Elliottia racemosa, Georgia plume

2019

Abstract

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Figure 1—Georgia plume in flower. James Henderson, Golden Delight Honey, Bugwood.org.

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ABSTRACT

Georgia plume is a rare, state-threatened, small tree or shrub native to Georgia. It is most common on sandy ridges and sandhill bluffs. It grows in oak-pine and longleaf pine woodlands and mixed bottomland and riparian forests. It reproduces by cloning; reproduction from seed has never been observed in the wild. Obstacles to sexual reproduction include lack of successful pollination in small populations with low genetic diversity and low rates of seed germination and seedling establishment.

Georgia plume is apparently a fire-adapted species, but information on its postfire response is very limited. It sprouts after top-kill by fire, and exposure to charate may improve germination of its seeds. The oak-pine and longleaf pine woodlands in which it grows historically experienced surface fires at frequent intervals (<10 years). Limited information suggests that prescribed fire may promote sprouting in Georgia plume, and prescribed fire, selective thinning, and/or reducing surrounding vegetation are recommended to protect and promote Georgia plume populations. However, given the limited knowledge of Georgia plume's postfire response, managers are cautioned to closely monitor Georgia plume's postfire response and modify future burn plans as needed. Clearcutting or heavy logging may reduce populations if dense growth of associated shrubs follows these treatments.

INTRODUCTION

TAXONOMY
The scientific name of Georgia plume is *Elliottia racemosa* Muhl. ex Ell. It is in the heath family (Ericaceae) [11, 12, 24, 30, 57]. There are only two North American species in the *Elliottia* genus: Georgia plume and copperbush. Their distributions do not overlap: copperbush is native to Alaska and the Pacific Northwest [57].

See table A1 for a complete list of common and scientific names of plant species discussed in this Species Review and links to other FEIS Species Reviews.

SYNONYMS
None

LIFE FORM
Tree-shrub

DISTRIBUTION AND PLANT COMMUNITIES

GENERAL DISTRIBUTION

Georgia plume is endemic to the coastal plain and Piedmont regions of south-central and eastern Georgia [9, 11, 23] (fig. 2), where it occurs in fragmented, declining populations [9, 30, 42]. Georgia plume once occurred in South Carolina [6]; however, those plants may have been cultivated (Bozeman 1999, Georgia Department of Natural Resources, personal communication cited in [17]). Georgia plume is hardy as far north as New England [12], and it has been planted in the Northeast as an ornamental [9].

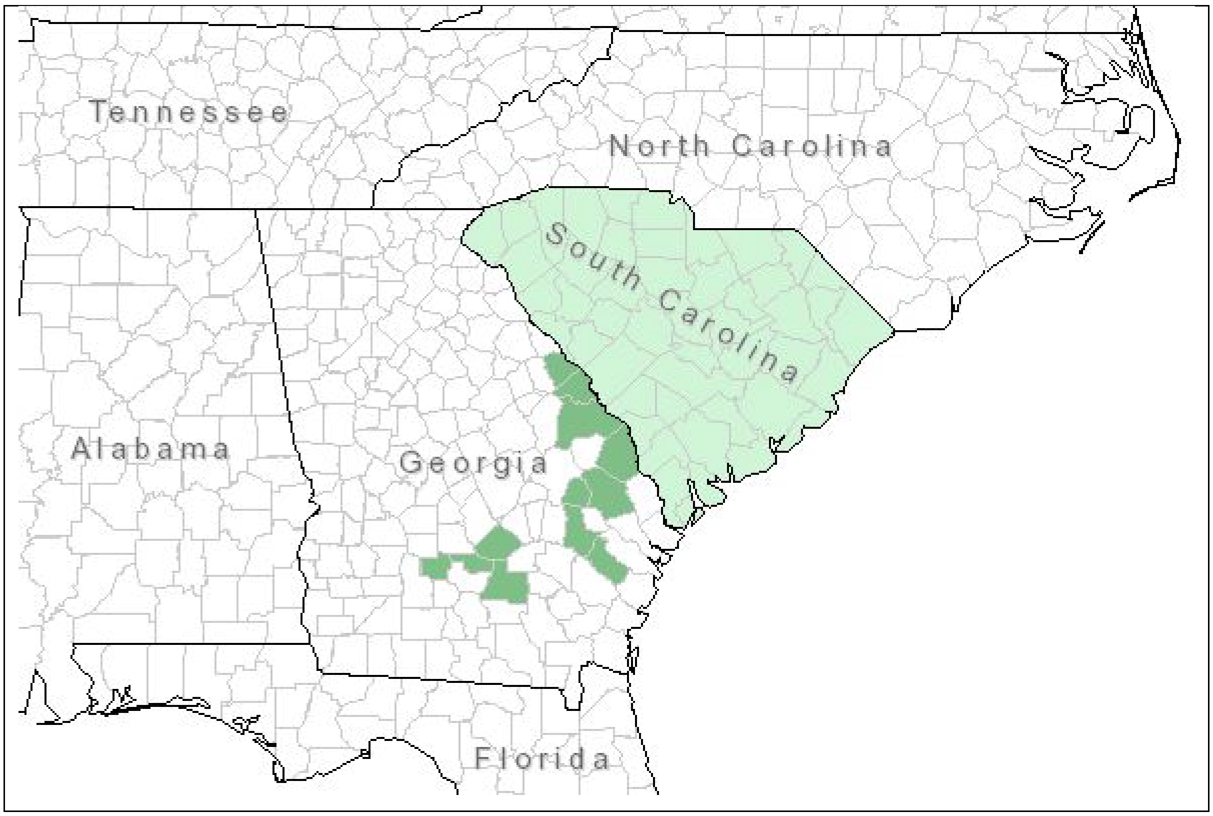

Figure 2—Approximate distribution of Georgia plume. Map courtesy of Natural Resources Conservation Service, U.S. Department of Agriculture [57].

In the late 1980s, there were about 70 Georgia plume populations [9] As of 2010, about half those populations had "winked out" (i.e., apparently no longer existed) [22] ; there were <24 populations across 16 counties [40, 42]. Only 16 of 28 putative populations surveyed still contained Georgia plume plants [40, 42]. These populations ranged from 0.02 to 2,553 acres (0.01-1,033 ha) in size, with 13 of these <2.5 acres (1 ha). Most populations (75%) had <45 individuals, and >33% had ≤12 individuals [40]. Populations are most frequent along the Altamaha, Ogeechee, Savannah, and Canoochee river drainages [9, 12]; most of these occupy <0.7 acre (0.3 ha) [40]. The largest population is in the Big Hammock Natural Area, Tattnall County [9, 40, 42]. It contains >1,000 genetically distinct individuals (i.e., different clones) [42]. The Georgia Department of Natural Resources provides a map where extant populations occur and possibly extirpated populations (searched for but not relocated for 5 to >20 years) once occurred.

