

**SPECIES: *Triadica sebifera***

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**INTRODUCTORY**SPECIES: *Triadica sebifera*

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Jeff Hutchison, Archbold Biological Station

**AUTHORSHIP AND CITATION:**

Meyer, Rachele. 2005. *Triadica sebifera*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/> [ ].

**FEIS ABBREVIATION:**

TRISEB

**SYNONYMS:**

*Sapium sebiferum* (L.) Roxb. [[36](#),[88](#),[132](#),[134](#)]

**NRCS PLANT CODE [[129](#)]:**

TRSE6

**COMMON NAMES:**

tallowtree  
Chinese tallow  
popcorn tree  
Florida aspen  
chicken tree

**TAXONOMY:**

The scientific name of tallowtree is *Triadica sebifera* (L.) Small (Euphorbiaceae) [[30,57,129](#)].

**LIFE FORM:**

Tree

**FEDERAL LEGAL STATUS:**

None

**OTHER STATUS:**

Tallowtree is considered a noxious weed in Florida. Its sale there was prohibited in 1998 [[127](#)]. The Southern Region of the Forest Service has listed it as a Category 1 weed species [[128](#)]. It is also included in the top 10 exotic pest plants in Georgia by the Georgia Exotic Pest Plant Council [[34](#)] and listed as a "red alert" species in California by the California Invasive Pest Plant Council [[9](#)].

## DISTRIBUTION AND OCCURRENCE

**SPECIES:** *Triadica sebifera*

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Cheryl McCormick, The University of Georgia, IPM Images

**GENERAL DISTRIBUTION:**

Tallowtree is a native of China and Japan [[29,68,69,76,131,134](#)]. It has been introduced to many areas including Taiwan, India, Martinique, Sudan, southern France and the southeastern United States [[5,68,109](#)]. Tallowtree was initially introduced to South Carolina in the 1700s. It was more widely introduced, due to use as an ornamental and attempts to establish it as a commercial crop starting in the early 1900s [[52,107,124](#)]. In the United States it occurs from North Carolina south to Florida and west through Louisiana and Arkansas to Texas [[5,57,129](#)]. In addition, tallowtree occurs in Puerto Rico [[128](#)] and recently established in Sacramento County and the San Francisco Bay Area of California from ornamental plantings [[9,75](#)]. Tallowtree populations are suspected to occur in Tennessee [[77](#)], but this has not been confirmed.

[Plants database](#) [[129](#)] provides a distributional map of tallowtree. The following lists include ecosystems with varying levels of tallowtree occurrence, and are not necessarily exhaustive or definitive.

**ECOSYSTEMS** [[33](#)]:

FRES12 Longleaf-slash pine  
 FRES13 Loblolly-shortleaf pine  
 FRES14 Oak-pine  
 FRES15 Oak-hickory  
 FRES16 Oak-gum-cypress  
 FRES32 Texas savanna  
 FRES39 Prairie

FRES41 Wet grasslands

STATES/PROVINCES: ([key to state/province abbreviations](#))

**UNITED STATES**

AL	AR	CA	FL	GA	LA
MS	NC	SC	TX	PR	

BLM PHYSIOGRAPHIC REGIONS [[4](#)]:

None

KUCHLER [[63](#)] PLANT ASSOCIATIONS:

K061 Mesquite-acacia savanna  
K062 Mesquite-live oak savanna  
K076 Blackland prairie  
K077 Bluestem-sacahuista prairie  
K078 Southern cordgrass prairie  
K079 Palmetto prairie  
K080 Marl everglades  
K088 Fayette prairie  
K089 Black Belt  
K090 Live oak-sea oats  
K092 Everglades  
K100 Oak-hickory forest  
K111 Oak-hickory-pine  
K112 Southern mixed forest  
K113 Southern floodplain forest  
K114 Pocosin  
K115 Sand pine scrub

SAF COVER TYPES [[31](#)]:

61 River birch-sycamore  
68 Mesquite  
69 Sand pine  
70 Longleaf pine  
73 Southern redcedar  
74 Cabbage palmetto  
80 Loblolly pine-shortleaf pine  
81 Loblolly pine  
82 Loblolly pine-hardwood  
83 Longleaf pine-slash pine  
84 Slash pine  
85 Slash pine-hardwood  
87 Sweetgum-yellow-poplar  
88 Willow oak-water oak-diamondleaf (laurel) oak  
89 Live oak  
91 Swamp chestnut oak-cherrybark oak  
92 Sweetgum-willow oak  
93 Sugarberry-American elm-green ash  
94 Sycamore-sweetgum-American elm  
96 Overcup oak-water hickory  
97 Atlantic white-cedar  
98 Pond pine  
100 Pondcypress  
101 Baldcypress  
102 Baldcypress-tupelo  
103 Water tupelo-swamp tupelo

104 Sweetbay-swamp tupelo-redbay

111 South Florida slash pine

SRM (RANGELAND) COVER TYPES [111]:

711 Bluestem-sacahuista prairie

717 Little bluestem-Indiangrass-Texas wintergrass

719 Mesquite-liveoak-seacoast bluestem

726 Cordgrass

728 Mesquite-granjeno-acacia

806 Gulf Coast salt marsh

807 Gulf Coast fresh marsh

808 Sand pine scrub

809 Mixed hardwood and pine

810 Longleaf pine-turkey oak

811 South Florida flatwoods

812 North Florida flatwoods

813 Cutthroat seeps

814 Cabbage palm flatwoods

815 Upland hardwood hammocks

816 Cabbage palm hammocks

817 Oak hammocks

818 Florida salt marsh

819 Freshwater marsh and ponds

821 Pitcher plant bogs

822 Slough

HABITAT TYPES AND PLANT COMMUNITIES:

Tallowtree can invade several communities including those of the Gulf coastal prairies and many types of forests in the southeastern U.S. Several areas of coastal prairie have been converted to tallowtree woodland. Cameron and Spencer [12] report scattered sugarberry (*Celtis laevigata*) and black willow (*Salix nigra*) within a tallowtree woodland in the coastal prairie about 35 miles (56 km) southeast of Houston. The most common species in nearby tallowtree woodland sites of the coastal prairie by Alvin, Texas were sugarberry, yaupon (*Ilex vomitoria*), stiff dogwood (*Cornus foemina*), and American elm (*Ulmus americana*) [7]. However, their densities and coverages were much lower (maximum 93 stems/ha, combined covers <2% for all stands) than that of tallowtree (up to 4,432 stems/ha, several stands with coverage >80%) [6,7]. Tallowtree can also become a major component of many forested habitats [47,55,81,84]. Helm and others [47] describe tallowtree stands on South Carolina's Bull Island. Tallowtree, cabbage palmetto (*Sabal palmetto*), loblolly pine (*Pinus taeda*), redbay (*Persea borbonia*), and in some areas southern bayberry (*Morella cerifera*) were codominants. Tallowtree stands had a dense shrub layer (9,689 stems/ha), of which 79% (7,656 stems/ha) were tallowtree stems. American beautyberry (*Callicarpa americana*) (625 stems/ha) and dwarf palmetto (*S. minor*) (469 stems/ha) were the next most common shrubs. The most common species in the herbaceous layer were tallowtree seedlings (9.5% cover), yaupon (3.9%), bedstraws (*Galium* spp.) (1.6%), southern redcedar (*Juniperus virginiana* var. *silicicola*) (1.3%), southern bayberry (1.3%), redbay (1.3%), and southern dewberry (*Rubus trivialis*) (1.6%) [47]. The extent to which tallowtree has invaded other wet [55,81] and riparian [84] forests is discussed below.

Tallowtree invades grassland communities and is especially successful in coastal prairies [7,37]. In these areas big bluestems (*Andropogon* spp.), little bluestems (*Schizachyrium* spp.), blazing stars (*Liatris* spp.), coneflowers (*Echinacea* spp.) and prairie coneflowers (*Ratibida* spp.), occur with cordgrasses (*Spartina* spp.) morningglories (*Ipomoea* spp.), pine lilies (*Eustoma* spp.) and sundews (*Drosera* spp.) [37]. As tallowtree invades, graminoid cover declines [7]. Kincaid and Cameron [59] reported tallowtree in two categories of coastal prairie. In one type it occurred with goldenrods (*Solidago* spp.). The 2nd type included little bluestem (*Schizachyrium scoparium*), groundsel-tree (*Baccharis halimifolia*), southern dewberry, blue mistflower (*Conoclinium coelestinum*), gulf cordgrass (*Spartina spartinae*), and bushy bluestem (*Andropogon glomeratus*), in addition to goldenrods and tallowtree [59]. Streng and Harcombe [126] report density of 13/ha for tallowtree larger than 1.6 feet (0.5 m) tall in a grass-sedge (*Carex* spp) meadow typical of southern bogs. Trees were sparse and included longleaf pine (*P. palustris*), loblolly pine, black tupelo (*Nyssa sylvatica*), sweetgum (*Liquidambar styraciflua*) and sweetbay (*Magnolia virginiana*). The dominant grass was little bluestem. Sundews, tenangle pipewort (*Eriocaulon*

*decangulare*), clubmosses (*Lycopodium* spp.), coastalplain yelloweyed grass (*Xyris ambigua*) and sedges such as beaksedges (*Rhynchospora* spp.) and hairy umbrella-sedge (*Fuirena squarrosa*) were common [126].

