Paulownia tomentosa

INTRODUCTORY

Princesstree in postfire habitat in Linville Gorge
Wilderness Area, North Carolina.
Photo by Dane Kuppinger.

AUTHORSHIP AND CITATION:
Innes, Robin J. 2009. Paulownia tomentosa. 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/ [2010, February 8].

FEIS ABBREVIATION:
PAUTOM

NRCS PLANT CODE [140]:

PATO2

COMMON NAMES:
princesstree
princess tree
princess-tree
paulownia
royal paulownia
empress tree
imperial-tree
kiri tree

TAXONOMY:
The scientific name of princesstree is *Paulownia tomentosa* (Thunb.) Sieb. & Zucc. ex Steud. [45,73]. A review [3] stated that botanists have historically debated the taxonomic classification of princesstree, placing it within either the figwort (Scrophulariaceae) or trumpet-creeper (Bignoniaceae) family. Based on floral anatomy, embryo morphology, and seed morphology, princesstree is placed in Scrophulariaceae, a family of mostly herbaceous species [3,62,158]. Princesstree is a popular ornamental, and several cultivars have been developed [62,115,123].

SYNONYMS:
Paulownia imperialis Sieb. & Zucc. [62]

LIFE FORM:
Tree

FEDERAL LEGAL STATUS:
None

OTHER STATUS:
Information on state-level noxious weed status of plants in the United States is available at Plants Database.

DISTRIBUTION AND OCCURRENCE

SPECIES: Paulownia tomentosa

- GENERAL DISTRIBUTION
- HABITAT TYPES AND PLANT COMMUNITIES

GENERAL DISTRIBUTION:
Princesstree is nonnative in North America. It occurs from Montreal, Canada, south to Florida and west to Texas and Indiana; it has also been planted in coastal Washington [101] and California [62]. Princesstree has escaped from cultivation and spread extensively to portions of the southeastern and middle Atlantic states [63,95,126]. It is invasive from Pennsylvania south to Georgia and west to Missouri (see Impacts) [10,71]. The Plants Database provides a distributional map of princesstree in the United States.

Princesstree is native to eastern and central China [63,158], where it occurs south of the 32 °F (0 °C) isotherm (see Climate) [63]. With the exception of Antarctica, princesstree has been cultivated in every continent of the world [30,34,37,57,61,62,63,78,133,149]. It was most frequently introduced as a crop tree but also as an ornamental. Princesstree appears to be less invasive in Europe than in North America [43,115,133]. However, it has received research attention in Europe due to increases in the number of localities where it has been observed since the 1980s [43]. In Australia, princesstree is considered potentially invasive [30,62]; invasiveness in other foreign countries had not been reported as of this writing (2009).

HABITAT TYPES AND PLANT COMMUNITIES:
Plant community associations of nonnative species are often difficult to describe accurately because detailed survey information is lacking, there are gaps in understandings of nonnative species' ecological characteristics, and nonnative species may still be expanding their North American range. Therefore, princesstree may occur in plant communities other than those discussed here and listed in the Fire Regime Table.

Princesstree occurs in a variety of habitats and plant associations throughout the eastern United States that are similar to those of its native range (see Site Characteristics). It may be a minor, occasional, or important component of plant communities of which it is a part. For example, in debris avalanches following Hurricane Camille in central Virginia, princesstree established at densities ranging from 75 to 310 stems/ha on 3 of 4 study sites dominated by yellow-poplar (*Liriodendron tulipifera*), sweet birch (*Betula lenta*), black locust (*Robinia pseudoacacia*), and red maple (*Acer rubrum*); in this study, its importance value ranked 12th among 15 tree species recorded [64]. In a streamside forest in central Virginia, it had the lowest importance value among the 4 dominant forest trees of the study area (yellow-poplar, sweet birch, and sycamore (*Platanus occidentalis*)) [146]. In northern Delaware, princesstree was present in 1 of 12 study sites; the site was a relatively undisturbed hardwood forest dominated by yellow-poplar, American beech (*Fagus grandifolia*), black oak, (*Quercus velutina*), white oak (*Q. alba*), and red oak (*Q. rubra*) [122]. In intact forest of Loess Bluff Ravines in western Kentucky, Bryant [22] reported low importance of princesstree in sugar maple (*Acer saccharum*)-American beech-sweetgum (*Liquidambar styraciflua*) forest; in this study, princesstree ranked 21st in relative importance among 27 tree species. Although Bryant [22] considered princesstree a minor component of plant communities across all 4 counties covered by Loess Bluff Ravines, Wilson [150] categorized it as a possible indicator species of the Backcut Loess habitat in Sandy Branch, a part of Loess Bluff Ravines in Carlisle County, Kentucky.

In other parts of the eastern United States, princesstree occurs in disturbed upland areas associated with early-successional species such as maple (*Acer* spp.), oak (*Quercus* spp.), and pine (*Pinus* spp.). Common associates on disturbed sites in Blue River Gorge in the Blue Ridge Mountains of Virginia include Virginia pine (*P. virginiana*), red maple, American elm (*Ulmus americana*), blackjack oak (*Q. marilandica*), eastern redbud (*Cercis canadensis*), sassafras (*Sassafras albidum*), sweet birch, and smooth sumac (*Rhus glabra*) [109]. Princesstree was described as an "aggressive" invasive species within disturbed areas at the Oak Ridge National Environmental Research Park in Tennessee; at this site, adjacent uplands were characterized by 2nd- and 3rd-growth oak-hickory-maple forests [44]. In the Great Smoky Mountains National Park, Tennessee, princesstree occurred by streams with yellow-poplar, sweet birch, and sycamore [8]. In eastern Pennsylvania, princesstree was a minor component in a 5-acre (2 ha) mixed-hardwood forest gap. Allegheny blackberry (*Rubus allegheniensis*) and American pokeweed (*Phytolacca americana*) dominated the vegetation of the tornado-formed gap [66]. Along the Green River Gorge, North Carolina, princesstree was locally abundant within disturbed cove hardwood forest dominated primarily by yellow-poplar and basswood (*Tilia americana*) [107]. Along a 250-mile (402 km) reach of the New River Gorge in West Virginia, princesstree was found at 5 of 34 sites; these sites included a yellow-poplar-white oak-red oak-sugar maple forest, midelevation quartzite rocky summits and cliff faces, a black willow-river birch (*Salix nigra-Betula nigra*) streambed, and disturbed areas [128]. In Bent Creek Experimental Forest in Asheville, North Carolina, it was a minor component in 4-year-old postclearcut forest dominated by yellow-poplar, sweet birch, black locust, and sassafras [89]. In the Appalachian Mountains from central Pennsylvania to northern Georgia, princesstree occurred in fire-adapted Table Mountain pine-pitch pine (*Pinus pungens-P. rigida*) forests, which commonly occur on xeric ridgetops and southwest-facing slopes at midelevations [40,148]. Princesstree occurs frequently on burned ridges with pitch pine and bigtooth aspen (*Populus grandidentata*) on Bull Run Mountain in northern Virginia [2]. In Great Falls Park in Fairfax County, Virginia, it occurred in American beech-white oak-red oak-yellow-poplar forest with American holly (*Ilex opaca*) and Christmas fern (*Polystichum acrostichoides*) in the understory [124]. At Inwood Hill Park in New York County, New York, princesstrees >4 inches (10 cm) DBH were found in valley forest and ridgetop communities at densities ranging from 0 to 13 stems/ha [46]:

Density per ha of subcanopy (10-30 cm DBH) and canopy (>30 cm DBH) princesstree found in 2 forest types in Inwood Hill Park, New York [46]		
	DBH (cm)	
Forest type	10-30	>30
Valley	0	9
Ridgetop	13	13

Sugar maple, yellow-poplar, red oak, chestnut oak, black locust, and black cherry (*Prunus serotina*) dominated the canopy and subcanopy of the valley forest community in this area. Yellow-poplar, white oak, and red oak dominated the canopy of the ridgetop community, while mulberry (*Morus* spp.), black cherry, plumleaf crab apple (*Pyrus prunifolia*), and red maple dominated the subcanopy [88]. For more information regarding the ecological range of princesstree, see Site Characteristics and Successional Status.

BOTANICAL AND ECOLOGICAL CHARACTERISTICS

SPECIES: Paulownia tomentosa

Princesstree in flower.
Photo courtesy of Leslie J. Mehrhoff, University of Connecticut, Bugwood.org

GENERAL BOTANICAL CHARACTERISTICS:

- **Botanical description**

- **Raunkiaer life form**

Botanical description: The following description of princesstree provides characteristics that may be relevant to fire ecology and is not meant for identification. Keys for identification are available (e.g., [45,63,104,108,158]).

