* has become widespread throughout NB66 and is positioned to become a dominant midstory tree, but it usually does not contribute to the overstory of mature hardwood forests in the Tallahassee Red Hills region.

An unanticipated observation was the minimal impact of new tree species that colonized NB66 following fire exclusion, including forest herbs and shrubs (Table 6, Appendix 1). Most new tree introductions were spurious and consisted of one or few individuals. Consequently, changes in species composition have scarcely altered patterns of dominance. Few forest undergrowth species have become established. This may be a reason why bird utilization of NB66 has remained low (Engstrom et al. 1984).

The presence of several large slash pines (*Pinus elliotii*, Table 2) suggests that the mesophication process began concurrently with plantation agriculture. *Pinus elliotii* originally occurred in wetlands and adjacent lowlands (Hebb and Clewell 1976) and colonized upland sites following disturbance (Forbes 1930, Clewell 2013). Occurrence of several large trees of *P. elliotii* on uplands at NB66 posed an enigma, because no seed source for these trees existed within dispersal range of NB66. At the Wade Tract on Arcadia Plantation, 26 km northeast of NB66 (30°45'48"N, 84°01'50"W), *P. elliotii* grows intermingled with *P. palustris* in an old-growth pine flatwoods bordering a swamp in a landscape that closely resembles that occurring next to NB66. This topographical correspondence suggests the possibility that *P. elliotii* formerly grew in pine flatwoods adjacent to NB66 when agricultural activities commenced in the mid-19th century. Seeds from those trees may have given rise to those recorded in Table 2.

In summary, the forest at NB66 shows little sign of impending change in species composition

and abundance, other than relatively short-term fluctuations in pine populations that will have little effect on longer-term community development. From the standpoint of community structure, the most significant transformation since 1966 has been the change in life form of hardwoods into normal tree stature, which were already present in 1966 from coppice. Of course, there have been secondary consequences of transformation, mainly the replacement of heliophytic herbs by hardwood leaf litter and lack of development of habitat that would attract recruitment of additional species from nearby forests. This observation is not necessarily an exclusive property of release from a fire trap. It seems to be a universal condition of secondary forests that developed on ex-arable lands in the Tallahassee Red Hills and elsewhere in the Southeast, wherever colonization by offsite species and mesophication prevail. Change in community structure but not species composition upon release from fire has been recorded elsewhere (Higgins et al. 2007) and is not unique to the Southeast.

Management Considerations

In this paper I have described the initial stages of escape of hardwoods from a fire trap. If NB66 continues to enjoy protection from fire and intentional disturbance, the site will provide added insights into fire trap processes. For that reason, consideration for maintaining NB66 as an experimental forest is germane. Table 1 was prepared to summarize the extent of the database as an aid for future investigators who consider conducting the next census. The comparison plot east of NB66 (Figure 1) must also be protected and burned frequently as an integral component of continuing investigations.

The indefinite direction of forest development is a matter of broader ecological concern. The long-term, documented history of NB66 makes it a candidate study site of global importance for investigation into dynamic processes in novel ecosystems. In particular, NB66 suggests that novel ecosystems may contain substantially less species diversity than original plant communities. The incapacity of NB66 to attract breeding birds may be a consequence of depressed levels of plant diversity. If lowered diversity is a general characteristic of novel ecosystems, then a global management strategy may be needed to introduce native species to augment biodiversity and ecological function.

The near absence of potentially alien species allows study of natural processes without the complication of invasive species. For that reason, I recommend the periodic and aggressive removal of alien species from NB66.

For purposes of ecological restoration, recovery of original vegetation is preferable to a novel ecosystem for several reasons offered by Clewell and Aronson (2013, p. 243–246). The appropriate ecological reference for upland restoration in the Tallahassee Red Hills would be SPOH or, if site conditions allowed, a longleaf pine savanna. If future fire management was unlikely, the target for restoration would be an oak-hickory forest dominated by hardwood species typical of SPOH woodland.

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APPENDIX 1. Vascular Plant Species Present at NB66 in 2010.

An asterisk (*) indicates species that were not recorded in 1966. Alien species, epiphytes, and offsite species are noted.

TREES

- Acer rubrum* L. offsite
Acer saccharum Marshall subsp. *floridanum* (Chapm.) Desmarais* offsite
Carpinus caroliniana Walter offsite
Carya glabra (Mill.) Sweet
Carya tomentosa Nutt.
Celtis occidentalis L.*
Cornus florida L.
Crataegus pulcherrima Ashe* offsite
Diospyros virginiana L. offsite
Fagus grandifolia Ehrh.* offsite
Fraxinus americana L.* offsite
Ilex opaca W.T.Aiton* offsite
Liquidambar styraciflua L. offsite
Magnolia grandiflora L.* offsite
Malus angustifolia (W.T.Aiton) Michx.
Morus rubra L.* offsite
Nyssa sylvatica Marshall
Osmanthus americanus (L.) Benth. & Hook. f. ex A.Gray* offsite