States**:**
GA [57]

SITE CHARACTERISTICS

Georgia plume typically grows at low elevations in well-drained soils. It occurs on dry sandstone bluffs and outcrops [11, 17, 22, 26, 37, 59], sandy ridges [17, 21, 26], hammocks [17, 21], and in mesic bottomlands [22, 42]. Georgia plume occurs up to about 390 feet (120 m) elevation [11]. It grows on talus slopes [10], Altamaha grit outcrops [14, 26], and ultramafic [14] (i.e., serpentine [10, 23]) soils. Soils supporting Georgia plume range from moist [11, 12, 37] to xeric [12, 37], but Georgia plume is most common in moist soils [10, 25] that are usually sands [25]. It is unusual on sites with high water tables. However, in Turner County, a population growing in poorly-drained, loamy sand that was occasionally flooded in winter and spring appeared "more vigorous" than a nearby population growing in deep, excessively drained sand [52]. Soil pH on sites supporting Georgia plume ranges from extremely acidic to strongly acidic (pH 3.5-5.2) [10, 22].

Several soil variables are associated with Georgia plume. In a habitat suitability study in the Big Hammock Natural Area, Georgia plume presence was positively associated with soil moisture, base saturation, cation exchange capacity, soil acidity, lime buffering capacity, and available soil iron and nickel ($P \leq 0.06$). Georgia plume presence also was positively associated with proximity to the Altamaha River ($P < 0.05$). Its presence was not significantly associated with degree of slope, aspect, elevation, soil organic matter, plant community composition, or overstory dominants; and it was negatively associated with available soil lead ($P \leq 0.06$) [22].

PLANT COMMUNITIES

Georgia plume grows in cabbage palmetto [42] and oak [10, 25, 35, 59] scrub; oak-pine [10, 25, 31, 42] woodlands; loblolly pine [21, 31] and longleaf pine [10, 21, 25, 26, 31, 35] woodlands and forests; longleaf pine woodland-bay swamp ecotones [3]; and mixed coniferous-deciduous bottomland [22, 42] and riparian [31, 52] forests. Typically, it is an ecotone species on sites transitioning from longleaf-scrub oak sandhill communities to more mesic coniferous-deciduous forests [26]. In woodland and forest understories, it often grows in association with cabbage palmetto (fig. 3) and farkleberry [22, 31, 59]. On sandstone outcrops, it grows in oak scrub and longleaf pine woodlands [59]. In Bulloch County, Georgia plume grows on sandy ridges vegetated with turkey oak-sand post oak scrub [19]. In the Big Hammock Natural Area, it grows in xeric turkey oak-myrtle oak scrub and Darlington oak-southern live oak hammocks [22]. NatureServe (2013, 2019) recognizes two associations with Georgia plume that occur on high, xeric dunes above rivers in eastern Georgia: longleaf pine-turkey oak coastal plain woodland [34] and myrtle oak-sand live oak-American witchhazel-Georgia plume shrubland [35].

Figure 3—A mixed bottomland coastal plain forest. The yellow arrows point to Georgia plume, the red arrow to cabbage palmetto. Image by Karan A. Rawlins, University of Georgia, Bugwood.org.

BOTANICAL AND ECOLOGICAL CHARACTERISTICS

GENERAL BOTANICAL CHARACTERISTICS

Botanical Description

This description covers characteristics that may be relevant to fire ecology and is not meant for identification. Identification keys are available online [12, 58].

Georgia plume is a deciduous small tree or shrub, typically 10 to 16 feet (3-5 m) tall [12] and <12 inches (30 cm) DBH [22]. Some individuals reach 35 feet (11 m) tall [22, 60] and 12 inches (30 cm) in diameter [9]. The trunk is usually single, although multiple trunks may grow after fire or other top-killing disturbances [14, 22, 37]. Bark is thin. Leaves are alternate and sometimes have soft trichomes or hairs underneath [14, 37]. The inflorescence is a 40- to 80-flowered raceme [12, 25]. The petals are not fused (fig. 4), making Georgia plume a more "primitive" member of the heath family than genera with fused petals [9] (e.g., *Gaylussacia* and *Vaccinium* spp.).

Figure 4—A Georgia plume raceme. Creative Commons image by Jason Hollinger.

The fruit is a small, winged [17, 47, 60], four- to five-parted capsule, 0.3 to 0.5 inch (7-12 mm) long [11, 12]. The seeds are very small, from 0.08 to 0.1 inch (2.0-2.5 mm) across. There are about 40 to 100 seeds/capsule. Roots are described as “shallow” [25], although depths to which Georgia plume roots grow in the soil were not reported as of 2019.

Stand Structure: Surveys across Georgia plume’s distribution found Georgia plume usually grows in tree form, but it grows in shrubby thickets on burned sites [42]. Georgia plume produces root sprouts (see Regeneration Processes). After a top-killing disturbance, it tends to form thickets due to clonal growth [25, 40]. Kruse (2019, Georgia Department of Natural Resources) observed a Georgia plume stand near the top of a sandridge in the Big Hammock Natural Area that had stems of approximately the same height. Presumably, this same height/age structure was due to sprouting after a wildfire in the 1980s [26].

Figure 5—Georgia plume root crowns and roots. Image by John Ruter, University of Georgia, Bugwood.org.

Raunkiaer Life Form
Phanerophyte
Geophyte [49]

SEASONAL DEVELOPMENT

Georgia plume flowers from June to August in Georgia [6, 9, 12, 14, 25], with sporadic flowering into September [37]. Heaviest flowering is in July [25]. Flowering occurs progressively later in northern locations where it is cultivated [9]. Individual plants flower for about 3 weeks [22]. Individual racemes flower for about 10 days, with flowers opening sequentially up the racemes. Individual flowers remain open for about 2 days before they abscise their petals [47]. Georgia plume is protandrous: it sheds pollen before the ovules are mature [47]. Flowers are receptive to pollen only when they are fully open and petals are either abscising or already abscised [43, 44], and the period of pollen viability is "extremely short" [42]. If fruits develop (see Seed Production), they generally mature in late summer [37]; some fruiting may continue into December [1, 37]. If seeds develop, they disperse in fall [47].