Princesstree is a deciduous tree [10,62] that may reach 69 to 105 feet (21-32 m) in height and 3.9 to 6.6 feet (1.2-2.0 m) DBH at maturity, although it is typically smaller [10,41,49,126]. At maturity, it has thin, flaky bark [126]. Princesstree tends to be branchy or multistemmed when grown in the open but can have a straight bole in forests [78,130,133]. Branches are stout but brittle, because the pith is chambered or hollow and markedly flattened at the nodes [10,41,126]. Leaves of adult trees are typically 6 to 12 inches (15-30 cm) long and 4 to 8 inches (10-20 cm) wide. However, leaves of juvenile plants and those of stump sprouts may be much larger; for example, juvenile leaves have been observed as long as 3 feet (0.9 m) [51,138], and leaves of stump sprouts may reach 20 to 30 inches (50-80 cm) or more in length (see Vegetative regeneration) [10,41,108,126]. Brittle branches and large leaves make princesstree prone to wind damage and as a result, twigs, seed capsules, and other debris frequently accumulate under the tree canopy [15,62,115,130]. The inflorescence is a large, erect terminal panicle 6 to 12 inches (15-30 cm) long with 2- to 2.5-inch (5-6 cm) long, tubular flowers. The fruit is an oval, 2-part capsule, 1 to 2 inches (2.5- 4 cm) long and 1 inch (2.5 cm) in diameter [10,41,62,126]. Each part of the capsule has 2 compartments that contain very small (1.5-3 mm long), winged seeds [10,17,108]. The capsules and large, fully-developed flower buds are conspicuous in winter [126]. Roots can be relatively shallow to deep and well developed, apparently depending upon soil conditions. They are typically widely spreading without a strong taproot [4,10,29,62,63,79,130,158].

A clumped stand structure can result from even-aged seedling establishment after disturbance or from expansion through root sprouting [41,96]. Establishment of princesstree in streamside forest in Virginia associated with the large-scale disturbance of Hurricane Camille resulted in even-aged princesstree stands 10 years after the hurricane [146]. Forty-three percent of recorded princesstree populations in Austria resided within monospecific stands; this was attributed to the species' ability to invade extremely dry sites after disturbance [43].

Life span: Princesstree is apparently short lived. According to a review, mature princesstrees are often structurally unsound and rarely live more than 70 years [10]. However, another review reports that its life span is over 125 years [78].

Raunkiaer [110] life form:
Phanerophyte
Geophyte

SEASONAL DEVELOPMENT:
According to reviews, princesstree pollen is fully developed before winter [62], and pollination occurs in spring [10,102]. Flowers bloom before the leaves begin to emerge in late April or early May [41,65,123]. Leaf expansion begins about 2 weeks after flowering. Flower buds begin to appear in the leaf axils in late July or early August [24,51,63]. They develop through summer, mature in October, and are visible as terminal panicles after leaves fall in autumn [24,51]. Leaves are retained in autumn until after the first frost [123]. Seeds mature in September, and capsules ripen and open in October [27]. The capsules may remain on the tree for long periods [65]. The capsules break open and seeds are disseminated by wind throughout winter and into spring [16].

REGENERATION PROCESSES:

- **Pollination and breeding system**
- **Seed production**
- **Seed dispersal**
- **Seed banking**
- **Germination**
- **Seedling establishment**

- **Plant growth**
- **Vegetative regeneration**

Princesstree reproduces from seed and by sprouting from adventitious buds on stems and roots [37,63]. It apparently sprouts with or without top-kill [101]. Both methods of reproduction are important to its reproductive success and invasiveness.

Pollination and breeding system: Flowers are pollinated by a variety of nectar- and pollen-feeding insects [10,102].

Seed production: Princesstree produces many small, light seeds. Seeds weigh about 0.17 mg each [16,31,138]. A single seed capsule may contain as many as 2,000 seeds [10,62], so an individual tree may produce 20 million or more seeds/year [130]. In a review, Bonner [17] provides the following information on princesstree fruit and seed collected in southeast Arkansas:

Measures of princesstree fruits and seeds in Arkansas [17]	
Fruits/L	88
Seeds/fruit	2,033
Seeds (g)/fruit (L)	28
Seeds/g	6,200
Moisture content (% fresh weight)	7

Princesstree reaches reproductive age early. Time to maturity depends upon environmental conditions. It may flower in favorable environments in its 4th or 5th year [78,79,101]; under cultivation it may flower as early as the 3rd year [130]. Hu [63] reports that *Paulownia* first flowers at 8 to 10 years of age under "suitable" conditions in China.

Seed dispersal: The small, light, winged seeds of princesstree are easily transported by wind and water over considerable distances [10,41]. Field observations suggest that seedlings are occasionally located more than 2 miles (3 km) from parent trees in mountainous regions of North Carolina and Tennessee [79,84]. This evidence led Kuppinger [79] to suggest that "only the largest blocks of uninvaded forest may have areas where invasion of princesstree is precluded by distance-induced dispersal limitations".

Seed banking: Although there is disagreement regarding the persistence of princesstree seeds within the seed bank, it appears that princesstree develops a transient seed bank. Seeds can survive in the soil seed bank for at least 2 to 3 years [67,79,90]. They may persist longer [36,90], but long-term field studies on princesstree seed longevity were lacking as of 2009 [17].

Some studies found evidence for a persistent princesstree seed bank. The species composition and density of seeds within the seed bank of 2nd-growth deciduous forest soils were examined in eastern Tennessee. Seeds were collected at 3 depths (litter layer, 0-2 inches (0-5 cm), and 2-4 inches (5-10 cm)) and germinated in a greenhouse. Viable princesstree seeds were found at each depth, but a majority (82%) of the germinants emerged from the 0- to 2-inch and 2- to 4-inch soil depths. The author concluded that the presence of viable seeds at depths as great as 4 inches (10 cm) was a strong indication that princesstree seeds may accumulate and remain dormant in the seed bank for long periods of time, and that this species "might be expected to appear should the canopy open up and early successional conditions prevail" [36]. In field experiments in Ohio, mortality of princesstree seeds was relatively low (21% (SE 3.3)) after 3 years. Seed dormancy was variable and significantly affected by harvest date, soil profile position, and location ($P<0.001$ for all variables). The author concluded that princesstree formed a persistent seed bank and estimated that seeds could survive in the soil for up to 15 years [90].

In contrast, no evidence of a persistent princesstree seed bank was found in soils of American beech-northern red oak-white oak-black oak-scarlet oak (*Q. coccinea*) forest in southeastern Pennsylvania. In this study, low seed survival rates (<30%) and low germination (1.7%) under field conditions over the course of 2 years suggested that princesstree did not form a persistent seed bank. These authors characterized princesstree's seed bank as large, with very high turnover and little between-year build-up, and suggested that seed banking was probably not important to princesstree regeneration [67]. High density of princesstree seeds within the seed bank may not indicate high rates of germination and establishment after disturbance. Hyatt [66] observed that princesstree seeds "rarely, if ever, germinate" in wildlands and "when they do germinate, they rarely survive more than a year" (see Seedling establishment).

Long-distance dispersal and prolific seed production of princesstree apparently allow it to establish a transient seed bank from on- and off-site sources. In 2nd-growth deciduous forest soils of Tennessee, viable princesstree seed was found in the seed bank, though no mature princesstrees were present in the overstory [36]. Similarly, though no mature princesstrees were present within the vegetative overstory, seed was observed in the seed bank of the pine (pitch pine and shortleaf pine (*Pinus echinata*)) barrens region of southern New Jersey and a Delaware River tidal freshwater marsh in northern New Jersey [86,92]. In debris avalanches following Hurricane Camille, princesstree established at densities up to 310 stems/ha, despite its absence from adjacent, undisturbed hardwood forest [64]. Similarly, it was very abundant (18%) in the seed bank in southeastern Pennsylvania at a site dominated by oak (red oak, white oak, and black oak) and American beech; however, only 2 mature princesstrees were present [66].

Germination: Princesstree seed longevity appears to be relatively short (see Seed banking). Seed germination capacity decreases from the time of dispersal even under optimal storage conditions in the laboratory [27,34,51,52]. One study found that cold-stratified seeds frequently maintained high germination rates (>90%) in the laboratory even after 3 years [17]. Other studies report that germination of cold-stored seeds appeared to decline sharply after 4 years, with highest germination occurring <2 years from the time of dispersal [26,51,52].