Tallowtree occurs in several woodlands in the southeastern U.S., including those that are very wet. For instance, it has been recorded in bottomlands and swamps with species such as baldcypress (*Taxodium distichum*), water tupelo (*Nyssa aquatica*), and pumpkin ash (*Fraxinus profunda*) [18,28,45]. In Louisiana, Rosen and others [103] found tallowtree in a Big Branch Marsh National Wildlife Refuge community dominated by swamp tupelo (*N. biflora*) with a mid-story dominated by riverflat hawthorn (*Crataegus opaca*). South of this site along the Bayou Sauvage Ridge, the bottomland forest is dominated by live oak, sugarberry, black willow, and dwarf palmetto. The understory is comprised of tallowtree saplings, red maple (*Acer rubrum*), common persimmon (*Diospyros virginiana*), poisonbean (*Sesbania drummondii*) and deciduous holly (*I. decidua*) [133]. All of these species, except dwarf palmetto and red maple, were reported by Neyland and Meyer [81] as occurring with tallowtree in the Cheniers of southwestern Louisiana. In addition, green hawthorn (*C. viridis*), American elm, buttonbush (*Cephalanthus occidentalis*), honeylocust (*Gleditsia triacanthos*), and southern bayberry occurred on at least 1 of the 5 sites where tallowtree was invading. Tallowtree had the highest relative densities of all woody species on sites where it occurred, with an average density of 2.23 individuals per 5 m<sup>2</sup> plot and an average frequency of 35% over the 6 sites investigated [81]. Jubinsky [55] reported high densities of tallowtree in wetlands and along the shore of Lake Jackson in Florida. Despite it only being present at the site for approximately 20 years, tallowtree had the highest density (0.452/m<sup>2</sup>), the highest relative frequency (0.636), and the 2nd highest mean DBH-based coverage (6.69 cm<sup>2</sup>/m<sup>2</sup>) of woody species. The only species with more coverage was sweetgum, and neither sweetgum nor any other woody species present, which included common elderberry (*Sambucus nigra* ssp. *canadensis*), oaks, black willow, and stiff dogwood, had densities greater than 0.055/m<sup>2</sup> [55]. Tallowtree has been reported in saturated pine flatwoods of the slash pine/saltmeadow cordgrass-black rush-switchgrass (*Pinus elliottii* var. *elliottii*/*Spartina patens*-*Juncus roemerianus*-*Panicum virgatum*) association within Big Branch March National Wildlife Refuge. Tallowtree occurred in this type in areas with infrequent fire along with Jesuit's bark (*Iva frutescens*), saltwater false willow (*B. angustifolia*), southern bayberry, dwarf palmetto, and groundsel-tree [103].

Tallowtree occurs in floodplain and riparian woodlands of the southeastern U.S. Nixon and Willet [83] report small (0.4 to 4.0 inches (1-10 cm) DBH) tallowtrees occurring with baldcypress, black willow, sugarberry, sycamore (*Platanus occidentalis*), green ash (*F. pennsylvanica*), common persimmon, planertree (*Planera aquatica*), water hickory (*Carya aquatica*) and hawthorns (*Crataegus* spp.) in a community along the Trinity River in Texas. Tallowtree occurred but was less abundant in 2 other communities along the Trinity River. These associations contained sugarberry, common persimmon, black willow, and American elm as well as water hickory, green ash, and eastern swampprivet (*Forestiera acuminata*). One of these types was dominated by planertree and contained water locust (*G. aquatica*) and baldcypress while the other was dominated by sycamore and contained hawthorns and had a very low frequency of eastern cottonwoods (*Populus deltoides*) [83]. Tallowtree occurred with sweetgum, deciduous holly, swamp chestnut oak (*Q. michauxii*), water oak (*Q. nigra*), and American hornbeam (*Carpinus caroliniana*) in the floodplain forest along the Neches River in the Big Thicket National Preserve, Texas [42,45]. In addition to these species, Hall and Harcombe [42] reported laurel oak (*Q. laurifolia*), overcup oak (*Q. lyrata*), water hickory, and American holly (*Ilex opaca*). Oliver [84] found large variation in the importance of tallowtree in oak-elm (*Ulmus* spp.) dominated riparian forests at the Armand Bayou Nature Center in Texas. In the western sites tallowtree was very common, occurring with 90% frequency and accounting for 38% of the basal area. In contrast, tallowtree occurred with a frequency of 44% and comprised only 6% of the total basal area on eastern sites. Sweetgum, yaupon, and American beautyberry were also more likely to occur in the western plots [84]. In the floodplain of the Neches River in Village Creek State Park, Texas, tallowtree, water tupelo, river birch (*Betula nigra*), water oak, and redbay were reported as overtaking a longleaf pine/bluestem stand due to a lack of fire. Understory species included yaupon, flowering dogwood (*Cornus florida*), American beautyberry, poison-ivy (*Toxicodendron radicans*), little bluestem, panicums (*Dichantherium* spp.), and various sedges [95].

In California, tallowtree is known to occur on the American River in a wildland preserve adjacent to housing. The riparian vegetation is dominated by valley oak (*Q. lobata*), Fremont cottonwood (*Populus fremontii*), Oregon ash (*Fraxinus latifolia*), and California boxelder (*Acer negundo* var. *californicum*). Along with poison-oak (*T. diversilobum*), nonnative species including giant reed (*Arundo donax*), poison hemlock (*Conium maculatum*), Himalayan blackberry (*Rubus discolor*), and bigleaf periwinkle (*Vinca major*) form the understory [75].

In addition, tallowtree occurs in mixed woodlands of the southeastern U.S. Loblolly pine is a common species in the mixed forest types in which tallowtree occurs [45,47,93,103]. In the mixed pine-hardwood study areas used by Renne

and others [93] to investigate bird dispersal of tallowtree seed, loblolly pine occurred with longleaf pine, live oak, laurel oak, sweetgum, water tupelo, and hickories (*Carya* spp.). The overstory dominants in a mesic forest invaded by tallowtree in Weir Woods Preserve, Texas, were loblolly pine, water oak, American beech (*Fagus grandifolia*), southern magnolia (*Magnolia grandiflora*), and white oak (*Q. alba*). Other common species included sweetgum, red maple, and black tupelo, while American holly, flowering dogwood, and yaupon were abundant understory species [45]. Sweetgum, blackgum, southern red oak (*Q. falcata*), bottomland post oak (*Q. similis*) and/or loblolly pine were canopy dominants in mixed woods of Big Branch Marsh National Wildlife Refuge. Understory vegetation was varied and included flameleaf sumac (*Rhus copallinum*), Canadian blacksnakeroot (*Sanicula canadensis*), climbing dogbane (*Trachelospermum difforme*), American hornbeam, and sawtooth blackberry (*Rubus argutus*), as well as tallowtree [103]. Renne and others [93] observed few tallowtrees in a longleaf pine-turkey oak (*Q. laevis*) forest of Georgetown County, South Carolina. Although very rare, tallowtree was present in an oak-hickory-pine forest of Big Thicket National Preserve in Texas [45].

## BOTANICAL AND ECOLOGICAL CHARACTERISTICS

SPECIES: *Triadica sebifera*

- [GENERAL BOTANICAL CHARACTERISTICS](#)
- [RAUNKIAER LIFE FORM](#)
- [REGENERATION PROCESSES](#)
- [SITE CHARACTERISTICS](#)
- [SUCCESSIONAL STATUS](#)
- [SEASONAL DEVELOPMENT](#)



Chuck Barger, The University of Georgia, IPM images

### GENERAL BOTANICAL CHARACTERISTICS:

This description provides characteristics that may be relevant to fire ecology, and is not meant for identification. Keys for identification are available (e.g. [36,88,134]).

Tallowtree is a quick-growing, deciduous, nonnative tree capable of root and basal sprouting [29,36,37,68,77,107]. Rockwood and Geary [96] reported growth to 13 feet (4 m) 1.7 years after planting, while Sheld and Cowles [107] observed resprout growth to 11 to 12 feet (~3.5 m) 1 year after cutting, and to more than 18 feet (>5.5 m) 2 years after cutting. In addition to resprouting from the base of the plant, root sprouting by tallowtree can result in new growth up to 16 feet (5 m) from the original stem [37]. Tallowtrees typically grow to between 24 and 35 feet (7-11 m) tall [76,131], but sizes up to 65 feet (20 m) tall and over 3 feet (1 m) in diameter have been reported [39].