Figure 6—Fall foliage of Georgia plume. Image by John Ruter, University of Georgia, Bugwood.org.

REGENERATION PROCESSES

Georgia plume reproduces by cloning [17, 47]. Seeds rarely survive to the ripening stage. Since 1773, when Georgia plume was first documented as a new species, no surveys have detected either ripe seeds [9] or seedlings [17, 44] in the wild. A 2007 flora reported that of nine populations occurring on public or private conservation lands, none was producing seedlings [6]. In 1876, a botanist asked a question about Georgia plume that still remains relevant: "What is the cause of the sterility, and the change of condition since the period when it must have been propagated by seed?" [50].

Vegetative Regeneration

Georgia plume spreads clonally from root sprouts [12, 17, 19, 52], with or without disturbance [21], and it sprouts from the roots after disturbances that damage or top-kill aboveground tissues [9] (see Plant Response to Fire). A survey in Turner County noted Georgia plume root sprouts on sites disturbed by logging [52]. Surveys across Georgia plume's distribution found root sprouts in 7 of 16 populations, with 3 populations growing only in the thicket form that develops after root sprouting [40]. Field observations indicate that ability to sprout is not strongly tied to stem size or age. Hodges (2019, The Nature Conservancy) observed that some old plants sprout after disturbance, with "no relationship between age class and resprouting" [21].

Pollination and Breeding System

Pollination and breeding system of Georgia plume are not well understood, and studies to better understand both were ongoing as of 2019. Many populations are composed of a few, inbred clones, so their genetic diversity is likely low [9].

Flowering is not limiting in most populations. Prolific flowering is reported among and across populations, with 21 of 28 populations surveyed in the late 2000s containing flowering plants [42]. However, pollination failure is common. Pollen viability was low to moderate in four wild populations [44, 45, 47], ranging from 25% to 42% [45]. Population sizes were not provided. In small populations, low viability may be due to inbreeding [53].

Based on infertility of small, clonal populations [9, 17] and results of pollination experiments, Georgia plume is apparently self-incompatible and requires cross-pollination [17, 43, 48]. A protandrous mating system tends to promote cross-fertilization [47]. Large populations consisting of more than one clone have better chances of cross-pollination than small populations consisting of a single or few clones [5, 9, 14]. Small or isolated Georgia plume populations may cross-breed with closely related individuals, resulting in low genetic diversity [47].

It is unclear whether Georgia plume requires insects or other animals for cross-pollination. Butterflies [31] and various Hymenoptera species [52], including ants (fig. 4) and bees [60], visit Georgia plume flowers. In 1902, Harper noted that that the flowers "were frequented by a large number of insects…One would suppose that this would ensure fertilization, but apparently it does not, for no fruit of *Elliottia racemosa* has yet been seen". He proposed extinction of a past pollinator as possible cause of pollination failure [19], although other causes have also been proposed (see Other Management Considerations). Successful hand-pollination of flowers in the laboratory led Radcliff (2009) to speculate that failure of insect-mediated pollination may partially explain poor Georgia plume regeneration in the wild [47].

Seed Production

Although flowering may be abundant, Georgia plume's seed set is low to nonexistent [17, 22, 44]. Field observations show that the smaller the population, the less likely it is to produce seeds (Bozeman 1987, Georgia Department of Natural Resources, personal communication cited in [9]). Seed set was observed in a large population on 400 acres (160 ha) in the Big Hammock Natural Area [31], although seed viability was not tested.

Genetic studies found that small Georgia plume populations consist of just one to a few distinct genotypes, suggesting that the number of genetically distinct individuals is low [17, 18, 42]. Low genetic variability may contribute to lack of sexual (seed) reproduction in the wild [17, 41]. A 1999 study found low genetic diversity within and among 10 Georgia plume populations. Most genetic variation (82%) occurred within populations. Populations with the lowest genetic variability had the lowest seed set [17].

Seed Dispersal

Since seeds are rarely produced in the wild, no information was available on patterns of seed dispersal. When seeds are produced, the seed wings may aid in dispersing seeds away from the parent plant.

Seed Banking

No information was available on this topic. A germination study [1] suggests that historically, Georgia plume may have stored seeds in the soil (see Postfire Seedling Establishment).

Germination

Germination requirements of Georgia plume were not well known as of 2019. In a greenhouse study, seeds collected in the wild and from plants cultivated in an arboretum had low viability [13]. However, some seeds collected in the wild and grown in a greenhouse have produced seedlings [14], suggesting that environmental factors, as well as pollination failure, may limit reproduction from seeds [5, 14].

Researchers speculate that fresh seeds are dormant [1, 13], although the mechanism of dormancy is unknown [13]. Fordham (1969) suggests that seeds may enter secondary dormancy if they do not germinate the spring after dispersal [13]. A laboratory study found fresh seeds had very low germination rate, while cold-stratified seed had relatively high germination rates (table 1) [9].

Table 1—Germination of Georgia plume seeds in the laboratory [9].

Seed lot (90 seeds/lot)	Days of cold stratification	Days to 1st germination	Number of seeds germinated	% germination
1	0	56	1	1
2	42	19	64	71
3	66	21	66	73
4	64	21	74	82

Chafin [5] stated that "the absence of fire likely limits reproduction in some ways not yet discovered". A laboratory study suggests that charate may increase germination rates [1] (see Postfire Seedling Establishment). Seeds that disseminate the first growing season after fire are likely exposed to charate solution as rain washes through the soil. Exposure to charate solution, coupled with low winter temperatures (i.e., overwinter stratification), may break seed dormancy [1], although this had not been tested as of 2019.

Seedling Establishment and Plant Growth

Mycorrhizae may be needed for seedling development [9, 31]. Laboratory-germinated Georgia plume seeds only established when mycorrhizae from the parent plant were incorporated in the potting mix [9].

Diameter growth of Georgia plume trees is reportedly slow, with boles rarely exceeding 0.04 inch (1 mm) expansion in radius per year [31]. However, growth of root sprouts after a top-killing disturbance can be rapid (see Postfire Sprouting).