Unlike seeds of many native trees that commonly occur with princesstree (e.g., oak, beech (*Fagus* spp.), and aspen (*Populus* spp.)), princesstree seeds can maintain high viability despite dehydration [9]. The seeds require light for germination [18,157]. The light requirement for germination was considered "unusually high" when compared with other species [31]. The actual period of illumination required ranges from minutes to hours and varies with seed source, year, and storage conditions [18,55].

Princesstree seeds are not dormant when dispersed from the mother plant [17,79,155]. In Arkansas, 90% of seeds germinated within 19 days of collection [17]. Thus, fresh, wind-blown seeds dispersed in late summer and early fall may germinate immediately if they reach suitable habitat [63]. Secondary dormancy can be induced by unfavorable environmental conditions after dispersal. Seeds can be readily induced into secondary dormancy in the laboratory by moist or dry stratification at cold temperatures (approximately 40 °F (4 °C)) or imbibing seeds in darkness [55,157].

The effect of secondary dormancy on germination is highly variable and partially depends upon the amount of time in darkness and the duration of the low temperature exposure [54,79]. Secondary dormancy may alter the time to germination and the rate of germination in this species, and in some cases, it may reduce or eliminate the light requirement of the seed and expand the range of temperatures in which germination occurs [7,17,27,28,51,52,54,157]. Seeds overwintered in the seed bank may achieve high germination rates in the spring [7,27] despite low light or temperature. Seeds may acquire secondary dormancy but fail to germinate if the conditions for breaking the dormancy are not met. In the laboratory, numerous mechanisms break secondary dormancy in princesstree (see [90] and [54] for more information). Smoke was an important chemical stimulus for the germination of seeds in the laboratory (see Fire Management Considerations) [132].

According to reviews, princesstree prefers high light, exposed mineral soil, and adequate moisture for germination and establishment [18,26,63,130]; however, results of experimental studies are variable and often difficult to reconcile given the effect of environmental conditions on germination capacity and dormancy. In field experiments in Ohio, germination of naturally cold-stratified seeds was measured on different substrates and across light (intact forest, edge, and 7-year-old clearcut) and substrate (bare mineral soil, sand, gravel, cobble, top soil, and leaf litter) gradients. Germination was low overall (15%) and occurred only under full light (clearcut). During the 1st year of the study, a drought year, germination was observed only in cobble and gravel. In the 2nd year, with average precipitation, germination was significantly greater on bare mineral soil than any other substrate (P=0.05). The difference in germination between the 2 years was attributed to presence of moist microclimates in the cobble and gravel during the drought. Seeds buried 2 inches (5 cm) in the soil had greater tendency to become dormant and had lower mortality than seeds stored at the soil surface [90]. In contrast, a greenhouse study subjected seeds that had been dry-stored at ambient temperatures to 2 light treatment levels (full sun and 50% shade), 2 surface-cover treatment levels (bare soil and 1-inch (2 cm) litter cover), and 3 seed position treatments (litter surface, soil surface, and 1 inch beneath the soil surface). Germination rates under 50% shade were significantly higher than germination rates under full sun, with the highest germination levels recorded under 50% shade in bare soil on the soil surface ($P<0.001$ for all variables). In addition, germination was significantly lower when litter was present than when litter was absent regardless of light level, and buried seeds had significantly lower germination rates than those on the soil surface ($P<0.001$ for all variables) [79]. Despite their contrasts, these studies agree that leaf litter inhibits germination of seeds and that buried seeds will likely remain dormant until disturbance brings them up to the soil surface. See Site Characteristics for additional information on the effects of soil moisture, pH, fertility, and texture on seed germination.

Seedling establishment: Princesstree seedling establishment may be infrequent and widely scattered [26,62,66,129,152]. For example, on Staten Island, New York, seedlings volunteered on a restored landfill site planted with native woody species. A year after restoration plantings, princesstree count on fifty 10 × 30 meter plots totaled 1 seedling, among the lowest of 32 volunteer taxa [113]. Many studies have detailed the difficulties of establishing princesstree in plantations in the United States under intense silvicultural practices and controlled environmental conditions (e.g., [13,127]). Even so, princesstree has successfully expanded its range through seeding establishment [113] and may be more common than indicated in the literature. For example, princesstree was characterized as the 2nd and 5th most successful nonnative tree invading native communities in the Northeast [102] and Southeast [97] as of 1986 and 2008, respectively (see Impacts).

Plant growth: Once established, princesstree growth may be rapid [41,58], and survival may be high [129] even in harsh environments, but reports are variable. Aboveground growth of seedlings is typically slow during the first year [34,62], when seedlings invest heavily in belowground growth [90,91]. Johnson and others [70] report a 220% increase in root growth of young seedlings over a 3-year period in field experiments in Virginia. Rapid seedling root development makes this species difficult to control (see Control). A shift in emphasis from belowground to aboveground biomass accumulation occurs between the 1st and 2nd year [90]. In reviews, height increases of over 7 feet (2 m)/year have been reported for cultivated *Paulownia* seedlings [37]. Many authors report findings on perhaps extraordinary individuals. A 20-year-old princesstree observed in Kentucky had a diameter of 14 inches (36 cm) and reached a height of 62 feet (19 m) [144]. Typically, however, growth rate is much less. For example, mean annual height growth of seedlings after direct seeding on surface-mine spoils in eastern Kentucky averaged 24 inches (60 cm)/year [129]:

Establishment and growth of princesstree 1 and 5 years after direct seeding on surface-mine spoils in eastern Kentucky [129]

Stocking* after 1st growing season (%)	Stocking* after 5 years (%)	Survival after 5 years (%)	Mean height after 1 year (cm)	Mean height after 5 years (cm)	Mean annual growth/year (cm)
1	<1	80	11.3	250.5	60

*Stocking defined as the percent of direct-seeded plots (n=1,080) with princesstree seedlings.

Johnson and others [70] report high survival of seedlings on control plots 1 year after planting (99.5% in 1994) but decreased survival in subsequent years (range: 44.8% in 1995 to 10.7% in 2000). Low survival of seedlings in this and other studies has been attributed to late spring frosts, drought, disease, damaging wind, herbivory, and interference from neighboring vegetation [15,70,90,98,105].

Light availability can impact seedling establishment, survival, and growth. Photoperiod is an important factor influencing seedling height growth, with rate and duration of height growth increasing with lengthening photoperiod in the laboratory (e.g., [24,68,116]). Photoperiod also influences root development. Root length of princesstree seedlings increased nearly 2-fold when the photoperiod was increased from 8 to 12 hours in the laboratory ($P=0.05$); increasing photoperiod beyond 12 hours further increased mean root length, but not significantly [24]. When the effects of herbivory were removed, princesstree seedlings planted in 7-year-old clearcut oak (white, red, and black oak)-hickory (pignut (*Carya glabra*) and shagbark hickory (*C. ovata*)) forest had greater percent survivorship (70.5% (SE 5.9)) than seedlings in either edges (47.5% (SE 3.6)) or intact forests (48.5% (SE 6.3), $P<0.05$), perhaps due to greater light availability in clearcuts. Plants in low light (intact forest) had slower growth rates, thinner leaves, and higher specific leaf area and leaf area ratios than those in edges and clearcuts [90]. See Site Characteristics for additional information on the effects of soil moisture, pH, fertility, and texture on seedling establishment and plant growth.

Vegetative regeneration: Vegetative regeneration is important to princesstree's persistence and spread because sprouting may allow an individual to persist after defoliation or disturbance. Princesstree sprouts from adventitious buds on stems and roots, apparently with or without top-kill [4,10,29,37,62,63,79,115,130,158]. Sprouts generally grow faster than seedlings. For example, root sprouts may grow to over 15 feet (5 m) in a single season [10]. Thus, coppicing is a common strategy employed by nurseries and plantation farmers to stimulate rapid growth of seedlings (e.g., [130]), which are typically slow growing initially (see Plant growth). In a common garden experiment, seedlings subjected to cutting sprouted at 4 weeks after germination even in low light, although older seedlings and those grown in full sun were more likely to survive and produce new shoots. Cut plants had greater mortality than uncut plants overall [91].