The lifespan of tallowtree is uncertain. Scheld and others [106] report that tallowtree is short-lived, only surviving 40 to 50 years. Grace and others [39] state that tallowtrees over 50 years old become "somewhat senescent," and Jones and McLeod [52] note a lifespan of under 100 years. However, roots can live longer [52]. Trees of varying age can occupy a single stand. The following table shows the mean annual mortality and recruitment rates (fraction of saplings/year) of small and large tallowtree saplings in a 9.9 acre (4 ha) floodplain forest site along the Neches River in the Big Thicket Preserve, Texas, over 14 years [42].

	Small saplings	Large saplings
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	(50-140 cm tall)	( $\geq 140$ cm)
Mortality rate	0.100	0.013
Recruitment rate	0.642	0.347

Tallowtree leaves are alternate, simple, and typically oval to round [68,69], but can also be rhombic [68]. They range from 1.4 to 3.3 inches (3.5-8.5 cm) long and from 1.4 to 3.5 inches (3.5-9.0 cm) wide [68,88]. The length of petioles ranges from 0.6 to 3.5 inches (1.5-9.0 cm) [68]. Sharma and others [109] found a maximum leaf area of  $2.7 \pm 0.2$  inches<sup>2</sup> ( $17.36 \pm 1.23$  cm<sup>2</sup>), a mature leaf moisture content of  $66.3 \pm 1.3\%$ , and a 41.1% translocation of total leaf nitrogen to twigs before leaf fall. Trunks can be gnarled [68] with fissured bark [77] that thickens as the tree grows [37]. Tiny, imperfect flowers occur in terminal spikes 2.4 to 7.9 inches (6-20 cm) long, with fascicles of up to 5 pistillate flowers near the base and fascicles of up to 15 staminate flowers along the spike [29,35,36,68,77,88]. Fruits are capsules about 9.5 to 19 mm in diameter [68,77]. They contain 3 wax-coated seeds about 6 to 10 mm long and 4.3 to 6.1 mm wide [68,77].

Tallowtree contains several potentially harmful chemicals. The milky sap of tallowtree is reportedly poisonous [29,35,69]. Seip and others [108] identified compounds from tallowtree roots as skin irritants and tumor producers. Although the chemicals have not yet been identified, there is some evidence that tallowtree has an allelopathic effect on loblolly pine germination and seedling growth [40]. Tallowtree has not been shown to have an allelopathic effect on species such as little bluestem [58], black willow [20], or baldcypress [20,23]. Little bluestem exposed to tallowtree extracts exhibited significantly ( $p < 0.05$ ) larger mass [58]. Baldcypress exposed to certain tallowtree extracts exhibited increased germination rates and/or growth, although variation was observed across seasons and treatments (leaves, litter, and soil extracts) [23]. Tallowtree was also shown to have consistently higher germination and growth rates in tallowtree-exposed treatments, which suggests that at least in some communities increased performance of conspecifics may be more important in tallowtree's success than limiting the success of sympatric species [23].

RAUNKIAER [90] LIFE FORM:

[Phanerophyte](#)

REGENERATION PROCESSES:

Tallowtree regenerates by seed and root sprouts. Tallowtree sprouts after incurring damage.

**Breeding system:** Imperfect flowers of both sexes occur on the same inflorescence [29,35,36,68,77,88]. There are 2 inflorescence types called "grape-like" and "eagle claw" that differ in morphology and development [8,68].

**Pollination:** Mechanisms of tallowtree pollination are uncertain. Tallowtree is a honey tree used by beekeepers [77] and was the dominant pollen in 1 of 7 samples examined in Louisiana [66]. However, the extent to which bees, other insects, and/or wind pollinate tallowtree has not been investigated.

**Seed production:** Tallowtree is capable of producing large amounts of seed. Lin and others [68] investigated seed yields from tallowtree grown in Taiwan. "Grape-type" inflorescences produced more seed than "eagle claw" inflorescences and habitat was also shown to influence seed production. Average yields were approximately 1 pound (0.453 kg) for 5-year-old trees, 7.4 pounds (3.379 kg) for 10-year-old trees, and reached a maximum of approximately 26.4 pounds (11.989 kg) in 20-year-old trees. Mean seed weight over all sites for seeds from "eagle claw" inflorescences was 0.112 g and 0.121 g for seeds from "grape like" inflorescences, giving an approximate average seed production of a 20-year-old tree of 100,000 seeds [68]. In northern India seed production ranged from 3,276 in a tree with a diameter of 2.4 inches (6 cm) to 45,276 in a tree with a diameter of 8.0 inches (20.4 cm) [109]. Renne and others [93] estimated mean tallowtree seed crop as 1,681,000 ( $s_x = 113,000$ ) in a 16,900 feet<sup>2</sup> (1,570 m<sup>2</sup>) area of coastal South Carolina.

**Seed dispersal:** Tallowtree seeds are dispersed by water and birds. Literature reviews by Bruce and others [8] and Jubinsky [55] report the dispersal of tallowtree seeds by water. Birds removed an estimated  $675,000 \pm 56,000$  seeds or about 40% of the total seed crop in a South Carolina study area [93]. Conway and others [22] observed 24 different bird species eating tallowtree seeds in coastal Texas, while Renne and others [93] saw 14 species feeding on tallowtree seeds in South Carolina. Red-bellied woodpeckers, northern cardinals, northern flickers, and red-winged

blackbirds are common dispersal agents [22,92,93].

**Seed banking:** Tallowtree apparently produces a seed bank that persists for at least a short period [39]. Cameron and others [10] found that tallowtree seeds could germinate in a greenhouse after 7 years of cold storage at 39 °F (4 °C) the 1st year and 32 °F (0 °C) the following years, with the maximum germination rate after 2 years storage. After 1 year of storage in a paper bag placed in sheltered area outdoors, Renne and others [94] found a significant ( $p=0.0001$ ) decrease in emergence over fresh seed. However, in an experiment specifically addressing persistence of tallowtree seedlings in the soil, they found no statistically significant ( $p>0.05$ ) difference in germination rates between seeds buried for 1 year and those buried for 2 years. Germination rates of seeds that had been buried for 1 and 2 years ranged between about 15% and 55% across habitat types. Maritime evergreen forest, with a comparatively open overstory of loblolly pine and live oak and high densities of shrubs and vines in the understory, was the only habitat in which seeds buried for 2 years had significantly ( $p = 0.0077$ ) higher germination rates than seeds buried for 1 year [94].

**Germination:** Tallowtree germination and time to germination are influenced by several factors, including season of planting, digestion by birds, and seed characteristics, such as size and age, which result in a wide range of reported germination rates both across and within studies. For instance, Conway and others [21] did not obtain germination rates higher than 10%, while germination rates as low as 0% and up to 94% were observed by Cameron and others [10]. Renne and others [94] also reported a wide range of germination rates (13% to 80%) .

The effect of time of planting and its associated light and temperature conditions differs between studies. Singh and others [119] found similar germination rates 60 days after planting for tallowtree seeds planted in February (60%) and in May (62%). Nijjer and others [82] noted that peak germination of tallowtree seeds in the field occurs in April and May. In contrast, Cameron and others [10] found a significant ( $p<0.001$ ) increase in germination rate after 120 days when seeds were planted in January and February (average 58%-59%) compared to late fall (21%-46%) or early spring (22%-36%) in a greenhouse with "natural" photoperiod and temperature. Several benefits of winter germination are suggested, including decreased activity of possible seed predators, increased light due to a more open canopy, and decreased interspecific competition for nutrients or light due to fewer annuals and dormancy in perennials [10]. However, Nijjer and others [82] found significantly ( $p<0.05$ ) higher germination in light (~15%) and dark (~15%) treatments than in light cycle (6%) treatments, implying that the darkness associated with canopy cover would not inhibit tallowtree germination. They also found a significant ( $p<0.0001$ ) effect of temperature, with constant temperatures of 90 °F (32 °C) and 60 °F (16 °C) having lower germination rates (~0%) than the cycling temperature regime (~6%-15%) of 16 hours at 90 °F (32 °C) and 8 hours at 60 °F (16 °C). Given that temperature fluctuations occur more often in open areas, such as canopy gaps, it is suggested that tallowtree may have higher germination in disturbed habitats [82].