SUCCESSIONAL STATUS

Georgia plume tolerates both open and shady sites [14, 40, 42]. Surveys across Georgia plume's distribution found it was most common in understories. Of 16 populations, 2 grew in the overstory, 12 in the understory, and 2 in both [40]. Canopies of plant communities with Georgia plume were mostly open to partially closed, with only two Georgia plume populations observed under closed canopies [42]. However, in the Big Hammock Natural Area, presence of Georgia plume was not significantly associated with the degree of canopy openness [22].

Georgia plume growth and cover may increase after disturbances that open or remove the canopy. Fire or light thinning may promote Georgia plume. Carlile (2019, Fort Stewart Military Reservation) observed that loblolly bay and other shade-tolerant species tend to replace Georgia plume successionally in the absence of fire or other top-killing disturbances [3]. However, heavy logging may reduce Georgia plume cover. Dense growth of other shrubs after clearcutting or heavy thinning has apparently excluded Georgia plume from many sites [35, 55], and heavy logging is cited as a cause of declining populations (see Other Management Considerations).

FIRE EFFECTS AND MANAGEMENT

FIRE EFFECTS

Immediate Fire Effects on Plant

Fire top-kills Georgia plume [1, 9, 14, 25, 31, 38]. Effects to Georgia plume by fire severity or intensity were unstudied as of 2019. The Georgia Department of Natural Resources (2013 fact sheet) suggests that young plants survive low-intensity fire, and that old plants are unlikely to survive intense or "hot" fire [14]. However, relationships between stem age, stem size, and sprouting have not been established. Old plants may sprout when young ones do not (Hodges 2019, personal communication [21]).

Postfire Regeneration Strategy

Tree with root sprouts
Shrub with root sprouts [54]

FIRE ADAPTATIONS AND PLANT RESPONSE TO FIRE

Postfire Sprouting: Georgia plume sprouts from the roots after damage or top-kill by fire [1, 4, 9, 14, 25, 31, 42, 48]. Multiple sprouts form thickets on burns [26, 42]. Given Georgia plume's failure to reproduce from seeds, Miller (1978) stated that postfire sprouting explains why Georgia plume "is still here today" [31]. Flowering may occur in postfire year 1 or 2, with flowering in postfire year 2 more common. Radcliff (2019, Atlanta Botanical Garden, personal communication) stated that postfire sprouts usually require time to grow before they can flower [48]. Managers have observed "vigorous" sprouting in postfire year 1, with flowering in postfire year 2 [21, 48]. Averett and Affolter (2002) suggested that new shoots may flower and produce seeds in the first postfire growing season [1], although they did not provide data. Carlile (1997, Fort Stewart Military Reservation, personal observation cited in [3]) observed Georgia plume sprouts flowering the first growing season after a prescribed fire in a longleaf pine woodland on the Fort Stewart Military Reservation.

In an unpublished case study of three populations (two burned, one unburned), early spring prescribed fire in a longleaf pine woodland on the Fort Stewart Military Reservation increased stem production in two populations of Georgia plume, but decreased maximum stem height for at least 1 year after the fire. The unburned population showed no change in stem production or maximum stem height (table 2). For the unburned population, tall stems (3-10 feet (1-3 m)) were the most frequent height class in both pre- and postfire years. For burned populations, stems were taller before than after fire; in postfire year 1, stems in <6-inch (15-cm) height classes were most frequent. The unburned population had more total racemes and more fruiting racemes after than before fire. For burned populations, the mean number of racemes was significantly less after fire than before fire in one population, but not in the other. The number of fruiting racemes was similar before and after fire in both burned populations. Seed production—or its absence—was not noted, but fruit production was negligible in the burned populations and extremely low in the unburned population. Prescribed burning was conducted when air temperatures were low (40 °F (4 °C)), relative humidity was moderate (50%), and winds were light from the north. Comparisons of burned plots and unburned control plots are shown in table 2 (plot size: 2 x 42 m, *n* = 42 plots) [38]. After another early spring fire in Fort Stewart Military Reservation, Georgia plume was observed flowering through late December of postfire year 1. Some sprouts were as tall as 10 feet (3 m) by then (Carlile 1997, Fort Stewart Military Reservation, personal observation cited in [3]).

Table 2—Overstory canopy cover, and growth and regeneration of two burned Georgia plume populations and an unburned control population, before and after an early spring prescribed fire. The study was conducted in a longleaf pine/pineland threeawn woodland on the Fort Stewart Military Reservation, Georgia. Data are means. Statistical comparisons (*P* values) are between pre- and postfire years within populations [38].			
	Prefire (2002)	Postfire year 1 (2003)	*P* value
--Overstory canopy cover (%)--			
Burned population 1	90.41	89.66	0.60
Burned population 2	95.94	94.54	0.40
Unburned population	92.78	94.32	0.30
--Stems/plant---			
Burned population 1	5.27	7.10	<0.001
Burned population 2	2.23	4.73	<0.001
Unburned population	2.40	2.41	0.91
--Height (m) of tallest stem/plant--			
Burned population 1	0.595	0.463	<0.001
Burned population 2	0.83	0.59	<0.001
Unburned population	1.02	1.08	0.25
---Total # of stems--			
Burned populations 1 & 2	2,690	4,272	<0.001
Unburned population	392	393	*P* value not provided
---Stem survival and regeneration--			
Burned populations 1 & 2[b]			
Stem mortality (%)	NA[a]	91.2	NA
Stem survival (%)	NA	8.8	NA
Stem increase (%)	not provided	63.0	NA
New stems (%)	NA	94.4	NA
---# of plants killed--			
Burned population 1	NA	4	NA
Burned population 2	NA	15	NA
Unburned population	NA	0	NA
---Flower and fruit abundance---			
Burned population 1			
# of racemes	0.147	0.241	0.4
# of fruits	0.0028	0.0582	0.34
# of fruiting racemes	0.0027	0.0277	0.37

Burned population 2			
# of racemes	2.22	0.22	<0.001
# of fruits	0	0.005	0.32
# of fruiting racemes	0	0.003	0.32
Unburned population			
# of racemes	7.87	16.42	<0.001
# of fruits	1.99	1.50	0.52
# of fruiting racemes	0.45	1.15	0.01
---# of new plants[c]--			
Burned population 1	NA	23	NA
Burned population 2	NA	4	NA
Unburned population	NA	4	NA
[a]Not applicable. [b]Data not available for unburned population. [c]Stems >6 inches (15 cm) away from another stem were considered separate individuals.			