SITE CHARACTERISTICS:
Little information is available on princesstree's natural habitat in China, largely because princesstree has a long history of cultivation there, and much of its native range has been altered by human activities [62]. In China, princesstree is a minor component of the deciduous mesophytic forest, growing chiefly in mesic ravines, open valleys, and disturbed areas associated with species of maple, ash (*Fraxinus* spp.), oak, chestnut (*Castanea* spp.), basswood (*Tilia* spp.), and pine [62,63]. The following distribution information of princesstree in China is provided by Zhu and others [158]:

Distribution of princesstree in its native range in China [158]	
Range	
Latitude	28-40 °N
Longitude	105-128 °E
Altitude (m)	1,500
Temperature (°C)	
Maximum	40
Minimum	-20
Rainfall	
Annual (mm)	500-1,500
Dry months	September to March
Soil	
pH	5-8.5
Texture	light clay to sand

In the eastern United States, princesstree occurs in a variety of disturbed, high-light environments including forest gaps and edges, streambanks and scoured riparian areas, steep rocky slopes—particularly south slopes where solar radiation is high—roadsides, fencerows, vacant lots, and "waste" places [10,11,31,41,49,51,58,71,85,93,108,112,126,130,138,146,147,153]. Seed germination and seedling establishment are optimum in disturbed areas with exposed mineral soil, high light, and little to no litter (see Germination) [18,63,130]; thus, princesstree frequently establishes and spreads after disturbances that create these conditions, such as fire, windstorms, pestilence, floods, landslides, and anthropogenic disturbances such as construction, cultivation, mining, and logging [10,44,51,64,84,90,97,113,118,131,146]. See Impacts for more information.

Soils: According to reviews, princesstree tolerates a variety of soil types and conditions including low fertility, high acidity, and drought [10,37,112,130] but grows best on moist, uncompacted, well-drained soils [14,17,37,51,52,127,133,138]. In Virginia, field observations suggest that drought may have reduced princesstree seedling survival and growth [70]. In field experiments in Ohio, overall survivorship of experimentally planted seedlings across 3 habitats (intact forest, edge, and clearcut) was reduced in a drought year ($P<0.0001$) [90].

Best growth of princesstree is obtained within strongly acidic to mildly alkaline pH levels (range: 5.5-7.5) [14,52,95,127,130,133,136,143,158]. High soil acidity adversely affects germination and seedling growth [136]. Germination, as well as seedling root and shoot growth, are typically poor at soil pH of <4.0, but seedling growth may be reduced at soil pH of <5.0 [95,136]. Seeds are likely killed at soil pH of <2.5. A gradual increase in seed germination was observed in the laboratory from pH 4 to pH 7, with 79% and 98% germination at pH 4.0 and 7.0, respectively. Time required for maximum seed germination was negatively correlated with acidity ($r^2=0.96$, $P<0.05$). Princesstrees in treatments with soil pH of <5.0 germinated more quickly and primary root growth occurred more slowly than princesstrees in treatments with soil pH of >6.0 [136]

Soil texture may play a role in princesstree's invasiveness. In general, sandy or loamy soils with low clay content appear optimum [14,52,127,158]. In China, princesstree generally grows on soils where clay content is <10% [158]. In the United States, production guides recommend planting princesstree on soils with <30% clay content [52,74]. In urban wetlands of northeastern New Jersey, princesstree abundance increased as soil sand content increased (odds ratio=0.91, $P=0.001$) and clay content decreased (odds ratio=1.07, $P=0.01$) [42]. Princesstree growers in the southeastern Piedmont region of Virginia reported decreased growth and survival on heavy clay soils; however, intense soil disturbance (i.e., soil trenching) ameliorated the effects of heavy clays [70].

In general, survival of seedlings appears highest in disturbed soils. For example, in field experiments in Illinois, survival of seedlings was significantly higher ($P=0.01$) on sites that had been plowed and disked (68%) than on zero-till sites (40%); these results were attributed to improved aeration of the uncompacted soils and to reduced cover of fescue (*Vulpia* spp.) and other annual grasses that resulted from the disturbance [5].

Nitrogen and phosphorus are essential for tree growth. Since fire may result in substantial short- and long-term changes in availability of these nutrients (see [76] for a review), knowledge of princesstree's nitrogen and phosphorus requirements may yield important information regarding its postfire establishment and spread. In general, princesstree is tolerant of low soil fertility but grows better in fertile soils, responding favorably to fertilizer by increasing growth [15,37,127]. Melhuish and others [95] report that nitrogen and phosphorus levels providing the best growth for princesstree seedlings in a field experiment (100 N:5 P) were about half those required by native red maple, indicating that princesstree may be more competitive than red maple in soils low in nitrogen and phosphorus. However, the authors note that the study was limited in scope and that further tests—including higher phosphorus levels—should be conducted [95]. Results of Jia and Ingestad [69] suggest that higher levels of phosphorus than those reported by Mehuish and others [95] are optimal for princesstree. These authors conducted an experiment to determine the optimum nutrient proportions for princesstree and found that high relative growth rate was obtained at 100 N:75 K:20 P:8 Ca:9 Mg [69]. High nitrogen levels may allow princesstree to increase chlorophyll content of leaves and maintain growth in low light [90]. *Paulownia* is endomycorrhizal [37,106], but according to Donald [37] the genus is not strongly dependent upon symbiotic fungi for resource uptake.

Climate: Cold climates may limit princesstree's establishment and spread. Early and late frosts and minimum winter temperatures apparently limit princesstree's establishment and spread in the United States [43,70,98,127,158]. In China, princesstree occurs south of the 32 °F (0 °C) isotherm [62,63] in areas that receive mean annual rainfall from 20 to 120 inches (500-3,000 mm) [37]. In the United States, it is typically not invasive in regions where temperatures drop below 32 °F (0 °C) for long periods [38,63,95,126]. USDA hardiness zones 7 to 10, where average annual minimum temperatures range from 0 to 40 °F (-18 to 4 °C) [72], are considered most favorable for princesstree [10].

When fully dormant, mature princesstrees can withstand temperatures as low as -13 °F (-25 °C), but individual plants are more susceptible to frost damage when actively growing or young and are damaged by 14 °F (-10 °C) or lower temperatures [37]. Damage to seeds by low temperatures is unknown, but seeds can be dry-stored at -4 °F (-20 °C) without losing viability [114]. Princesstree may be top-killed by low temperatures [13,37,48,81,98,126]. Following damage by cold, plants typically sprout [13,37,98,126]. In some cases flower buds are damaged by extreme cold, as observed by Braun [19] in Ohio. Thus, the reproductive potential of an individual can be greatly limited in cold climates even if individual trees survive. Predicted climate change might result in princesstree spreading beyond its current distribution, pushing altitudinal limits upwards and latitudinal limits northward of its current range [118].

SUCCESSIONAL STATUS:
Princesstree is an early-successional species that is intolerant of shade [53,90,147]. It possesses many characteristics often associated with early-successional species and invasive behavior: 1) copious production of small, wind-dispersed seeds, 2) rapid growth of seedlings, 3) strong shade intolerance and "poor competitive ability", 4) early age to first reproduction (<10 years), and 5) sprouting ability [63]. Apparently due to growth interference by neighboring vegetation and an inability to reproduce in shade, princesstree is a transient invader following disturbance [79].

Princesstree is frequently described as having "poor competitive ability", particularly during the first few years of age [4,12,14,16,34,37,52,63,138]. Many authors have demonstrated that treating neighboring vegetation with herbicides increases princesstree seedling survival and growth (e.g., [4,12,145]). However, the influence of neighboring vegetation on princesstree is variable. Hyatt and Casper [67] concluded that native Allegheny blackberry in an eastern Pennsylvania mixed-hardwood forest gap inhibited American pokeweed seed input and increased seed mortality ($P<0.05$); however, no significant effect on princesstree seed input, germination, or survival was observed [67].

Field observations in Illinois suggested that if other vegetation overtops and shades princesstree within the 1st year of establishment, princesstree survival may be low [4]. A shift in the distribution of princesstree seedling heights during the first 4 years following fire in the Linville Gorge Wilderness Area, North Carolina, suggested that surviving individuals were those that grew faster than and thus stayed above the regenerating vegetation or were in a location where regeneration of all vegetation was slow. The author surmised that although similar shifts occur in most species over time, the relative rapidity of the shift suggested that a lack of persistence of princesstree in some portions of the postfire landscape may be due to its "poor competitive ability" [79].

If princesstree seedlings grow fast enough to remain in the canopy, survival may be high. Seedlings over 5 feet (1.5 m) tall can create sufficient leaf surface area to shade out undergrowth [15]. Longbrake [90] concluded that once princesstree establishes, "competition will not hinder its invasive potential"; instead, light availability is apparently the dominant factor influencing its growth. Seedlings can acclimate to low light; however, growth is slower [91] and according to Zhu and others [158], around 70% shade may be fatal to princesstree saplings.