Digestion by birds and depth of burial affect germination of tallowtree seeds. Seed burial and avian digestion significantly increased germination in a greenhouse experiment [94]. Seeds buried to a depth of 1 cm exhibited a 56% germination rate while only 17.5% of seeds placed on the soil surface germinated ( $p<0.0001$ ). In addition, seeds that had passed through an avian digestive tract had significantly ( $p<0.0001$ ) higher germination rates (51%) than seeds that had no evidence of being handled by birds ("unhandled", 22.5%). There was an interaction effect as well ( $p<0.0005$ ), with the highest germination rate (81%) observed in eaten and buried seeds. Buried seeds also germinated faster (~7 days) than surface seeds (eaten, 13.1 days; unhandled, 42.2 days). Emergence of buried seeds was significantly ( $p\leq 0.0003$ ) higher in acid-treated (83.0%) and digested seeds (76.5%) than unhandled seeds (39.5%). Freshly collected seeds (75.3%) emerged at a significantly ( $p=0.0001$ ) higher rate than 1-year-old seeds (44.5%). Freshly collected, digested seeds had the highest emergence rate (~83%), but the interaction of these 2 treatments was not statistically significant ( $p=0.06$ ) [94]. Siril and others [120] found that chemical treatment with concentrated sulfuric acid significantly ( $p<0.001$ ) affected tallowtree germination rates, with the 10-minute treatment resulting in the highest mean germination (76.8%) of all treatments. This treatment and the 14-minute sulfuric acid treatment also exhibited the fastest mean time for germination (36.4 days) of all treatments. However, exposure to sulfuric acid for more than 10 minutes resulted in significant ( $p<0.05$ ) decreases in germination compared to the 10-minute treatment [120]. Although complete removal of the tallow seed coating with a surgical blade resulted in an increase in germination rate (62.3%), splitting the tallow seed coating resulted in a substantial decline in germination rate (17.3%) [120]. In addition, lack of a difference in germination between uneaten seeds collected after yellow-warbler feeding activities and those collected from trees [22] indicates that digestion of the seed, not handling by the birds, results in enhanced germination.

Seed source has also been shown to have a large effect on germination rates. Germination rate of tallowtree seeds from Florida was significantly higher than seed from all other locations, while germination rates of seeds from Houston, Taiwan, and Georgia were significantly higher than seeds from South Carolina [10]. The reason for this may be differences in developmental stage of seeds from plants at different latitudes. However, the Florida and Houston sites were similar in latitude. The following table displays the number of trees sampled from each location (n), and the mean germination rates after 120 days and standard errors for seeds from these areas [10].

Locality	n	Total percent germinated
Florida	9	52.4 ± 5.9
Houston	53	24.3 ± 2.7
Taiwan	36	28.8 ± 3.3
Georgia	9	30.9 ± 6.3
South Carolina	15	5.7 ± 3.1

In addition, seeds from 3 areas of northern India exhibited significant ( $p=0.001$ ) differences in germination. Again the trend was for higher germination rates in seeds from lower latitudes, with untreated seeds from the southernmost site having a 59.0% germination rate and untreated seeds from the northernmost site having a 48.3% germination rates [120].

Tallowtree seed characteristics such as size and age also affect germination rate. Large seeds had significantly ( $p<0.05$ ) higher germination rates ( $\geq 0.15$  g = 87.1%) than medium (0.1 - 0.14 g = 35.4%) and small seeds ( $<0.1$  g = 10.4%) [120]. Age of tallowtree seeds has also been demonstrated to have a significant ( $p<0.0001$ ) affect on germination rate [10]. After 4 to 5 years storage in cold, dry, conditions (39 °F (4 °C) the 1st year and 32 °F (0 °C) the following years), mean germination rate started falling and by 7 years was quite low (0%-12%). The following table shows tallowtree germination rates for seeds of varying ages planted at different times of the year; the interaction between these variables was significant ( $p<0.0004$ ) [10].

Age (yrs) of seeds	Date of Planting					
	Nov 2	Nov 30	Jan 2	Feb 1	Mar 6	Apr 5
7	0	0	12 ± 3.7	6 ± 2.5	2 ± 2.0	0
5	18 ± 8.0	48 ± 5.8	52 ± 13.6	36 ± 22.3	20 ± 3.2	20 ± 5.5
4	36 ± 9.3	60 ± 8.4	64 ± 5.1	80 ± 4.5	40 ± 5.5	28 ± 7.3
2	44 ± 9.3	82 ± 3.7	94 ± 2.5	84 ± 4.0	76 ± 7.5	46 ± 7.5
0	8 ± 5.8	40 ± 4.5	66 ± 6.8	92 ± 5.8	40 ± 8.4	14 ± 4.0

Water immersion has not been shown to have a significant effect on tallowtree germination. Tallowtree seeds soaked in water for 96 hours or less exhibited insignificant ( $p>0.05$ ) increases in germination rates, while seeds soaked for 192 hours resulted in insignificant ( $p>0.05$ ) decreases in germination rate [120]. Similarly, Conway and others [21] found insignificant ( $p=0.359$ ) differences between soaking, soaking and chilling, and control treatments. Germination of seeds immersed in 176 °F (80 °C) water for 15 minutes (59.0%) was similar to the control (53.7%) [120]. In addition, Bruce [6] found no significant ( $p=0.224$ ) effect of watering frequency on germination in a greenhouse experiment.

Germination of native species is typically similar to or higher than tallowtree germination and can occur over a broader range of conditions [6,82]. However, regardless of low germination rates, such as those reported by Conway and others ( $<10\%$ ) [21,22] and Nijjer and others ( $<15\%$ ) [82], high seed production can cause difficulties in controlling tallowtree invasions [21]. The possibility of increased germination of tallowtree seeds in areas where tallowtree is already present [20,23] causes additional concern. However, Bruce [6] demonstrated that the success of tallowtree seedlings in closed canopy tallowtree woodlands can be very low.

**Seedling establishment/growth:** Tallowtree seedlings are capable of quick growth and are able to survive in a variety of conditions. Seeds that germinated up to 15 weeks after planting exhibited survival rates between 80% and 100% [16]. Growth rate of tallowtree seedlings has been reported as equal to or greater than many native seedlings in most conditions [6,52,53] and is a factor in its success invading coastal prairies [6]. Growth rates from 0.03 inch per day (0.076 cm/day) were recorded in canopy gaps of tallowtree forest and coastal prairie, and up to 0.13 inch per day

(0.33 cm/day) in cleared grassland plots. Average height of tallowtree seedlings at the end of the 1991 growing season was 8.7 inches (22 cm) [6].

The effect of several factors on tallowtree seedling performance have been investigated. Jones [51] investigated the effect of growing tallowtree with red maple, sweetgum, and tallowtree. He found that after 42 days, the species growing with tallowtree had a significant ( $p < 0.01$ ) effect on tallowtree seedling biomass, with seedlings in tallowtree-only pots smaller than those in grown in mixed-species pots. After 96 days there was no longer a significant ( $p = 0.10$ ) difference between tallowtree seedlings in inter- and intraspecific treatments. However, there was a significant ( $p = 0.03$ ) interaction between associated species (red maple vs. sweetgum) and heating pots to temperatures between 88 °F (31 °C) and 93 °F (34 °C) [51]. Planting tallowtree from Texas with Italian ryegrass (*Lolium multiflorum*) had no significant effect on shoot growth, shoot mass, or root mass of tallowtree seedlings [101]. In addition, nutrient supplementation (3 g nitrogen/m<sup>2</sup>, 1 g phosphorus/m<sup>2</sup>, 2 g potassium/m<sup>2</sup>) and root damage (roots cut 2 inches (5 cm) below the soil surface) did not significantly affect stem growth, root mass, or shoot mass of tallowtree seedlings from Texas [101]. However, Rogers and Siemann [99] observed a significant ( $p < 0.0001$ ) effect of nitrogen application on tallowtree seedling height and diameter growth rates, as well as shoot and root mass. Roots of nearby plants invading the area containing tallowtree roots resulted in a significant ( $p < 0.05$ ) decrease in total tallowtree seedling mass, total height, and leaf area [54].

Timing of planting was not found to have a significant effect on seedling emergence or survival [94]. Tallowtree seedlings emerged throughout the growing season in coastal forests with established tallowtree. Seeds planted in December and those planted in February showed no significant difference in total emergence ( $p = 0.5308$ ) or number of tallowtrees emerged by sampling date ( $p > 0.10$ ). Similarly there was no significant effect of planting date on seedling survival either across habitats ( $p = 0.8851$ ) or within habitats ( $p > 0.20$ ) [94].

Information on the effects of site characteristics such as water and soil conditions on establishment of tallowtree are discussed in the [Site Characteristics](#) section below, while the effect of light is addressed in the [Shade tolerance](#) section.

**Asexual regeneration:** Tallowtree spreads locally by root sprouts [39,77] and has strong sprouting capabilities following damage [8,19,39,77]. Root sprouting up to 16 feet (5 m) from the tree trunk has been reported [37]. Scheld and Cowles [107] reported prolific sprouting within a month of cutting tallowtree. Rockwood and Geary [96] found that tallowtree coppiced consistently and reported growth of over 26 feet (8 m) after 24 months.