Postfire Seedling Establishment: Enhanced germination of Georgia plume seeds using charate suggests that Georgia plume might have historically stored seed in the soil, and that fire may promote germination of Georgia plume seeds. A laboratory study found seed lots collected from a large population near Glenville had higher germination rates when watered with a charate solution (44.0%) than with a control solution of distilled water (22.7%) ($P = 0.06$). A fungal infection killed many seeds in both the charate and control seed lots. When fungal-killed seeds were excluded from the analysis, germination rates were 70.6% with the charate solution and 41.7% with the control solution ($P = 0.003$) [1].

No information was found in English-language literature on fire effects to and postfire growth responses of the other species in the *Elliotia* genus: copperbush, bract-bearing elliotia, and panicle-flowered elliotia. The latter two species are native to Japan [32, 36].

FUELS AND FIRE REGIMES

Fuels

Where Georgia plume grows in productive plant communities (e.g., longleaf pine and bottomland forests), fuels accumulate quickly in both the canopy and on the surface (e.g., [8, 20, 61]). In populations across Georgia plume's distribution, most soil cover (75%) consisted of groundlayer vegetation; bare ground was uncommon. Duff thickness ranged from 0 to 2 inches (0-5 cm) on 15 of 16 sites with Georgia plume; duff thickness on the other site ranged from 2 to 12 inches (5-30 cm) [42]. NatureServe (2013) reports that fuel accumulation is slow in longleaf pine associations on the xeric river dunes where Georgia plume sometimes grows [34].

Information on flammability of Georgia plume was not found in the literature.

Fire Regimes

Georgia plume occurs in fire-adapted ecosystems [5, 33]. In 2009 surveys, 6 of 16 populations, or one-third, occurred on sites showing evidence of recent fire (charred tree bark or char in litter and soil) [42]. The six populations were growing on sandhills, sandstone outcrops, flatwoods, and mixed bottomland forests [40]. Sites supporting a large population in the Big Hammock Natural Area have a history of selective logging of pines and hardwoods and of "frequent wildfire". The author concluded that "Possibly Elliottia's occurrence on these sites is due to its ability to sprout more readily following fire than its associates" [31]. Historically, frequent fire likely maintained an open canopy on sites with Georgia plume, promoting flowering and reducing litter around Georgia plume stems. Kruse (2019, The Nature Conservancy) observed that Georgia plume trunks tend to decay if moist litter builds up around them [14].

Historically, oak-pine and longleaf pine woodlands experienced frequent surface fires at mean intervals of ≤10 years (e.g., [2, 34, 39, 51]). LANDFIRE modeled mean fire intervals of 7 years for Atlantic coastal oak-pine communities [28] and of 4 years for longleaf pine communities [29]. Fire in longleaf pine associations on xeric river dunes may have historically been less frequent than in longleaf pine associations on more mesic sites, which have heavier fuel loads [34]. Bozeman (1978, U.S. Department of the Interior, Fish and Wildlife Service, personal communication cited in [59]) stated that myrtle oak-Chapman oak scrub communities transitioning to oak-pine forests had historical fire intervals of 30 to 40 years. A habitat suitability model for Georgia plume predicted that oak, pine, and forested wetlands with short (6-25 years) to moderate (26-45 years) return intervals were most favorable for Georgia plume. Results were based on fire history and other site data collected from 16 Georgia plume populations [42].

Some mixed coniferous-deciduous bottomland and riparian forests had longer fire intervals and more mixed-severity fires than pine and oak-pine woodlands [27]. However, information is lacking on how often Georgia plume historically occurred in closed-canopy bottomland and riparian forests. Since it is most common on sites with open to partially closed canopies [40] , it is likely that Georgia plume was most common in bottomland and riparian forests in which fire and/or other disturbances were frequent enough to prevent canopy closure.

See these FEIS publications for further information on historical fire regimes in plant communities in which Georgia plume occurs:

- Fire regimes of Gulf and Atlantic coastal oak-pine communities
- Fire regimes of longleaf pine communities

FIRE MANAGEMENT CONSIDERATIONS

Georgia plume has been called a "fire-adapted species" [33]. Because it evolved in plant communities (e.g., oak-pine and longleaf pine) that experienced frequent, low-intensity fires [1, 5] and has a strong postfire sprouting response, fire exclusion has been suggested as one factor in the decline of Georgia plume populations [14, 22]. Some researchers speculate that frequent fire is necessary for Georgia plume recruitment and long-term maintenance [5, 33], and that on many sites, disruption of the historical fire regime might have resulted in seed germination failure of Georgia plume [1, 6].

As of 2019, there was only one study [38] with data on the effects of prescribed fire on Georgia plume (see Postfire Sprouting). Prescribed fire may benefit Georgia plume by reducing surrounding vegetation, promoting sprouting and possibly, promoting seedling recruitment [37, 41]. Averett and Affolter (2002) suggest that "controlled burns may be a useful technique for enhancing seedling recruitment in natural populations" [1]. Prescribed fire did not increase fruit production of Georgia plume in the only fire study available [38]; however, Georgia plume's postfire response was only monitored for 1 year, and flowering is more likely in later postfire years [21, 48]. Closely monitoring Georgia plume's postfire response [6, 14] and modifying future burn plans as needed [14] are recommended if prescribed burning is conducted. Porter (2010) recommends keeping severity of prescribed fires low around Georgia plume plants [42]. Similarly, the Georgia Department of Natural Resources (2007 and 2013 fact sheets) recommends low-intensity prescribed fires to promote Georgia plume growth [5, 14]. They recommend application of winter prescribed fire for old plants, which may be more sensitive to fire damage than young plants [5, 14]. However, some large or old plants sprout after top-kill (Hodges 2019, personal observation) [21], and further studies are needed on the relationship between stem age and/or size and the ability of Georgia plume to sprout. Glitzen et al. (2003) suggest that in longleaf pine woodlands, prescribed surface fire every 4 years may be a good interval for conservation of Georgia plume and other rare shrubs [16]. Further recommendations on using prescribed fire to protect and promote Georgia plume were not available as of 2019.

MANAGEMENT CONSIDERATIONS

FEDERAL LEGAL STATUS

None [56]

OTHER STATUS

State of Georgia: Threatened (S2-S3) [14]
Georgia Plant Conservation Alliance: Priority Concern [15]
NatureServe: Imperiled (G2) [35]

IMPORTANCE TO WILDLIFE AND LIVESTOCK

Insects visit Georgia plume flowers [31, 52, 60]. There was no further information on wildlife or livestock use of Georgia plume as food or cover.