Ostrya virginiana (Mill.) K.Koch* offsite
Pinus echinata (Chapm. ex Engelm.) Vasey ex Sarg.
Pinus elliotii Engelm. offsite
Pinus palustris Mill.
Pinus taeda L. offsite
Prunus americanus Marshall* offsite
Prunus caroliniana (Mill.) Aiton* offsite
Prunus serotina Ehrh. offsite
Prunus umbellata Elliott
Quercus alba L.
Quercus falcata Michx.
Quercus hemisphaerica W.Bartram ex Willd.
Quercus laurifolia Michx.* offsite
Quercus michauxii Nutt.* offsite
Quercus nigra L. offsite
Quercus stellata Wangenh.
Quercus virginiana Mill. offsite
Sassafras albidum (Nutt.) Nees
Vaccinium arboreum Marshall

SHRUBS

Aralia spinosa L.* offsite
Callicarpa americana L.
Crataegus uniflora Münchh.
Elaeagnus pungens Thunb.* alien
Hypericum hypericoides (L.) Crantz
Ilex vomitoria Aiton*
Ligustrum sinense Lour.* alien
Myrica cerifera L.
Nandina domestica Thunb. alien
Rhus copallinum L.
Rubus cuneifolius Pursh
Rubus trivialis Michx.
Sebastiania fruticosa (W.Bartram) Fernald* offsite
Vaccinium elliotii Chapm.
Vaccinium stamineum L.
Viburnum rufidulum Raf.*

WOODY VINES

Ampelopsis arborea (L.) Koehne* offsite
Campsis radicans (L.) Seem. ex Bureau
Gelsemium sempervirens (L.) W.T.Aiton
Parthenocissus quinquefolia (L.) Planch.
Toxicodendron radicans (L.) Kuntze
Smilax bona-nox L.
Smilax glauca Walter
Smilax laurifolia L.* offsite
Smilax smallii Morong
Smilax tamnoides L.*
Vitis aestivalis Michx.
Vitis rotundifolia Michx.

GRASSES AND SEDGES

Andropogon virginicus L.
Chasmanthium sessiliflorum (Poir.) Yates*
Dichanthelium acuminatum (Sw.) Gould & C.A.Clark
Dichanthelium boscii (Poir.) Gould & C.A.Clark
Eragrostis hirsuta (Michx.) Nees
Gynopogon ambiguus (Michx.) Britton et al.
Oplismenus hirtellus (L.) P. Beauv.* offsite
Panicum anceps Michx.
Paspalum setaceum Michx.*
Rhynchospora harveyi Boott
Saccharum brevibarbe (Michx.) Pers. offsite
Scleria ciliata Michx.

Sorghastrum nutans (L.) Nash
Tridens flavus (L.) Hitchc.

FORBS

Acalypha gracilens A.Gray
Ageratina aromatica (L.) Spach
Ageratina jucunda (Greene) Clewell & Wooten
Aristolochia serpentaria L.*
Asplenium platyneuron (L.) Britton et al.*
Botrychium biternatum (Sav.) Underw.*
Chamaecrista fasciculata (Michx.) Greene
Cnidioscolus stimulosus (Michx.) Engelm. & A.Gray
Conoclinium coelestinum (L.) DC. offsite
Conyza canadensis (L.) Cronquist
Crotalaria spectabilis Roth alien
Desmodium floridanum Chapm.
Desmodium glabellum (Michx.) DC.*
Desmodium laevigatum (Nutt.) DC.
Desmodium lineatum DC.
Desmodium nudiflorum Muhl. ex Willd.*
Desmodium paniculatum (L.) DC.
Desmodium viridiflorum (L.) DC.
Dioscorea aff. *villosa* L.*
Elephantopus elatus Bertol. offsite
Erythrina herbacea L.
Eupatorium compositifolium Walter
Eupatorium hyssopifolium L.
Euphorbia pubentissima Michx.
Fleischmannia incarnata (Walter) R.M.King & H.Rob.
Galactia macreei M.A.Curtis
Galium hispidulum Michx.*
Gentiana villosa L.
Lespedeza procumbens Michx.
Lespedeza repens (L.) W.P.C.Barton
Lobelia puberula Nutt.
Lygodium japonicum (Thunb.) Sw.* alien
Matalea gonocarpus (Walter) Shinnners*
Mitchella repens L.*
Monotropa uniflora L.*
Physalis arenicola Kearney
Pleopeltis polypodioides (L.) E.G.Andrews & Windham epiphyte
Sanicula canadensis L.* offsite
Scutellaria lateriflora L.* offsite
Solidago odora Aiton
Symphyotrichum dumosum (L.) G.L.Nelson
Symphyotrichum lateriflorum (L.) A Löve & D. Löve*
Thelypteris dentata (Forssk.) E.P.St. John* offsite
Tillandsia usneoides (L.) L. epiphyte
Tragia urens L.
Trichostema dichotomum L.
Vernonia angustifolia Michx.
Yucca filamentosa L.