Recovery of midsuccessional vegetation after disturbance may create unsuitable conditions for princesstree. Without repeated canopy-opening disturbance, princesstree is likely to remain suppressed in the understory [64,90]. It is rarely present in the canopy of mature forests [64,93]. Even if it persists in the tree canopy, the requirements of high light and bare soil for seed germination may lead to reproductive failure beneath the canopy of mature trees [64]. Hu [62] suggests that by the time *Paulownia* grows to maturity, the seeds it produces likely cannot survive within the same habitat as the parent plant because the succeeding vegetation has "modified the physical environment so much that no new *Paulownia* has any chance to get established". Thus, princesstree may not alter the successional pathways of some native ecosystems.

Relatively poor quality sites—for example, those with low fertility and frequent drought—may provide better survival for princesstree in the long term [4]. Over time in the Linville Gorge Wilderness Area, princesstree became increasingly limited to the most xeric portions of the landscape, such as slopes and ridgetops, where native plant regeneration was low. The distribution of princesstree 1 and 4 years after fire indicated that princesstree habitat contracted over this 4-year period; habitat losses were more concentrated on mesic sites, at relatively low elevations, and on relatively flat slopes. Princesstree was reduced mainly where fire severity was low, moisture availability was high, and native plants were regenerating well [79].

Princesstree in postfire habitat in Linville Gorge Wilderness Area, North Carolina.
Photo by Dane Kuppinger.

The frequency and scale of disturbance may be important to establishment and persistence of princesstree [90]. Several reviews note that princesstree invasion of native forests may be primarily facilitated by large-scale disturbances, which are more likely to result in reduced interference from other vegetation, high light, and exposed mineral soil necessary for optimal establishment [24,144,146,147]. Establishment of princesstree in a streamside forest after Hurricane Camille peaked immediately following the hurricane and decreased over time. Sixteen years after the disturbance, no new individuals were recruited. The author attributed this to a lack of disturbance since the hurricane and overshading by native vegetation [146]. No new princesstrees were recruited 3 years after the initial postfire recruitment phase in Linville Gorge Wilderness Area. Approximately 5,000 acres (2,000 ha) of the Wilderness Area burned [111], with severity ranging from low-severity surface fire to high-severity crown fire [79]. Princesstree recruitment after postfire year 3 may have failed due to increased competition for light by regenerating native vegetation that limited germination of seeds after that time (see Impacts) [79]. Although frequent disturbance may sometimes promote establishment and spread of princesstree, there are exceptions. For example, princesstree established on sandy and silty bars of Plummers Island, Maryland, along with eastern cottonwood (*Populus deltoides*), green ash (*Fraxinus pennsylvanica*), southern catalpa (*Catalpa bignonioides*), sycamore, silver maple (*Acer saccharinum*), and boxelder (*Acer negundo*), but was rarely able to survive past the first year's growth because princesstree seedlings died when the bars flooded the following winter [117].

FIRE EFFECTS AND MANAGEMENT

SPECIES: Paulownia tomentosa

- FIRE EFFECTS
- FUELS AND FIRE REGIMES
- FIRE MANAGEMENT CONSIDERATIONS

Princesstree in postfire habitat in Linville Gorge Wilderness Area, North Carolina.
Photo by Dane Kuppinger.

FIRE EFFECTS:

- **Immediate fire effect on plant**
- **Postfire regeneration strategy**
- **Fire adaptations and plant response to fire**

Immediate fire effect on plant: The aboveground portion of princesstree is probably easily killed by fire. The brittle branches, thin, flaky bark, and large leaves with a high surface-to-volume ratio suggest that it has good potential for crowning fires; however, crowning fire behavior has not been reported for princesstree as of this writing (2009). Although princesstree roots are frequently shallow [4,10,29,62,63,130,158], even the most severe fires rarely damage plant tissues below 2 inches (10 cm) in the soil [119]; thus, many roots are probably insulated from heat damage by soil and likely survive low- to moderate-severity fire.

The effect of fire on seeds depends upon fire severity. In a laboratory experiment, Kuppinger [79] found a significant negative relationship between germination and the maximum temperature experienced by princesstree seeds ($P<0.05$). In this study, a series of "burn events" were simulated by placing seeds in a wire mesh bag at 3 depths (on the litter surface, on the soil surface, and buried at 0.8-inch (2 cm) depth) and exposing them to a range of fire temperatures (approximate range: 77-437 °F (25-225 °C)) for as long as 210 seconds. After the burn events, seeds were germinated in a greenhouse. Results showed that seeds were exposed to decreased temperatures with increasing soil depth, making princesstree seeds on the soil surface more vulnerable to fire-induced mortality than those in the soil. Less than 0.1% of seeds from all depths germinated when soil surface temperatures exceeded 212 °F (100 °C) [79]. Since soil surface temperatures during fire frequently exceed this (see [32] for a review), mortality of unburied princesstree seeds during wildfire is likely. This evidence suggests that princesstree seeds may only survive fire when buried, or if on the soil surface, when fires are of very low severity [79].

Postfire regeneration strategy [125]:
Tree with adventitious buds, a sprouting root crown, and root suckers
Geophyte, growing points deep in soil

[Ground residual colonizer](#) (on site, initial community)
[Initial off-site colonizer](#) (off site, initial community)
[Secondary colonizer](#) (on- or off-site seed sources)

Fire adaptations and plant response to fire: Highly shade-intolerant, princesstree requires large-scale disturbances such as fire, landslides, flood scour, or other land scarification for optimal stand establishment [63]. The small, wind-dispersed seeds germinate almost exclusively on open sites with exposed mineral soil [18,63]. These traits are similar to those of many native fire-dependent species, such as Table Mountain pine and pitch pine [148]. Princesstree may grow rapidly after fire. For example, in oak-pine forest in Linville Gorge Wilderness Area dominated by scarlet oak, chestnut oak, pitch pine, and Table Mountain pine, seedlings grew to 14 feet (4 m) tall 4 years after fire [40]. Furthermore, princesstree's ability to sprout from adventitious buds along its bole, root crown, and/or roots after partial to complete top-kill [63] likely allows it to persist after fire. Thus, prescribed fire meant to enhance regeneration and maintenance of native, fire-dependent forest species may also create conditions suitable for princesstree regeneration.

Establishment of princesstree after wildfires has been reported in the fire-dependent Table Mountain pine-pitch pine forests of the southern Appalachians (e.g., [40,84,111]). On the western rim of the Linville Gorge Wilderness Area, Dumas and others [40] examined the effects of a fall 2000 wildfire in primarily xeric oak-pine forest. This area had not been burned in 50 years and had succeeded to a mixed-hardwoods community with a dense mountain-laurel (*Kalmia latifolia*) understory [111]. Throughout Linville Gorge Wilderness Area, fire severity ranged from low-severity surface fire to high-severity crown fire (see Kuppinger [79] for more information). In this area, the fire was a low-severity surface fire, with crowning mainly restricted to stands of pitch pine and Table Mountain pine that had been killed by southern pine beetle. Two years after fire, little overstory mortality was evident in healthy stands. Most of the understory, composed primarily of mountain-laurel, was top-killed and had subsequently sprouted. The fire reduced surface organic horizons nearly 50% in burned plots relative to unburned plots and increased light penetration about 15%, resulting in greater soil temperature extremes but no differences in available nitrogen or phosphorus. Rates of soil respiration and litter decomposition tended to be lower in burned than unburned plots. This low-intensity surface fire caused postfire basal sprouting of trees and shrubs, increased species richness in the herb layer, and allowed the establishment of pitch pine and princesstree seedlings. Princesstree had not been detected in the 12,002-acre (4,857 ha) Wilderness Area prior to the fire, but seedlings had "rapidly increased in number and height" by postfire year 4 [40]. Potential brevity of princesstree seeds in the soil seed bank and susceptibility of seeds to fire-induced mortality suggests that princesstree may have established in the Linville Gorge Wilderness Area from seed dispersed after the fire rather than from dormant seed present in the soil seed bank prior to the fire (see Fire Management Considerations and Seed banking) [79,111].

Landscapes with high fire severity may provide quality habitat for princesstree [79]. Kuppinger [79] examined postfire establishment and spread by princesstree across 5 sites in western North Carolina and eastern Tennessee that burned in 2000 and 2001. Data collected in postfire years 1 and 4 were compared. General patterns emerged, including a positive association with relatively dry, upland reaches of the landscape, a negative association with remaining vegetation cover taller than 3.3 feet (1 m), and a negative association with decreasing hill shade.