VALUE FOR RESTORATION OF DISTURBED SITES

Georgia plume is difficult to propagate [9, 13, 47] and does not transplant well [9, 13], so it is not used for restoration. Outplanting conducted in the early 2000s was not successful (Krus 2010, Georgia Department of Natural Resources, personal communication cited in [22]). Failure of most nursery-grown plants to establish may be due to failure to establish mycorrhizal associations [31]. Procedures for tissue culture propagation of Georgia plume have been successfully developed, with the goal of safeguarding, augmenting, and reintroducing populations [46, 47, 48]. Tissue-cultured plants moved to the Atlanta Botanical Garden were still growing as of 2019 (Radcliff 2019, Atlanta Botanical Garden, personal communication) [48].

OTHER USES

Georgia plume is cultivated as an ornamental, although it is difficult to grow and prone to fungal diseases [12].

OTHER MANAGEMENT CONSIDERATIONS

Suggested causes for Georgia plume's decline include fire exclusion [14, 22]; clearing for agriculture [7, 35, 37, 40, 41, 42] and forestry [37, 40, 41, 42]; urbanization [41]; and failure of insect-mediated pollination in the wild [19, 47]. Losses to agricultural clearing were noted by the late 1800s [55] and to timber by the 1920s [55], although such losses were likely incurred earlier. Surveys in 2009 found that for Georgia plume populations that have winked out since the 1980s, 58% of losses were due to human activity [40, 41, 42].

Safeguarding existing populations [14, 40], in vitro propagation, artificial (anthropogenic) cross-pollination in the field [47], overcoming obstacles to sexual reproduction [14, 40], and reintroductions on sites where populations have disappeared [40] are recommended for Georgia plume conservation. Besides prescribed fire, selective thinning [14, 37], reducing surrounding understory vegetation [6, 14], and protecting sites with Georgia plume from clearcutting [6, 14] are recommended to protect and promote Georgia plume. Clearcutting or heavy logging may be detrimental to Georgia plume populations [35].

Although deliberate genetic manipulation of rare and endangered populations is controversial, Godt and Hamrick (1999) suggest that artificial cross-pollination among Georgia plume populations may be warranted in order to increase genetic diversity in populations with low genetic diversity [17].

APPENDIX

Table A1: Common and scientific names of plant species mentioned in this Species Review. Links go to other FEIS Species Reviews.

Common name	Scientific name
--Trees--	
American witchhazel	*Hamamelis virginiana*
bay	*Gordonia, Magnolia, Persea* spp.
Darlington oak	*Quercus hemisphaerica*
Georgia plume	*Elliottia racemosa*, this review
huckleberries	*Gaylussacia*, *Vaccinium* spp.
loblolly bay	*Gordonia lasianthus*
loblolly pine	*Pinus taeda*
longleaf pine	*Pinus palustris*
oak	*Quercus* spp.
pine	*Pinus* spp.
turkey oak	*Quercus laevis*
southern live oak	*Quercus virginiana*
--Shrubs--	
bract-bearing elliotia	*Elliotia bracteata*
cabbage palmetto	*Sabal palmetto*
Chapman oak	*Quercus chapmanii*
copperbush	*Elliottia pyroliflora*
farkleberry	*Vaccinium arboreum*
myrtle oak	*Quercus myrtifolia*
panicle-flowered elliotia	*Elliottia paniculata*
sand post oak	*Quercus margaretta*
--Grasses--	
pineland threeawn	*Aristida stricta*

REFERENCES

1. Avertt, Jack M.; Affolter, James M. 2002. Charred wood treatments simulate germination of Georgia plume seeds (Georgia). Ecological Restoration. 20(1): 69-70. [93304]

2. Bailey, Andrew D.; Mickler, Robert; Frost, Cecil. 2007. Presettlement fire regime and vegetation mapping in southeastern coastal plain forest ecosystems. In: Butler, Bret W.; Cook, Wayne, comps. The fire environment--Innovations, management, and policy; conference proceedings; 2007 March 26-30; Destin, FL. Proceedings RMRS-P-46CD. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 275-286. [71106]

3. Carlile, Lawrence D. 1997. Fire effects on threatened and endangered species and habitats of Fort Stewart Military Reservation, Georgia. In: Greenlee, Jason M., ed. Proceedings: First conference on fire effects on rare and endangered species and habitats; 1995 November 13-16; Coeur d'Alene, ID. Fairfield, WA: International Association of Wildland Fire: 227-231. [52064]

4. Carlile, Lawrence D. 2019. Personal communication [Email to Janet Fryer]. 24 May. Unpublished data and information regarding Georgia plume postfire recovery. Fort Stewart, GA: Fish and Wildlife Branch, Fort Stewart Military Reservation, U.S. Army. On file with: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT; FEIS files. [93336]

5. Chafin, Linda G. 2007. Fact sheet: Georgia plume. Georgia Department of Natural Resources, Wildlife Resources Division. (Producer). Available: https://georgiawildlife.com/sites/default/files/wrd/pdf/fact-sheets/georgia_plume_2010.pdf [2019, May 5]. [93314]

6. Chafin, Linda G. 2007. Field guide to the rare plants of Georgia. Athens, GA: The University of Georgia. 526 p. [93278]

7. Coile, Nancy C. 1981. Flora of Elbert County, Georgia. Castanea. 46(3): 173-194. [73970]

8. Dasgupta, Swarvanu; Qu, John J.; Hao, Xianjun; Bhoi, Sanjeeb. 2007. Evaluating remotely sensed live fuel moisture estimations for fire behavior predictions in Georgia, USA. Remote Sensing of Environment. 108(2): 138-150. [79564]

9. Del Tredici, Peter. 1987. Lost and found: Elliottia racemosa. Arnoldia. 47(4): 3-8. [93280]

10. Duncan, Wilbur H.; Duncan, Marion B. 1978. Elliottia in the Piedmont of Georgia. Castanea. 43(3): 182-184. [93282]

11. Duncan, Wilbur H.; Duncan, Marion B. 1988. Trees of the southeastern United States. Athens, GA: The University of Georgia Press. 322 p. [12764]