#### SITE CHARACTERISTICS:

Tallowtree is most successful in wet, open habitats. It is flood tolerant [77] and is often found along the shores of water bodies, in floodplains, and in swampy areas [28,35,36,77,81,134]. However, it can also occur in drier, upland habitats [35,36,77,94,134]. Tallowtree can invade intact habitats and is quite successful in disturbed areas [17,81,121,134]. Thin woodlands, canopy gaps, and open understory appear more easily colonized by tallowtree than closed canopy forests [29,45,81,84,115]. Tallowtree typically occurs at low elevations [29,35,36,133] but can grow at higher elevations. In a southern New Mexico experimental planting, tallowtree survived and grew at 3,770 feet (1,150 m) [62]. Plantations at elevations between 1,300 and 2,300 feet (400-700 m) in Taiwan [68] and between 4,000 and 5,000 feet (1,200-1,600 m) in northern India have been reported [109]. Although tallowtree has been reported to withstand some exposure to freezing temperatures [96], substantial damage has been observed after 36 hours of below freezing temperatures [8]. Tallowtree is likely limited in the north by cold temperatures [8,56].

**Water:** Tallowtree prefers wet sites but can grow in drier areas. Average annual precipitation in tallowtree-invaded habitats near Houston ranged from 42.1 to 55.9 inches (1,070-1,420 mm) [115]. In Taiwan average annual precipitation ranges between 52.6 inches and 147 inches (1,336-3,733 mm) in habitats where tallowtree occurs [68]. However, in plantations in New Mexico that were irrigated for 2 months after transplanting, tallowtree exhibited 90.6% survival and grew to an average height of 55 inches (140.3 cm) over 2 growing seasons in an area with an average annual precipitation of 9.6 inches (243 mm) [62]. Tallowtree seedlings can construct a taproot system quickly and survive dry periods [107]. Barrilleaux and Grace [3] found that tallowtree could survive and grow when watered monthly. However, significantly ( $p = 0.0001$ ) larger total plant biomass was observed in more frequently watered plants. Singh and others [119] found that plants grew taller, had larger stem diameters, and produced seed at an earlier age when grown in waterlogged conditions compared to those grown on agricultural sites. Soil moisture has also been shown to affect seedling survival. Bruce [6] found significantly ( $p < 0.01$ ) lower seedling survival in dry soil (23% soil moisture) compared to treatments with  $\geq 31\%$  soil moisture. There are typically fewer tallowtrees in

drier habitats than nearby wet sites [45,94].

Several studies have investigated tallowtree tolerance of freshwater and saltwater flooding [13,14,15,16,54,73,115,133]. Tallowtree can produce hypertrophied lenticels, adventitious roots, and thicker feeder roots when flooded [13,54]. Siemann and Rogers [115] found no significant effect of flooding duration (to stem base or higher) on tallowtree survival ( $p>0.31$ ) or mass ( $p>0.35$ ) in a floodplain forest. They observed mean flooding depths of 14 inches (35 cm) with a range of 8 to 20 inches (20-52 cm) and an average flooding duration of 35 days (range 14-61). Tallowtree can survive and grow in most flooding treatments, but tallowtrees in drained treatments generally have significantly ( $p<0.05$ ) smaller root biomass and significantly ( $p<0.05$ ) larger heights, stem diameters, and leaf biomass [13,14,16,54]. Tallowtrees in drained soil also exhibit significantly ( $p=0.0001$ ) increased photosynthesis compared to flooded (to 2.0 inches (5 cm) above the soil surface) plants [73]. The reduction in tallowtree size due to flooding to 1.0 inch (2.5 cm) above the soil surface was significantly ( $p<0.0001$ ) larger than the reduction in water tupelo under 100% light, but not under 20% light ( $p>0.03$ ) [54].

The effect of saline water on tallowtree has also been investigated [13,14,15,73]. Watering or flooding (to 2.0 inches (5 cm) above the soil surface) with 10 ppt saline water has significant ( $p<0.05$ ) effects on height, photosynthesis, and root and stem biomass [13,14,73]. Saline (10 ppt) watering resulted in a significant ( $p<0.05$ ) decline in tallowtree height and photosynthesis ( $p=0.0005$ ) compared to watering with freshwater or less saline water (2 ppt) [13,14]. Flooding with 10 ppt saline water was the only treatment that resulted in tallowtree mortality, with all 4-month-old plants dying after 6 weeks [13,14,73]. Tallowtree saplings that were approximately 6 weeks older survived longer under these conditions [13,73]. Tallowtree was only slightly affected by saline (20-27 ppt) flooding of up to 2 days, and after 5 days survival was 60% [15]. No tallowtree mortality was reported for simulated storm surge treatments (21 ppt salinity for 48 hours). Tip dieback did occur, mainly in plants that were flooded with freshwater before the simulation [13,14].

**Soil:** Tallowtree occurs in acidic to slightly basic soils. Tallowtree plantations in Taiwan were reported to have soil with pH values between 3.9 and 8.5 [68]. Tallowtree in India grew in soils with a pH of 5.65 at depths between 0 and 3.9 inches (0-10 cm). Deeper soil samples, from 35.4 to 47.2 inches (90-120 cm), had a pH of 5.35 [80]. Soils of trial plantations in India had mean pH values between 6.1 and 6.6 [70]. Streng and Harcombe [126] reported a mean soil pH of 4.7 in a tallowtree-containing meadow in Texas. In an tallowtree experiment performed by Conner and others [16] the soil used had a pH of 6.1.

Tallowtree can grow on a wide range of soil textures from clay [6,107] to loam [6,80] to sandy [48,88] soils. Bruce [6] found that tallowtree generally grew better in clay soil. This was more noticeable in dry (23% soil moisture) treatments than wet ( $\geq 31\%$  moisture) treatments.

Tallowtree is tolerant of slightly saline soils [68,77,107]. In field experiments, tallowtree performed best on eastern and central coastal prairie sites which had electrical conductivities from 140  $\mu\text{S}$  to 634  $\mu\text{S}$  [3]. Tallowtree had higher mortality and lower growth on soils from western sites. Although other factors may be influencing this pattern, a likely cause is high salinity (mean electrical conductivity of 3070  $\mu\text{S}$ ) on the western sites [3].

Nutrient conditions in tallowtree plantations have been investigated. Lin and others [68] reported soil with organic matter between 0% and 4.5% and total nitrogen between 0% and 0.20% on tallowtree plantation sites in Taiwan. Available phosphorus was between 1 and 18 kg/ha and available potassium was between 70 and 230 kg/ha on these sites [68]. Narain and others [80] reported similar organic carbon (1.573%) and total nitrogen (0.17%) values for a plantation in India. In another study of tallowtree cultivation in India, mean organic carbon ranged between 0.71% and 1.64% dry mass across 2 sites and 5 years. This same study reported average total nitrogen values between 0.10% and 0.25% dry mass, mean exchangeable potassium between 2.0 mg/100g soil and 6.43 mg/100g soil, mean exchangeable calcium from 30.6 mg/100g soil to 87.03 mg/100g soil and average exchangeable magnesium values between 2.3 mg/100g soil and 8.46 mg/100g soil [70]. In Texas, at the University of Houston Coastal Center, experimental tallowtree plantations were developed on sites low in nitrogen and phosphorus [107].

Addition of nutrients, mainly nitrogen, has not been shown to have a significant ( $p=0.4$ ) effect on tallowtree survival [114] and has had mixed results on tallowtree growth. Rogers and Siemann [101] found that stem growth, shoot mass and root mass of tallowtree from Texas were not significantly affected by a total nutrient supplementation of 6 g nitrogen/m<sup>2</sup>, 2 g phosphorus/m<sup>2</sup>, and 4 g potassium/m<sup>2</sup>. Tallowtree diameter growth rate was not significantly affected by nitrogen supplementation in one study [100], but was significantly ( $p<0.0001$ ) increased in another study

[99]. Although a greenhouse experiment resulted in an insignificant ( $p=0.087$ ) increase in shoot mass with increased nitrogen, Rogers and Siemann [100] found a significant effect of nitrogen addition on tallowtree shoot mass in a field experiment. Nitrogen treatments have been found to result in larger plant mass [99,114]. Height and diameter growth, shoot mass, and root mass of tallowtree seedlings were significantly increased by the addition of fertilizer (maximum of 9 g nitrogen/m<sup>2</sup>) in a 15-week experiment [99]. Tallowtree height growth also increased significantly with nitrogen supplementation ( $p=0.025$  in [100];  $p\leq 0.0001$  in [99]). Mean leaf area ( $p=0.0003$  in [100];  $p=0.0006$  in [98]) and individual leaf mass ( $p<0.0001$ ) [98] were significantly increased with increased nitrogen. Number of new leaves was significantly affected. Rogers and Siemann [100] found a significant decrease ( $p=0.036$ ), while Rogers and others [98] found a significant ( $p<0.0001$ ) increase. Rogers and others [98] also found an insignificant ( $p=0.0815$ ) declining trend in stomatal conductance with increases in nitrogen and a significant ( $p=0.0089$ ) nitrogen-shade interaction on petiole length, with more shade and nitrogen resulting in longer petioles [98]. The effects of nitrogen and shade have been the topic of several studies [99,100,114] and their results regarding the effect of shade are summarized in the [Shade tolerance](#) section.