Fire severity and intensity likely affect regeneration of princesstree. Because of variations in fuels and topography, fire creates a variety of microsites within each burned area. High-severity fire produces favorable conditions for princesstree germination and establishment but killing mature trees and some seeds, particularly those in the litter. Conversely, low-severity fire may not kill mature princesstree trees or their seeds but is less likely to create conditions necessary for germination and establishment. More information is needed about the establishment and persistence of princesstree seedlings and sprouts and their ability to compete with native vegetation after fire (see Successional Status) [144].

FUELS AND FIRE REGIMES:

Fuels: Princesstree may increase fuel loads locally but may not increase fire hazard and thus not affect fire regimes. Princesstree's growth habit suggests that it may contribute substantially to fuel loads. Princesstrees may produce large amounts of litter. The brittle branches break easily even when green, and branch die-back from frost is common, so the branches, large leaves, and numerous seed capsules accumulate under the tree canopy (e.g., [37,81,115,126]).

However, princesstree is not considered a fire hazard [44]. *Paulownia* wood has low thermal (0.063-0.086 Kcal m? ^{1} hr? ^{1} °C? ^{1}) and temperature conductivity (0.000561-0.000631 m? ^{1} hr? ^{1}) and thus very high heat insulation properties and low combustibility relative to other species [158]. Relatively high moisture content and low ignitability of chemicals in the plant partially explain its low combustibility and consumption in fire. Li and Oda [87] studied the characteristics of princesstree wood in the laboratory and found that "the thermal conductivity of princesstree is lowest among all types of wood", although the authors did not provide relative numbers. The porous microstructure of princesstree wood and its chemical composition help explain its light weight, relatively low combustibility, and "flame retardant" characteristics compared to other types of wood [87]. For more information on the cellular structure and physical characteristics of princesstree wood see Zhu and others [158] and Hu [62,63].

Fire regimes: Little information is available on the fire regime of plant communities in princesstree's native habitat in China. Its ability to sprout and establish from off-site, wind-dispersed seeds, its rapid growth rate, early age to seed production, and appearance in early-successional plant communities in North America (see Habitat Types and Plant Communities) suggest that princesstree is tolerant of short fire-return intervals and stand-replacing disturbances. Lack of persistence in shaded sites suggests that long fire-return intervals are not favorable.

It is difficult to assess how princesstree may alter fire regimes in North American ecosystems and plant communities where it is present. Its low heat of combustion relative to other species suggests that its populations could possibly alter properties of the native fuel bed (see Fuels). Further information, especially on postfire response of princesstree, is needed to increase understanding of the effects of princesstree on fire regimes in North America. The Fire Regime Table summarizes characteristics of fire regimes for vegetation communities in which princesstree may occur.

FIRE MANAGEMENT CONSIDERATIONS:
Because princesstree invades readily after disturbance, prescribed fire and fuels management activities may increase its populations. Thus, prescribed fire alone is not considered a control option for princesstree [44].

Princesstree may establish from the seed bank after fire. Viable princesstree seeds have been found in the soil seed bank of some forest communities (see Seed banking) [36,67], including the pine barrens region of southern New Jersey, where prescribed fire has been used since the 1930s [92]. However, princesstree seed mortality may be high after fire (see Immediate fire effect on plant), particularly, the "high severity fires most likely to produce the most suitable habitats for princesstree establishment" [79]. Thus, the establishment and spread of princesstree after fire may be primarily controlled by the yearly seed rain rather than an accumulation of seeds within the seed bank [79].

Preventing invasive plants from establishing in burned areas is the most effective and least costly management method. This may be accomplished through early detection and eradication, careful monitoring and follow-up, and limiting dispersal of invasive plant seed into burned areas. Evans and others [44] made the following management suggestions for preventing princesstree invasion after fire and fuels management activities. First, conduct control measures for princesstree before initiating silvicultural and/or prescribed fire treatment (see Control). This helps prevent mature trees from going to seed and reduces reproduction by sprouting. Second, plan late-season burns. Princesstree's response to fire depends upon the season fire occurs. Since seeds germinate in the first growing season following dispersal in the late summer and early fall if they encounter sufficient light levels and bare soil conditions, early spring fires are highly conducive to princesstree establishment and should be avoided [44]. Conversely, fire in the late summer and fall may kill seeds on the soil surface [79], possibly preventing princesstree establishment. Third, because seeds are easily transported, clean all equipment thoroughly before and after tree harvest, prescribed fire, or mechanical site preparation [44]. Fourth, because princesstree is promoted by activities that disturb the soil, monitor sites for new infestations whenever there is a nearby (<6 miles (10 km)) [79] seed source and follow up with additional control measures as needed. Particular attention should be paid to roadways, skid trails, and other disturbed grounds because these are likely corridors for invasion [44,84].

General recommendations for preventing invasive plants from establishing in weed-free burned areas include:

- incorporate cost of weed prevention and management into fire rehabilitation plans
- acquire restoration funding
- include weed prevention education in fire training

- minimize soil disturbance and vegetation removal during fire suppression and rehabilitation activities
- minimize the use of retardants containing nitrogen and phosphorus
- avoid areas dominated by high priority invasive plants when locating firelines, monitoring camps, staging areas, and helibases
- clean equipment and vehicles prior to entering burned areas
- regulate or prevent human and livestock entry into burned areas until desirable site vegetation has recovered sufficiently to resist invasion by undesirable vegetation
- monitor burned areas and areas of significant disturbance or traffic from management activity
- detect weeds early and eradicate before vegetative spread and/or seed dispersal
- eradicate small patches and contain or control large infestations within or adjacent to the burned area
- reestablish vegetation on bare ground as soon as possible
- avoid use of fertilizers in postfire rehabilitation and restoration
- use only certified weed-free seed mixes when revegetation is necessary

For more detailed information on these topics see the following publications: [6,20,50,139].

MANAGEMENT CONSIDERATIONS

SPECIES: Paulownia tomentosa

- IMPORTANCE TO WILDLIFE AND LIVESTOCK
- OTHER USES
- IMPACTS AND CONTROL

IMPORTANCE TO WILDLIFE AND LIVESTOCK:

Palatability/nutritional value: Domestic livestock and wildlife regularly consume princesstree leaves, flowers, and branches. In reviews, several authors mention the use of *Paulownia* leaves as fodder for domestic sheep, goats, pigs, and rabbits [29,34,37,74,78,149,158]. Leaves of 3 *Paulownia* species (*P. tomentosa*, *P. fortunei*, and *P. elongata*) were highly palatable to domestic goats in experimental studies and had "adequate" nutritional value for domestic goat browse as long as minerals were supplemented [108]. Leaves appear to be equally palatable to wildlife. High rates of herbivory were observed on young seedlings by unspecified burrowing animals and white-tailed deer in forest, edge, and clearcut habitats in Ohio [90]. Mitchem and others [98] suggested that white-tailed deer commonly browsed princesstree in Virginia. Little is known about princesstree seed predation, but field experiments in Ohio suggest that seed predation by wildlife may be minimal [90]. The rapid growth and coppicing ability of princesstree may allow it to establish despite heavy browsing pressure [74,91].

Cover value: No information is available on this topic.

OTHER USES:

Princesstree is valued in eastern Asia for its medicinal, ornamental, and timber uses [62,63]. In the United States, it has been widely planted as an ornamental (e.g., [41]), as a source of high-value export lumber (e.g., [10,26,57,96,106,130]), and for revegetation of land disturbed by coal mining (e.g., [143]). Except for its use as an ornamental, little attention was given to princesstree in the United States until the 1970s [58]. The United States began exporting princesstree wood to Japan in 1972. The logs obtained from wild-grown trees in the United States were of high quality, making prices for princesstree logs comparable to expensive native hardwoods such as black walnut (*Juglans nigra*) [57]. High prices encouraged interest in cultivating princesstree for timber production and led to much research regarding its cultivation on plantations and surface-mined lands [26,37,51,57,58,106,115,130,133]. Princesstree has since been extensively cultivated and grown in commercial plantations in the United States and throughout the world (see General Distribution) [96]. The commercial market for princesstree in the United States likely peaked in the late 1970s and early 1980s [58,106], when it was promoted as a "magic tree" [29] or as an "eco-friendly multi-purpose species" [34].

Frequent planting and increased propagule pressure may have resulted in increased invasibility of native communities by princesstree. The 1990s marked the first time that researchers and land managers began to see princesstree establish after fire in native xeric plant communities in the southern Appalachians [79]. Beginning in the early 1990s, focus in the literature gradually shifted from promotion to eradication of princesstree (see Impacts).