APPENDIX 2. Vascular Plant Species Recorded in Quadrats in the Comparison Plot in 2013.

Alien species are noted.

TREES

Diospyros virginiana L.
Liquidambar styraciflua L.
Malus angustifolia (Aiton) Michx.
Nyssa sylvatica Marshall

Pinus echinata Mill.
Pinus taeda L.
Prunus serotina Ehrh.
Quercus falcata Michx.
Quercus nigra L.
Quercus virginiana Mill.

SHRUBS

Callicarpa americana L.
Myrica cerifera L.
Rhus copallinum L.
Rubus cuneifolius Pursh
Toxicodendron vernix (L.) Kuntze
Vaccinium corymbosum L.

WOODY VINES

Campsis radicans (L.) Seem. ex Bureau
Gelsemium sempervirens (L.) W.T.Aiton
Smilax bona-nox L.
Smilax glauca Walter
Smilax rotundifolia L.
Smilax tamnoides L.
Vitis rotundifolia Michx.

GRASSES AND SEDGES

Andropogon virginicus L.
Aristida purpurascens Poir. var. *virgata* (Trin.) Allred
Cyperus ovatus Baldwin
Dichantherium aciculare (Desv. ex Poir.) Gould & C.A. Clark
Dichantherium boscii (Poir.) Gould & C.A. Clark
Dichantherium ovale (Elliott) Gould & C.A. Clark
Dichantherium ravenellii (Scribn. & Merr.) Gould
Digitaria serotina (Walter) Michx.
Eragrostis spectabilis (Pursh) Steud.
Gymnopogon ambiguus (Michx.) Britton et al.
Hackelochloa granularis (L.) Kuntze alien
Heteropogon melanocarpus (Elliott) Elliott ex Benth. alien
Panicum anceps Michx.
Paspalum notatum Flugge alien
Paspalum setaceum Michx.
Rhynchospora harveyi Boott
Rhynchospora grayii Kunth
Saccharum brevibarbe (Michx.) Pers. var. *contortum* (Baldwin ex Elliott) R.D. Webster
Schizachyrium tenerum Nees
Scleria ciliata Michx.
Setaria parviflora (Poir.) Kerguelen
Sorghastrum nutans (L.) Nash
Tridens flavus (L.) Hitchc.

FORBS

Acalypha gracilens A.Gray
Agalinis fasciculata (Elliott) Raf.

Ambrosia artemisiifolia L.
Centrocema virginianum (L.) Benth.
Chamaecrista fasciculata (Michx.) Greene
Chamaesyce hyssopifolia (L.) Small
Chrysopsis mariana (L.) Elliott
Conoclinium coelestinum (L.) DC.
Crotalaria rotundifolia J.F. Gmel.
Crotalaria spectabilis Roth alien
Desmodium ciliare (Muhl. ex Willd.) DC.
Desmodium floridanum Chapm.
Desmodium laevigatum (Nutt.) DC.
Desmodium lineatum DC.
Desmodium obtusum (Muhl. ex Willd.) DC.
Desmodium paniculatum (L.) DC.
Desmodium viridiflorum (L.) DC.
Diodea teres Walter
Dyschoriste oblongifolia (Michx.) Kuntze
Elephantopus elatus Bertol.
Erigeron strigosus Michx. ex Willd.
Eupatorium hyssopifolium L.
Galactia microphyllum (Chapm.) D.W. Hall & D.B. Ward ex Isely
Galium pilosum Aiton
Gentiana villosa L.
Habenaria quinqueseta (Michx.) Eaton
Helianthus angustifolius L.
Helianthus hirsutus Raf.
Hieracium gronovii L.
Houstonia procumbens (J.F. Gmel.) Standl.
Lactuca canadensis L.
Lespedeza angustifolia (Pursh) Ell.
Lespedeza cuneata (Dum. Cours.) G. Don alien
Lespedeza procumbens Michx.
Lespedeza repens (L.) W.P.C. Barton
Lespedeza virginica (L.) Britton
Liatris spicata (L.) Willd.
Monarda punctata L.
Passiflora incarnata L.
Phyllanthus urinaria L. alien
Physalis heterophylla Nees
Pityopsis graminifolia (Michx.) Nutt.
Pseudognaphalium obtusifolium (L.) Hilliard & B.L.Burt
Rhynchosia tomentosa (L.) Hook. & Arn.
Solidago canadensis L.
Solidago odora Aiton
Sericocarpus asteroides (L.) Britton et al.
Strophostyles umbellata (Muhl. ex Willd.) Britton
Symphotrichum dumosum (L.) G.L.Nelson
Tephrosia spicata (Walter) Torr. & A.Gray
Tragia smallii Shimmers
Trichostema dichotomum L.
Viola sp.