Tallowtree leaf fall can affect soil microbial communities and may alter nutrient dynamics. Stress from tannin input from tallowtree leaves may be responsible for changes in microbial life history characteristics [78]. In the laboratory, 2 common aquatic invertebrates were shown to have significantly ( $p<0.05$ ) higher mortality in tallowtree tannin treatments with available food, suggesting a disruption of regular feeding resulted in lower survival [11]. The effect of leached tannins is likely to have a persistent effect on aquatic organisms and seasonal effects on terrestrial invertebrates. Once tannins are leached tallowtree leaves are consumed by terrestrial isopods. Despite the initial lack of invertebrate feeding activity, Cameron and Spencer [12] report rapid tallowtree leaf decay. The average amount of leaf fall observed, 382.6 g/m<sup>2</sup>/year, is typical for southern deciduous trees. However the lignin to initial nitrogen concentration ratio was lower than other southern trees, which may partially explain tallowtree's rapid leaf decay. Concentrations of several nutrients, such as phosphorus, potassium, and zinc, were significantly ( $p<0.05$ ) higher in tallowtree woodland soil than in nearby prairie soil, while manganese and sodium concentrations were significantly ( $p<0.05$ ) lower. Cameron and Spencer [12] conclude that rapid leaf decay resulting in the release of nutrients may cause increased productivity in areas with tallowtree. Measurements of aboveground net primary productivity from DBH in tallowtree woodland (1,264 g/m<sup>2</sup>;  $s_x^- = 27$  g/m<sup>2</sup>) and from a modification of the peak live standing crop on unburned (462 g/m<sup>2</sup>;  $s_x^- = 49$  g/m<sup>2</sup>) and burned (624 g/m<sup>2</sup>;  $s_x^- = 63$  g/m<sup>2</sup>) grassland support this conclusion [44].

**Temperature:** Because of only limited tolerance to freezing, tallowtree establishment is restricted in the north [8,56]. Rockwood and Geary [96] report tallowtree survival after a December 1983 freeze, and Grace and others note [39] that tallowtree can grow after damage from exposure to cold. However, tallowtree suffered substantial damage after exposure to freezing temperatures for 36 hours. From these observations and a distributional map, the authors conclude that the northern boundary of tallowtree spread is in the 7b zone (average minimum winter temps of 5 °F to 10 °F (-12 °C to -15 °C)) of the USDA Plant Hardiness Zone map [8].

#### SUCCESSIONAL STATUS:

**Shade tolerance:** Although tallowtree can survive and grow in shade, it generally performs better in sunlight. Survival of tallowtree increased with increasing light levels. At 0.1% full sunlight tallowtree mortality was 5.3%, at 1% sunlight mortality was approximately 3.6%, and at 10% sunlight mortality was approximately 0.05% [67]. Tallowtree seedlings had greater net photosynthesis and dry mass ( $p<0.05$ ) than sycamore and cherrybark oak under 5% full sunlight [52]. Dry mass, height, and basal diameter of tallowtree grown in full sunlight were greater than tallowtrees grown in 5% full sunlight. Tallowtree in well-drained soil grown in 100% light had significantly ( $p<0.05$ ) larger mass than those grown in 20% light [54]. Jones and McLeod [53] reported "moderate growth in deep shade and rapid growth in full sunlight" and increases in tallowtree seedling height with increasing light between 5% and 20% full sunlight. The maximum tallowtree seedling dry mass occurred under 100% light, and absolute growth was greater in tallowtree than Carolina ash (*Fraxinus caroliniana*) under 5% and 100% full sunlight. In a grassland field experiment, tallowtree seedling survival was significantly reduced in shade treatments ( $p<0.01$ ) and significantly ( $p<0.05$ ) increased in increased-light treatments [114]. Siemann and Rogers [115] found a significant ( $p<0.05$ ) effect of light availability on tallowtree survival and growth in prairie sites, but not in mesic ( $p>0.16$ ) or floodplain ( $p>0.61$ ) forests. Leaf area ( $p<0.0001$ ) and number ( $p\leq 0.019$ ) have been shown to increase with increasing shade [98,100]. Significant ( $p<0.0001$ ) declines in stomatal conductance [98], root mass ( $p=0.025$ ), and root to shoot ratio ( $p<0.0001$ ) [100] have also been observed with increasing shade. At very high light levels tallowtree growth has been shown to decrease. For instance, Jones and McLeod [53] found that the tallest tallowtrees occurred in the intermediate (53% and 20%) light level treatments ( $p<0.05$ ). In addition, Rogers and Siemann [99] found that tallowtree grown in 37%

and 12% sunlight had significantly ( $p < 0.0001$ ) larger height growth rates than those grown in full sunlight. They suggest temperature or water stress resulting in photo-oxidation, despite daily watering, or photoinhibition may have caused this.

In the field, tallowtree seedlings perform much better in open habitats. Bruce [6] observed 100% mortality of tallowtree seedlings in a closed canopy tallowtree forest, while tallowtree seedlings survived and grew, in some cases very rapidly, in canopy gaps, grassland, and cleared sites. Tallowtree was also more prevalent on the edges of chenier woodland sites in Louisiana [81]. Oliver [84] suggests that tallowtree dominance in part of her Harris County, Texas, study area may be explained by the relatively open canopy, although it may also be due to higher moisture availability.

Several studies have investigated the interaction of shade with other variables. Most of these studies focus on nitrogen and shade; several of the results from these studies were discussed in the [Soil](#) section, such as the interaction of increasing shade and increasing nitrogen resulting in significantly ( $p = 0.0089$ ) longer petioles [98]. Siemann and Rogers [114] suggest that the increased growth of tallowtree in a shade and nitrogen addition experiment, along with increased tallowtree growth with increased light, implies tallowtree's response was not due to higher shade tolerance, but to better performance than prairie vegetation under the shaded, nitrogen-added, conditions. Light availability and flood tolerance may also interact. Reduction of tallowtree growth due to flooding under 20% sunlight was not significantly different from water tupelo, while tallowtree growth reductions under full light were significantly larger than those of water tupelo [54]. Quick seedling growth of flood-tolerant species may allow them to inhabit areas that would typically be occupied by more shade tolerant species [41,67].

#### SEASONAL DEVELOPMENT:

Tallowtree flowers from April until June and produces fruit between August and January in the southeastern U.S. [77,88].

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## FIRE ECOLOGY

SPECIES: *Triadica sebifera*

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- [FIRE ECOLOGY OR ADAPTATIONS](#)
- [POSTFIRE REGENERATION STRATEGY](#)

#### FIRE ECOLOGY OR ADAPTATIONS:

**Fire adaptations:** Tallowtree has several adaptations to fire. Bark that thickens with age insulates older trees. Tallowtree top-killed by fire can produce vigorous basal sprouts, and roots are capable of sprouting up to 16 feet (5 m) from the original stem [37]. Tallowtree has been observed sprouting after several years of annual burning [91]. In addition, it is not prone to crown fires and typically ignites only when fires are very intense. This and the lack of herbaceous fuels under tallowtree stands result in woodlands that are very resistant to burning [37].

Information regarding degree and mechanisms of colonization of burned sites is lacking. Surviving tallowtrees are the most likely source of seed. However, the ability of seeds in the seed bank to survive fire has not been investigated. Whether from a surviving tree, the seed bank, or dispersed from an off-site source, germination and establishment rates of tallowtree seeds on recently burned sites are unknown.

**Fire regimes:** There is a wide range of fire frequencies and severities in habitats where tallowtree occurs. Many tallowtree-containing habitats have evolved with short fire return intervals. Although no systematic research has been done, many observations suggest that sites within these habitats with relatively infrequent or irregular fire frequencies may be more easily colonized by tallowtree [37,38,95,103]. Frequent burning may decrease tallowtree recruitment or prevent establishment of tallowtree woodlands in coastal prairies [37,43]. Thus, reintroduction of fire into native plant communities adapted to a frequent fire regime may help prevent establishment and spread of tallowtree.

In tallowtree woodlands, the moisture and fuel conditions necessary to ignite and carry a fire occur very rarely [37].

The following table provides fire return intervals for plant communities and ecosystems where tallowtree is important. For further information, see the FEIS review of the dominant species listed below. This list is not inclusive for all plant communities in which tallowtree occurs. If you are interested in plant communities or ecosystems that are not listed below, see the complete [FEIS Fire Regime Table](#).