Wood products: The characteristics of princesstree wood make it suitable for a diversity of uses, and many reports have touted the unique physical and mechanical properties of princesstree wood (e.g., [38,58,62,63,106,115,123,130]). Its wood is used to make plywood and other house construction wood (other than for structural timber), paper, veneer, hand-carvings, clogs, musical instruments, furniture, and kitchen items such as rice pots, water pails, bowls, and spoons [34,37,51,57,62,63,78,106,115,133,138].

Reforestation and reclamation: Princesstree invades open, disturbed areas and often tolerates the harsh environmental conditions of surface mines [31]. Several studies have advocated using it for reclamation [25,26,31,95,130,136]. It has been planted on surface-mined lands throughout the eastern United States, including West Virginia, Kentucky, Tennessee, and Alabama [57,106,130,143]. However, several authors describe it as having limited importance for use in revegetation on coalmined sites due to the frequent difficulties of establishing princesstree relative to other species [129,133,143]. It was unclear how common the use of princesstree in reclamation was as of this writing (2009).

Agroforestry and cropping systems: The Chinese have developed intercropping and agroforestry systems for *Paulownia*, including princesstree, which have been evaluated extensively in the literature (e.g., [29,34,37,38,149,154]). Species of *Paulownia* other than princesstree are apparently preferred for these practices [74].

IMPACTS AND CONTROL:

Impacts: Princesstree is a moderate to severe threat to native plant communities in many eastern states. In general, it is considered moderately invasive in native communities of the northeastern United States [137]. In the Southeast, it is typically considered a substantial or severe threat to native communities [1,47,75,80,120,121]. Princesstree is considered moderately invasive in Virginia [142]. In a study using the Southern Research Stations Forest Inventory and Analysis database, cover estimates of princesstree totaled over 20,000 acres in 12 southeastern states [97]:

Estimates of area covered by princesstree in the Southeast as of 2008 [97]	
State	Acres
Alabama	2,284
Arkansas	82
Florida	82
Georgia	347
Kentucky	2,726
Louisiana	7
Mississippi	1,867
North Carolina	2,297
South Carolina	95
Tennessee	7,361
Texas (east)	Not detected
Virginia	6,331
Total acres covered	23,478

Princesstree is primarily a threat to native communities in heavily disturbed areas in the eastern United States. In the southern Appalachian Mountains it excludes native species in areas that experience frequent fire or in areas with naturally exposed soils and sunny aspects such as cliffs and rocky outcrops (see Site Characteristics) [70,84]. In the Great Smoky Mountains National Park and Linville Gorge Wilderness Area, its ability to colonize rocky or infertile sites makes it a threat to 2 rare, endangered species (Heller's blazing star (*Liatris helleri*), mountain goldenheather (*Hudsonia montana*)) that require these marginal habitats [44,79]. Its ability to sprout or establish by seed quickly after fire has allowed princesstree to replace native fire-dependent species such as Table Mountain pine and pitch pine in some areas of Great Smoky Mountains National Park [118].

Many studies report princesstree is of minor importance in intact forest and undisturbed environments [37]. For example, in New London County, Connecticut, it had increased in disturbed areas but had not spread to more mature plant associations; the remaining native terrestrial flora had not seriously declined despite a high percentage of nonnative species [59]. In western North Carolina and eastern Tennessee, there was no significant correlation between princesstree's presence or cover and native species cover or diversity; however, the author cautioned about the stability of this condition if princesstree cover were to increase [79]. Princesstree was not considered an "aggressive invader" in eastern forests lacking large-scale disturbance due to its habit of forming "small scattered populations in much the same way that it does in its natural environments in China" [147]. In China, Hu [63] speculated that the requirement for high light for germination and the small size of the seed—with little food reserve—probably contribute to the isolated occurrence of princesstrees there.

Kuppinger [79] concluded that princesstree in western North Carolina and eastern Tennessee "appears to be able to germinate and survive for a year or 2 across a much larger range of habitat conditions than will enable it to survive to maturity". The author continued by stating that "in situations where there is interest and resources for control efforts, (habitat models) indicate that control may be unnecessary over large portions of the landscape initially invaded by princesstree. In these areas, it is likely that regeneration of native vegetation will eventually exclude princesstree as it is apparently a poor competitor for space and light. Because of this, control efforts should be focused on the most xeric and exposed portions of the landscape where habitat models predict princesstree will persist and a high-light, low-competition environments will be maintained" [79].

Control: Princesstree control requires persistence due to its strong sprouting ability, rapid growth, and prolific seed production. Posttreatment monitoring and retreatment are essential. Treated areas should be checked once or more a year, with any new sprouts or seedlings retreated (cut, sprayed, or pulled) as soon as possible so that roots do not have time to build up carbohydrate reserves and grow larger. Princesstree's rapid root growth and sprouting ability underscore the need to eradicate seedlings when they are small and before they become established.

In all cases where invasive species are targeted for control, no matter what method is employed, the potential for other invasive species to fill their void must be considered [21]. Bean and others [10] review application methods for many of the control methods discussed below; however, the information provided herein is not intended to be either comprehensive or prescriptive in nature.

Fire: For information on the use of prescribed fire to control this species, see Fire Management Considerations.

Prevention: Managing to maintain the integrity of the native plant community and mitigate the factors enhancing ecosystem invasibility is likely to be more effective than managing solely to control the invader [60]. Maintaining high plant species richness in native communities is likely to decrease the invasibility of plant communities by princesstree because interference from neighboring vegetation may decrease princesstree's growth and survival (see Successional Status). Due to princesstree's preference for open, disturbed habitat, its establishment may be prevented by minimizing loss or disturbance of native communities [99,103]. For example, Williams [146] surmised that since light levels may be inadequate for the growth and survival of princesstree seedlings or sprouts, small forest gaps are unlikely to contribute to its population maintenance in most forests, whereas native early-successional forest trees such as yellow-poplar and black birch may occupy canopy gaps of various sizes [146]. Given this, planting of native species in the understory of existing stands may allow native species to increase while preventing princesstree germination [90].

Successful control of princesstree requires prevention of propagation and planting by restricting the sale and use of princesstree and increasing public education about its impacts on native communities. In 2006, Webster and others [144] stated that "a quick review of the forestry extension web sites of 24 land grant universities in the eastern United States revealed that 7 institutions still offer publications that promote invasive exotic woody plants for plantations, wildlife habitat improvement, and ornamental plantations". The authors suggest that the first step in preventing the introduction of princesstree is by "encouraging the use of native species in forestry and horticulture applications" [144].

Another method of preventing princesstree infestation is by developing and using a risk assessment model [35]. A risk assessment model combines information regarding current infestations with what is known about the species' biology. Land managers can then use the model to identify the probability of occurrence and areas at risk of invasion. Although a risk assessment model had not been developed for princesstree in the United States as of this writing (2009), McNab and Loftis [94] developed a model for oriental bittersweet (*Celastrus orbiculatus*) and suggested that such a model could be broadly applicable to princesstree and other invasive plants.

Weed prevention and control can be incorporated into many types of management plans, including those for logging and site preparation, grazing allotments, recreation management, research projects, road building and maintenance, and fire management [139]. See the Guide to noxious weed prevention practices for specific guidelines in preventing the spread of weed seeds and propagules under different management conditions.

Physical and/or mechanical: Mechanical methods can be an effective initial control measure for princesstree. Cut mature trees at ground level. To prevent seed production, cutting is most effective at the onset of flowering. Because princesstree spreads by suckering, root sprouts are common after treatment, and additional control methods such as repeated cutting for sprouts or an herbicidal control to prevent sprouting may be required [10]. Repeated cutting eventually exhausts the roots and kills the plant, but this may take several years [71]. Girdling kills the top of a tree but sprouts are common and may require a follow-up treatment with a foliar herbicide such as glyphosate or triclopyr. Seedlings can be controlled by hand-pulling; however, the entire root must be removed because broken root fragments may sprout [10].

Biological: Biocontrol could potentially reduce the invasiveness of princesstree in the United States [42], but no biocontrol methods are available as of this writing (2009). Ding and others [35] prioritized princesstree and 9 other species as targets for future biological control efforts based on information on their importance in introduced areas, availability of their host-specific insects or pathogens in China, and their potential biological control risk to introduced ecosystems. According to this study, princesstree has no congener species in the United States, making the potential biological control risk to introduced ecosystems low. Of 128 natural enemies in China, 19 may be potential biological control agents for use in the United States due to their narrow host ranges.