12. Flora of North America Editorial Committee, eds. 2019. Flora of North America north of Mexico, [Online]. Flora of North America Association (Producer). Available: http://www.efloras.org/flora_page.aspx?flora_id=1. [36990]

13. Fordham, Alfred J. 1969. Elliottia racemosa and its propagation. Arnoldia. 29(1): 59-62. [93283]

14. Georgia Department of Natural Resources. 2013. Wildlife Conservation Section Biotics Database, Georgia biodiversity portal: Plants. Georgia Department of Natural Resources, Wildlife Resources Division (Producer). Available: http://www.georgiawildlife.com [2019, April 24]. [93313]

15. Georgia Plant Conservation Alliance. 2019. Preserving Georgia's imperiled native species. Athens, GA: University of Georgia (Producer). Available: https://botgarden.uga.edu/conservation-science/georgia-plant-conservation-alliance/ [2019, May 10]. [93321]

16. Glitzenstein, Jeff S.; Streng, Donna R.; Wade, Dale D. 2003. Fire frequency effects on longleaf pine (Pinus palustris P. Miller) vegetation in South Carolina and northeast Florida, USA. Natural Areas Journal. 23(1): 22-37. [43553]

17. Godt, M. J. W.; Hamrick, J. L. 1999. Population genetic analysis of Elliottia racemosa (Ericaceae), a rare Georgia shrub. Molecular Ecology. 8(1): 75-82. [93284]

18. Godt, Mary Jo W.; Hamrick, J. L. 2001. Genetic diversity in rare southeastern plants. Natural Areas Journal. 21(1): 61-70. [93294]

19. Harper, Roland M. 1902. Notes on Elliottia racemosa. The Plant World. 5(5): 87-90. [93285]

20. Hiers, J. Kevin; O'Brien, Joseph J.; Mitchell, R. J.; Grego, John M.; Loudermilk, E. Louise. 2009. The wildland fuel cell concept: An approach to characterize fine-scale variation in fuels and fire in frequently burned longleaf pine forests. International Journal of Wildland Fire. 18: 315-325. [76373]

21. Hodges, Malcolm. 2019. Personal communication [Email to Janet Fryer]. 3 July. Unpublished information regarding Georgia plume sprouting and plant associations. Atlanta, GA: The Nature Conservancy. On file with: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT; FEIS files. [93397]

22. Jackson, Lara. 2010. Geospatial analysis and habitat suitability modeling of Elliottia racemosa (Georgia plume). Athens, GA: The University of Georgia. 85 p. Thesis. [93286]

23. Kartesz, J. T., The Biota of North America Program (BONAP). 2015. North American Plant Atlas, [Online]. Chapel Hill, NC: The Biota of North America Program (Producer). Available: http://bonap.net/napa [maps generated from Kartesz, J. T. 2010. Floristic synthesis of North America, Version 1.0. Biota of North America Program (BONAP). (in press)]. [91053]

24. Kartesz, J. T. The Biota of North America Program (BONAP). 2015. Taxonomic Data Center, [Online]. Chapel Hill, NC: The Biota of North America Program (Producer). Available: http://bonap.net/tdc [Maps generated from Kartesz, J. T. 2010. Floristic synthesis of North America, Version 1.0. Biota of North America Program (BONAP). [in press]. [84789]

25. Kral, Robert. 1983. Ericaceae: Elliottia racemosa Muhl. Paper 29. In: A report on some rare, threatened, or endangered forest-related vascular plants of the South. Volume II: Aquifoliaceae through Asteraceae and glossary. Tech. Publ. R8-TP 2. Atlanta, GA: U.S. Department of Agriculture, Forest Service, Southern Region: 829-832. [93295]

26. Kruse, Lisa. 2019. Personal communication [Email to Janet Fryer]. 11 June. Unpublished information regarding Georgia plume fire response and plant associations. Atlanta, GA: Georgia Department of Natural Resources. On file with: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT; FEIS files. [93426]

27. Lafon, Charles W.; Naito, Adam T.; Grissino-Mayer, Henri D.; Horn, Sally P.; Waldrop, Thomas A. 2017. Fire History of the Appalachian region: A review and synthesis. General Technical Report SRS-219. Asheville, NC: United States Department of Agriculture, Forest Service, Southern Research Station. 97 p. [91542]

28. LANDFIRE Biophysical Settings. 2009. Biophysical setting 5513350: Atlantic coastal plain dry and dry-mesic oak forest. In: LANDFIRE Biophysical Setting Model: Map zone 55, [Online]. In: Vegetation Dynamics Models. In: LANDFIRE. Washington, DC: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory; U.S. Geological Survey; Arlington, VA: The Nature Conservancy (Producers). Available: https://www.landfire.gov/national_veg_models_op2.php [2019, May 9]. [93319]

29. LANDFIRE Biophysical Settings. 2009. Biophysical setting 5513460: Atlantic coastal plain fall-line sandhills longleaf pine woodland. In: LANDFIRE Biophysical Setting Model: Map zone 55, [Online]. In: Vegetation Dynamics Models. In: LANDFIRE. Washington, DC: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory; U.S. Geological Survey; Arlington, VA: The Nature Conservancy (Producers). Available: https://www.landfire.gov/national_veg_models_op2.php [2019, May 9]. [93318]

30. Little, Elbert L., Jr. 1977. Atlas of United States trees. Volume 4. Minor eastern hardwoods. Misc. Pub. No. 1342. Washington, DC: U.S. Department of Agriculture, Forest Service. 17 p. [21683]

31. Miller, Howard A. 1978. Wildfire's child: The story of Elliottia, a primitive, slow-growing member of the heath family that is rare in more ways than one. American Forests. 83: 24-27. [93324]

32. Missouri Botanical Garden. 2019. Tropicos.org. St. Louis, MO: Missouri Botanical Garden (Producer). Available: http://www.tropicos.org/Home.aspx [2019, July 10]. [93429]

33. Moretz, C. Craig; Silman, Miles R. 2002. Is Elliottia racemosa a fire dependent species? Historic records and current observations. Southeastern Biology. 49(2): 193. Abstract. [93306]

34. NatureServe. 2013. International Ecological Classification Standard: Terrestrial Ecological Classifications of the United States and Canada. In: NatureServe Central Databases. Arlington, VA, (Producer). 1530 p. [89169]

35. NatureServe. 2019. NatureServe Explorer: An online encyclopedia of life, [Online]. Version 7.1. Arlington, VA: NatureServe (Producer). Available: http://www.natureserve.org/explorer. [69873]