Community or Ecosystem	Dominant Species	Fire Return Interval Range (years)
bluestem-Sacahuista prairie	<i>Andropogon littoralis-Spartina spartinae</i>	<10 [85]
sugarberry-America elm-green ash	<i>Celtis laevigata-Ulmus americana-Fraxinus pennsylvanica</i>	<35 to 200
Atlantic white-cedar	<i>Chamaecyparis thyoides</i>	35 to > 200 [132]
Everglades	<i>Mariscus jamaicensis</i>	<10 [79]
slash pine	<i>Pinus elliottii</i>	3-8
slash pine-hardwood	<i>Pinus elliottii</i> -variable	<35
sand pine	<i>Pinus elliottii</i> var. <i>elliottii</i>	25-45 [132]
South Florida slash pine	<i>Pinus elliottii</i> var. <i>densa</i>	1-15 [79,123,132]
longleaf-slash pine	<i>Pinus palustris-P. elliottii</i>	1-4 [79,132]
longleaf pine-scrub oak	<i>Pinus palustris-Quercus</i> spp.	6-10
pocosin	<i>Pinus serotina</i>	3-8
pond pine	<i>Pinus serotina</i>	3-8
loblolly pine	<i>Pinus taeda</i>	3-8
loblolly-shortleaf pine	<i>Pinus taeda-P. echinata</i>	10 to <35
sycamore-sweetgum-American elm	<i>Platanus occidentalis-Liquidambar styraciflua-Ulmus americana</i>	<35 to 200 [132]
eastern cottonwood	<i>Populus deltoides</i>	<35 to 200 [85]
mesquite	<i>Prosopis glandulosa</i>	<35 to <100 [74,85]
oak-hickory	<i>Quercus-Carya</i> spp.	<35 [132]
oak-gum-cypress	<i>Quercus-Nyssa</i> -spp.- <i>Taxodium distichum</i>	35 to >200 [79]
southeastern oak-pine	<i>Quercus-Pinus</i> spp.	<10
live oak	<i>Quercus virginiana</i>	10 to <100 [132]
cabbage palmetto-slash pine	<i>Sabal palmetto-Pinus elliottii</i>	<10 [79,132]
blackland prairie	<i>Schizachyrium scoparium-Nassella leucotricha</i>	<10
Fayette prairie	<i>Schizachyrium scoparium-Buchloe dactyloides</i>	<10 [132]
southern cordgrass prairie	<i>Spartina alterniflora</i>	1-3 [85]
baldcypress	<i>Taxodium distichum</i> var. <i>distichum</i>	100 to >300
pondcypress	<i>Taxodium distichum</i> var. <i>nutans</i>	<35 [79]

\*fire return interval varies widely; trends in variation are noted in the species review

#### POSTFIRE REGENERATION STRATEGY [125]:

Tree with adventitious bud/root crown/soboliferous species root sucker

Crown residual colonizer (on-site, initial community)

Secondary colonizer (on-site or off-site seed sources)

## FIRE EFFECTS

SPECIES: *Triadica sebifera*

- [IMMEDIATE FIRE EFFECT ON PLANT](#)
- [DISCUSSION AND QUALIFICATION OF FIRE EFFECT](#)
- [PLANT RESPONSE TO FIRE](#)
- [DISCUSSION AND QUALIFICATION OF PLANT RESPONSE](#)
- [FIRE MANAGEMENT CONSIDERATIONS](#)



James Grace, USGS Coastal Prairie Management and Restoration

### IMMEDIATE FIRE EFFECT ON PLANT:

Mature tallowtree typically survives or is top-killed by fire [37]. At the time of this writing (2005), there is no information regarding the effect of fire on tallowtree seeds.

### DISCUSSION AND QUALIFICATION OF FIRE EFFECT:

Tallowtree seedlings are more susceptible to fire than adults. The only immediate mortality Grace [37] observed after prescribed fire was that of 4-inch (10 cm) tall transplanted seedlings. Grace and others [38] reported decreasing mortality rate, generally decreasing occurrence of top-kill, and generally increasing survival rate with tallowtree height. The following table gives approximate values for these rates [38].

Height class	Died (%)	Top-killed (%)	Survived (%)
<0.1 m	100	0	0
0.1-1.0 m	40	~25	~35
1-2 m	~15	~60	~25
2-3 m	~3	~37	~60
3-4 m	0	~10	~90

Fuel biomass and continuity also affect tallowtree response. More tallowtree was burned in a prairie site (73-100%) than in an abandoned rice field (24-73%), because of a larger amount and more continuous fuels on the prairie site [37].

### PLANT RESPONSE TO FIRE:

Several factors influence the long-term impact of fire on tallowtree. Stage of development of the tallowtree stand is possibly the most important factor, due its influence on fuel characteristics (see the [Fire Ecology](#) section) [37,38]. Repeat burning of stands with enough fuels to carry a fire can eventually lead to declines in tallowtree dominance [37,38]. However, as tallowtree stands age they become increasingly resilient, due to increased ability of older trees to recover after fire and reduced severity of burns in woodlands with little fuel [37]. Once a "critical stand density" is reached burning will have little to no long-term impact on tallowtree stands [39]. This critical threshold is likely affected by season of burning and other fire and site characteristics [37,38,39].

### DISCUSSION AND QUALIFICATION OF PLANT RESPONSE:

Possible factors influencing tallowtree's response to fire include tree height, fuel characteristics, and season of burning. As already discussed, the height of tallowtree affects its ability to recover from fire. However, Grace and others [39] report that large isolated tallowtrees can be killed by repeated fires when there is enough herbaceous fuel

near their trunks. As mentioned in the [Fire Ecology](#) section, tallowtree persistence reduces fuel biomass over time [37,38]. Additionally, there is evidence that tallowtree stands in coastal prairies have understories that are forb-dominated. This results in a patchier, discontinuous fuel layer comprised of less flammable species than the original grassland vegetation [132]. These changes in fuel characteristics result in less severe fires, which are less likely to impact tallowtree [37,132]. Season of burning influences tallowtree's response to fire. Prescribed burns conducted during the growing season had larger long-term negative effects on tallowtree than those conducted when tallowtree was dormant, resulting in decreased growth and survival of basal sprouts [37,38].

Site conditions are also likely to have a large impact on tallowtree response. Soil moisture influences the impact a fire has on plants [46,110,118]. The amount of clay in soils may also affect tallowtree response by influencing water retention and insulating roots from the heat of a fire [122]. Conditions on some sites, such as slow fuel production or consistently wet fuels and soil, inhibit the use of fire as a tallowtree control technique in these areas.

There is some circumstantial evidence of lower tallowtree densities on burned compared to unburned sites. Smith and others [121] found more tallowtree in unburned than burned plots following prescribed burning in Cape Romain National Wildlife Refuge, South Carolina. Burns were conducted in winter and were of low severity, with most of the duff layer remaining unburned. Johns and others [49] reported lower tallowtree relative densities on a site which was successfully burned after clearcutting (41.5%) compared to larger tracts that had different postharvest treatments (85% and 80%). It is important to note that confounding factors, such as tallowtree seed availability or differences in site characteristics, were not eliminated as possible explanations for these observations.

#### FIRE MANAGEMENT CONSIDERATIONS:

Use of fire in communities with short presettlement fire return intervals is probably fire's most practical use in controlling tallowtree, since fire is most effective when used repeatedly and frequently. For example, repeated burning is used in combination with herbicides and mowing in the coastal prairie of the Armand Bayou Nature Center [43,84,91]. In addition to burning sprouts from tallowtree top-killed in previous burns and possibly causing increasing damage to older trees [37,38], the susceptibility of young tallowtree [38] means repetitive burns can substantially decrease recruitment. If conditions conducive to burning do not occur often enough to allow for burning frequencies that will reduce tallowtree dominance, other control methods are required. This will likely be the case in relatively mature tallowtree stands, wet areas, and sites where production of herbaceous fuels is low and/or patchy.

Potential for tallowtree to establish in the postfire environment is not documented in the literature. This is a concern due to its ability to establish following other types of disturbance [17,81,121,134]. Repeated burning mitigates, to some extent, the risk of postfire colonization of tallowtree. Managers using prescribed fire for other objectives should monitor burned sites for postfire establishment in areas where tallowtree occurs.

## MANAGEMENT CONSIDERATIONS

### SPECIES: *Triadica sebifera*

- [IMPORTANCE TO LIVESTOCK AND WILDLIFE](#)
- [OTHER USES](#)
- [IMPACTS AND CONTROL](#)

#### IMPORTANCE TO LIVESTOCK AND WILDLIFE:

Although tallowtree leaves, fruit and sap are toxic to many animals including cattle, several bird species eat the fruits and insects eat a limited amount of various parts.

**Palatability/nutritional value:** Tallowtree is toxic to several species including humans [29,35,69,124]. The toxic effect of tallowtree leaves and fruit on cattle was demonstrated by Russell and others [104]. However cattle have been reported to eat seedlings < 2.4 inches (6 cm) tall (M. Kramer pers comm in [8]). Sheep and goats are much less affected by tallowtree [104]. They have been reported to eat the leaves [2], although Sharma and others [109] note that goats in northern India do not eat tallowtree.

Several bird species eat tallowtree seeds [22,75,92,93] and are important dispersal agents. Winter residents eat tallowtree seeds more often than other birds ( $p < 0.001$ ) [22,92]. Species commonly observed eating tallowtree seeds include northern cardinals, red-winged blackbirds, gray catbirds, and red-bellied woodpeckers [22,92,93]. Baltimore orioles and yellow-rumped warblers comprised 72% of the foraging observations in coastal Texas [22], while northern flickers and American robins were important in South Carolina [92,93]. Given the importance of birds as dispersal agents and the possibility of competition with native plant species for dispersal agents [93], more research is needed on birds' preference for tallowtree seeds compared to native foods.

Few insects feed on tallowtree in the field. For example, Jones and Sharitz [54] observed much lower herbivory in tallowtree (mean 3.3%; range 0-5% of total leaf area) than in green ash (mean, 25.8%; range 5-75%). Much of the investigation of insect foraging on tallowtree has investigated the hypothesis that evolution of reduced defenses against herbivores due to low predation loads has allowed tallowtree to allocate more resources to increasing performance [113,115,116,117]. Despite evidence for reduced defenses compared to tallowtree from China [113,116,117], tallowtrees occurring in the southeastern U.S. do have some herbivory defense [71,102]. For instance, Cameron and LaPoint [11] showed that a terrestrial reducer ate leached and ground tallowtree leaves faster than unprocessed leaves. However, other species appear to benefit from eating tallowtree. Siemann and Rogers [117] found increased growth rates with increased amounts tallowtree foliage consumed ( $p < 0.05$ ) by grasshoppers. In laboratory trials, Lankau and others [65] found that grasshoppers preferred tallowtree over 3 native species ( $p < 0.05$ ). This and other experiments led them to conclude that behavioral avoidance of tallowtree, and not strong tree defenses, may cause the low tallowtree herbivory load. Other insects have been observed feeding on tallowtree. Johnson and Allain [50] reported a swarm of leaf-footed bugs feeding on the fruits of tallowtree in Brazoria National Wildlife Refuge, Texas, and on a prairie site approximately (80 km) northwest of Lafayette, Louisiana. Another Hemipteran has also been seen feeding on tallowtree fruits in this area, but at lower densities [50]. In addition, termites have infested tallowtree roots [61]. The effects of herbivory on tallowtree are discussed in the [Control: herbivory](#) section below.

Little information on the nutritional content of tallowtree is available. However, seeds have been reported to contain crude fat in quantities  $>25\%$  of dry matter [112]. In addition, the following table shows nutritional data (% dry matter) collected by Rockwood and included in a literature review by Rockwood and others [97].

Organic matter	Neutral detergent fiber, ash free	Digestibility by rumen microbes	Acid detergent fiber	Lignin	Nitrogen	Phosphorus
98.5	85.7	19.1	69.5	20.2	0.49	0.04

**Cover value:** The value of tallowtree as cover is uncertain. Small mammals such as cotton rats and harvest mice prefer other habitats over those containing tallowtree [59,60]. Use of specific layers of tallowtree forests by species of migrant birds, such as black-throated warblers and black and white warblers, suggest that tallowtree provides adequate cover for some bird species [24].

#### OTHER USES:

Tallowtree has many uses. The waxy seed coating is used in candles, soaps, and cosmetics in China and Japan [29,68,109,119]. It is also edible and can replace animal tallow when processed properly [109,119]. The seed oil is used in many applications. It is well known for its drying properties and is used in several products including varnishes, paints, and plastics [68,109]. In addition, tallowtree seed oil has potential as a biofuel, although the long-term effects of its use in engines has not been reported [1,105]. Meal from the seed kernel is high in protein and can be used as animal feed, fertilizer, or refined into flour for human use [109]. The leaves are used as a silk dye and as a fertilizer [68,109]. Tallowtree is also an important species in the honey industry [66,68,77]. Its use as an ornamental assists its spread into new areas [29,77]. Preliminary trial plantings suggested planting tallowtree as a cash crop was economically viable [106].

**Wood Products:** Although the white or yellow wood of tallowtree can be used for various objects, including printing blocks, toys, and furniture [68,109], it is most typically used as fuel. Several investigations of tallowtree's potential as a biomass fuel crop were conducted in the southeastern United States [96,97,107]. Tallowtree biomass production after 2 years was more than 5 dry tons per acre and on coppiced plots biomass production was over 7 tons per acre. Mean energy content of 18- to 24-year-old trees was 7,586 btu/lb with a range between 7,226 and 7,835 btu/lb [107]. Data from Rockwood and Geary [96] suggest annual yields could reach 24 dry metric tons per hectare.

**IMPACTS AND CONTROL: Impacts:** Invasion of coastal prairie and longleaf pine communities by tallowtree is a major concern, given the already limited distribution of these habitats [37,130]. The degree to which tallowtree can establish in these and other communities ([Distribution and Occurrence](#)), as well as the degree to which it can alter ecosystem processes such as fire frequency ([Fire Ecology](#)) and nutrient cycling ([Soil](#)), have been addressed in previous sections of this review. A summary of the literature investigating allelopathic effects of tallowtree is discussed in the [General Botanical Characteristics](#) section.

**Control:** Several reviews summarize different tallowtree control options [5,8,55,56,124]. In a literature review, Bruce and others [8] suggest that tallowtree control efforts should be maintained for 3 to 5 years and managed sites must be monitored. Due to tallowtree's ability to sprout following top-kill [37,96,107], these steps should be taken regardless of the method used. Ramsey and others [89] describe a technique for mapping tallowtree stands using infrared photography.

**Prevention:** : Fire and mowing are used to prevent tallowtree establishment. Details regarding the effects of fire on tallowtree can be found in the [Fire Effects](#) section. Regular mowing is used to prevent tallowtree invasion in the coastal prairie of Texas [43,84,115].

Educating the public about the consequences of using tallowtree as an ornamental and removing it from nurseries is an important step to reduce seed sources [72,87]. Putz and others [87] promoted replacing tallowtree with native species and enlisted the support of nurseries in Gainesville, Florida. Langeland [64] includes a list of ornamental species that are good alternatives to tallowtree in areas with an annual minimum temperature of 15 °F (-9.4 °C) or higher.

**Integrated management:** No information is available on this topic.

**Physical/mechanical:** As mentioned in the [Prevention](#) section, mowing can be used to prevent establishment of tallowtree. High-impact mechanical control techniques are typically used on insensitive sites, such as right-of-ways [5,56]. In more sensitive areas, mechanical treatment typically involves manual removal of seedlings and felling trees in place [8]. Due to the ability of tallowtree to resprout, mechanical techniques are almost always accompanied with herbicide application. Conway and others [25] conclude that mechanical harvest is best done during seed formation as this is when total nonstructural carbohydrate (TNC) concentrations in tallowtree roots are the lowest. Consideration should be given to reducing seeds left on a newly-cleared site, as successful recruitment is likely [5,56,124].

Flooding is not typically used in tallowtree control given its tolerance. However, Smith [122] has observed successful control of tallowtree with constant flooding for 36 months. Cutting below the water level has also been reported as a successful technique [5].

**Fire:** See the [Fire Management Considerations](#) section of this summary.

**Biological:** Only preliminary surveys of the feasibility of biological control of tallowtree have been undertaken [26,86,124].

**Herbivory:** : Grazing has been noted to prevent establishment of tallowtree [84]. However, in a personal communication cited by Bruce and others [8], Kramer reports that short-term rotation of high-density cattle herds is less successful in controlling tallowtree than in controlling groundsel-tree, despite cattle eating tallowtrees less than 2.4 inches tall (6 cm).

In addition, tallowtree appears to have at least short-term tolerance to herbivory by insects. Greenhouse experiments investigating the effect of herbivory have consistently found no effect of simulated insect herbivory on tallowtree from the southeastern U.S. under varying nutrient conditions [99,100,101]. However, an interaction between site and herbivory was observed in a field experiment, with tallowtree in grassland showing improved survival and mass with slightly decreased herbivore damage [115]. Despite overall higher damage from herbivores, tallowtree in the floodplain forest did not show any effects of decreased herbivory, suggesting that tallowtree is more susceptible to insect damage in areas with less suitable conditions. Although tallowtree shows high short-term herbivory tolerance,

there was a significant ( $p < 0.01$ ) negative correlation between amount of herbivory in the 1st year and survival from the start to the end of the 2nd growing season [115].

Chemical: Herbicides are widely used for controlling tallowtree [8,27,37,124], and guidance specifically for property owners is available [64]. Basal bark applications are preferred by many organizations including The Nature Conservancy and the Florida Department of Environmental Protection [5,8]. Conway and others [25] conclude that the period from "seed maturation until leaf fall" is the best time for foliar herbicide application, since the chemicals would be moved downward into the root system during this time, resulting in a higher probability of the death of the entire plant.

After chemical control, which is the most widely used tallowtree control method, seeds in the soil were reported sprouting 5 years after treatment began (Jubinsky unpub data in [8]).

Cultural: See [Prevention](#) for information regarding a public education campaign on tallowtree.

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