36. Ohwi, Jisaburo. 1965. Flora of Japan. Washington, DC: Smithsonian Institution. 1067 p. [50787]

37. Patrick, Thomas S.; Allison, James R.; Krakow. Gregory A. 1995. Protected plants of Georgia. Social Circle, GA: Georgia Department of Natural Resources, Wildlife Resources Division; Georgia Natural Heritage Program. 246 p. [93302]

38. Phillips, R. P. 2007. Elliotia racemosa Mulh.: Georgia plume response to dormant season fire. PowerPoint presentation. Fort Stewart, GA: Fort Stewart Fish and Wildlife Branch, Fort Stewart Military Reservation, U.S. Army; Statesboro, GA: Georgia Southern University. On file with: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT; FEIS files. [93335]

39. Platt, William J.; Glitzenstein, Jeff S.; Streng, Donna R. 1991. Evaluating pyrogenicity and its effects on vegetation in longleaf pine savannas. In: Proceedings, 17th Tall Timbers fire ecology conference; 1989 May 18-21; Tallahassee, FL. Tallahassee, FL: Tall Timbers Research Station: 143-161. [17606]

40. Porter, Justin A.; Berle, David; Wetzstein, Hazel Y. 2013. Integrating field and GIS-based surveys to map the distribution and characterize the ecological habitat for conservation management of Georgia plume, a rare endemic. HortScience. 48(2): 158–163. [93311]

41. Porter, Justin A.; Wetzstein, Hazel Y.; Berle, David; Wadl, Phillip A.; Trigiano, Robert N. 2012. Molecular analysis for conservation of Georgia plume, a threatened endemic, using random amplified polymorphic DNA. HortScience. 47(5): 563-569. [93287]

42. Porter, Justin. 2010. Conserving our biological heritage: Using GPS/GIS and molecular analysis as conservation management tools for Georgia plume (Elliottia racemosa). Athens, GA: The University of Georgia. 70 p. Thesis. [93296]

43. Radcliffe, Carrie A.; Affolter, James M.; Wetzstein, Hazel Y. 2009. Morphological and histological evaluations of flower development in Elliottia racemosa. HortScience. 44(4): 1055. [93289]

44. Radcliffe, Carrie A.; Affolter, James M.; Wetzstein, Hazel Y. 2009. Reproductive biology of Elliottia racemosa, a rare coastal plain endemic. Hortscience. 44(3): 563. Abstract. [93312]

45. Radcliffe, Carrie A.; Affolter, James M.; Wetzstein, Hazel Y. 2010. Floral morphology and development in Georgia plume, Elliottia racemosa (Ericaceae), a rare coastal plain endemic. Journal of the American Society for Horticultural Science. 135(6): 487–493. [93288]

46. Radcliffe, Carrie A.; Affolter, James M.; Wetzstein, Hazel Y. 2011. In vitro shoot regeneration of Georgia plume, Elliottia racemosa, from multiple genotypes collected from wild populations. HortScience. 46(2): 287–290. [93290]

47. Radcliffe, Carrie Amanda. 2009. Studies in reproductive biology and in vitro propagation as approaches to the conservation of Elliottia racemosa. Athens, GA: University of Georgia. 83 p. Thesis. [93358]

48. Radcliffe, Carrie Amanda. 2019. Personal communication [Email to Janet Fryer]. 11 June. Unpublished information regarding Georgia plume sexual regeneration. Atlanta, GA: Atlanta Botanical Garden, Department of Science & Conservation. On file with: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT; FEIS files. [93367]

49. Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. Oxford, England: Clarendon Press. 632 p. [2843]

50. Ravenel, H. W. 1876. Some rare southern plants. Bulletin of the Torrey Botanical Club. 6(15): 81-82. [93291]

51. Rebertus, Alan J.; Williamson, G. Bruce; Platt, William J. 1993. Impact of temporal variation in fire regime on savanna oaks and pines. In: Hermann, Sharon M., ed. The longleaf pine ecosystem: Ecology, restoration and management: Proceedings, 18th Tall Timbers fire ecology conference; 1991 May 30 - June 2; Tallahassee, FL. Tallahassee, FL: Tall Timbers Research: 215-225. [28371]

52. Ruter, John M.; Krewer, Gerard; Faircloth, Wayne R. 1995. A new location for Elliottia racemosa Muhl. ex Ell. (Ericaceae) in southwest Georgia. Castanea. 60(4): 370-371. [93292]

53. Santamour, Frank S., Jr. 1967. Cytology and sterility in Elliottia racemosa. Morris Arboretum Bulletin. 18(3): 60-63. [93293]

54. Stickney, Peter F. 1989. Seral origin of species comprising secondary plant succession in northern Rocky Mountain forests. FEIS workshop: Postfire regeneration. Unpublished draft on file at: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT. 10 p. [20090]

55. Trudell, Harry W. 1929. Rescuing Elliottia. Bartonia. 9: 11-15. [93315]

56. U.S. Department of Interior, Fish and Wildlife Service. 2019. Endangered Species Program, [Online]. U.S. Department of the Interior, Fish and Wildlife Service (Producer). Available: https://www.fws.gov/endangered/ [2019, April 15]. [86564]

57. USDA, NRCS. 2019. The PLANTS Database, [Online]. U.S. Department of Agriculture, Natural Resources Conservation Service, National Plant Data Team, Greensboro, NC (Producer). Available: https://plants.usda.gov/ [2019, April 12]. [34262]

58. Weakley, Alan S. 2008. Flora of the Carolinas, Virginia, Georgia, northern Florida, and surrounding areas: Working draft of 7 April 2008. Chapel Hill, NC: University of North Carolina Herbarium (NCU), North Carolina Botanical Garden, University of North Carolina at Chapel Hill. 1015 p. Available: http://www.herbarium.unc.edu/WeakleysFlora.pdf [2019, May 13]. [81727]

59. Wharton, Charles H. 1978. The natural environments of Georgia. Atlanta, GA: Georgia Department of Natural Resources. 227 p. [24582]

60. Wherry, Edgar T. 1971. Georgia's rare plant, Elliottia. Plants and Gardens. 27(2): 56-57. [93325]

61. Williamson, G. Bruce; Black, Edwin M. 1981. High temperature of forest fires under pines as a selective advantage over oaks. Nature. 293: 643-644. [9917]