Biological control of invasive species has a long history that indicates many factors must be considered before using biological controls. Refer to these sources [141,151] and the Weed control methods handbook [135] for background information and important considerations for developing and implementing biological control programs.

In the United States, native and nonnative invertebrates, fungi, and diseases are known to adversely affect princesstree. Several studies have reported mortality of seedlings due to root rots [13,62,63,123,127,138]. Stringer [127] described 2 fungi (*Rhizoctonia* sp., *Colletotrichum* sp.) that infected seedlings and caused die-back in field experiments in Kentucky. Several foliage diseases causing at least superficial damage to princesstrees have been reported in the United States, including *Phyllosticta paulowniae*, *Phyllactinia guttata*, and *Uncinula clintonii* ([70], Hepting 1971, cited in [16]). Princesstree is subject to minor damage by the Comstock mealybug (*Pseudococcus comstocki*), an introduced species from Asia [138] and saltmarsh caterpillar (*Estigmene acrea*), a native species [15].

Chemical: Herbicides may provide initial control of a new invasion or a severe infestation but are rarely a complete or long-term solution to invasive species management [23]. Herbicides are more effective on large infestations when incorporated into long-term management plans that include replacement of weeds with desirable species, careful land use management, and prevention of new infestations. Following stem control, total elimination requires surveillance and treatment of root sprouts and plant germinants that originate from the soil seed bank [96]. Control with herbicides is temporary because it does not change conditions that allow infestations to occur [156]. See The Nature

Conservancy's Weed control methods handbook [135] for consideration on the use of herbicides in wildlands and detailed information on specific chemicals.

According to reviews, systemic herbicides (e.g., triclopyr and glyphosate), which kill roots, currently provide the best chemical control for princesstree [10], although results may vary depending upon environmental conditions. These herbicides risk damage to nontarget species. When princesstree is interspersed with nontarget species, the foliage, stumps, or basal bark of individual trees can be treated with herbicides [10].

Integrated management: Princesstree can be controlled most effectively using integrated management. Cutting or girdling trees may prevent seed production. However, princesstree readily sprouts and repeated cutting or an herbicide treatment following cutting may be necessary [134]. Korostoff [77] reports that princesstree was eliminated in northwestern Pennsylvania by cutting followed by stump treatment with herbicide. Integrated management should include establishing desirable species in addition to considerations for killing the target plant.

APPENDIX: FIRE REGIME TABLE

SPECIES: Paulownia tomentosa

The following table provides fire regime information that may be relevant to princesstree habitats. Follow the links in the table to documents that provide more detailed information on these fire regimes. If you are interested in fire regimes of plant communities not listed here, see the Expanded Fire Regime Table.

Fire regime information on vegetation communities in which princesstree may occur. This information is taken from the LANDFIRE Rapid Assessment Vegetation Models [83], which were developed by local experts using available literature, local data, and/or expert opinion. This table summarizes fire regime characteristics for each plant community listed. The PDF file linked from each plant community name describes the model and synthesizes the knowledge available on vegetation composition, structure, and dynamics in that community. Cells are blank where information is not available in the Rapid Assessment Vegetation Model.

Southeast | Great Lakes | Northeast | South-central US | Southern Appalachians

Great Lakes

- Great Lakes Grassland
- Great Lakes Woodland
- Great Lakes Forested

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
Great Lakes Grassland					
Mosaic of bluestem prairie and oak-hickory	Replacement	79%	5	1	8
	Mixed	2%	260		
	Surface or low	20%	2		33

Great Lakes Woodland					
Northern oak savanna	Replacement	4%	110	50	500
	Mixed	9%	50	15	150
	Surface or low	87%	5	1	20
Great Lakes Forested					
Northern hardwood maple-beech-eastern hemlock	Replacement	60%	>1,000		
	Mixed	40%	>1,000		
Great Lakes floodplain forest	Mixed	7%	833		
	Surface or low	93%	61		
Maple-basswood	Replacement	33%	≥1,000		
	Surface or low	67%	500		
Maple-basswood mesic hardwood forest (Great Lakes)	Replacement	100%	>1,000	≥1,000	>1,000
Maple-basswood-oak-aspen	Replacement	4%	769		
	Mixed	7%	476		
	Surface or low	89%	35		
Oak-hickory	Replacement	13%	66	1	
	Mixed	11%	77	5	
	Surface or low	76%	11	2	25

Northeast

- Northeast Woodland
- Northeast Forested

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
Northeast Woodland					
Eastern woodland mosaic	Replacement	2%	200	100	300
	Mixed	9%	40	20	60
	Surface or low	89%	4	1	7
Rocky outcrop pine (Northeast)	Replacement	16%	128		
	Mixed	32%	65		
	Surface or low	52%	40		
Pine barrens	Replacement	10%	78		
	Mixed	25%	32		
	Surface or low	65%	12		

Oak-pine (eastern dry-xeric)	Replacement	4%	185		
	Mixed	7%	110		
	Surface or low	90%	8		
Northeast Forested					
Northern hardwoods (Northeast)	Replacement	39%	≥1,000		
	Mixed	61%	650		
Eastern white pine-northern hardwoods	Replacement	72%	475		
	Surface or low	28%	>1,000		
Northern hardwoods-eastern hemlock	Replacement	50%	≥1,000		
	Surface or low	50%	≥1,000		
Northern hardwoods-spruce	Replacement	100%	≥1,000	400	>1,000
Appalachian oak forest (dry-mesic)	Replacement	2%	625	500	≥1,000
	Mixed	6%	250	200	500
	Surface or low	92%	15	7	26
Beech-maple	Replacement	100%	>1,000		

South-central US

- South-central US Grassland
- South-central US Woodland
- South-central US Forested

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
South-central US Grassland					
Oak savanna	Replacement	3%	100	5	110
	Mixed	5%	60	5	250
	Surface or low	93%	3	1	4
South-central US Woodland					
Oak-hickory savanna	Replacement	1%	227		
	Surface or low	99%	3.2		
Interior Highlands dry oak/bluestem	Replacement	16%	25	10	100
	Mixed	4%	100	10	

woodland and glade	Surface or low	80%	5	2	7
Oak woodland-shrubland-grassland mosaic	Replacement	11%	50		
	Mixed	56%	10		
	Surface or low	33%	17		
Interior Highlands oak-hickory-pine	Replacement	3%	150	100	300
	Surface or low	97%	4	2	10
Pine bluestem	Replacement	4%	100		
	Surface or low	96%	4		
South-central US Forested					
Interior Highlands dry-mesic forest and woodland	Replacement	7%	250	50	300
	Mixed	18%	90	20	150
	Surface or low	75%	22	5	35
Gulf Coastal Plain pine flatwoods	Replacement	2%	190		
	Mixed	3%	170		
	Surface or low	95%	5		
West Gulf Coastal plain pine (uplands and flatwoods)	Replacement	4%	100	50	200
	Mixed	4%	100	50	
	Surface or low	93%	4	4	10
West Gulf Coastal Plain pine-hardwood woodland or forest upland	Replacement	3%	100	20	200
	Mixed	3%	100	25	
	Surface or low	94%	3	3	5
Southern floodplain	Replacement	42%	140		
	Surface or low	58%	100		
Southern floodplain (rare fire)	Replacement	42%	≥1,000		
	Surface or low	58%	714		

Southern Appalachians

- Southern Appalachians Grassland
- Southern Appalachians Woodland
- Southern Appalachians Forested

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
Southern Appalachians Grassland					
	Replacement	46%	15		

Bluestem-oak barrens	Mixed	10%	69		
	Surface or low	44%	16		
Eastern prairie-woodland mosaic	Replacement	50%	10		
	Mixed	1%	900		
	Surface or low	50%	10		
Southern Appalachians Woodland					
Appalachian shortleaf pine	Replacement	4%	125		
	Mixed	4%	155		
	Surface or low	92%	6		
Table Mountain-pitch pine	Replacement	5%	100		
	Mixed	3%	160		
	Surface or low	92%	5		
Oak-ash woodland	Replacement	23%	119		
	Mixed	28%	95		
	Surface or low	49%	55		
Southern Appalachians Forested					
Bottomland hardwood forest	Replacement	25%	435	200	≥1,000
	Mixed	24%	455	150	500
	Surface or low	51%	210	50	250
Mixed mesophytic hardwood	Replacement	11%	665		
	Mixed	10%	715		
	Surface or low	79%	90		
Appalachian oak-hickory-pine	Replacement	3%	180	30	500
	Mixed	8%	65	15	150
	Surface or low	89%	6	3	10
Eastern hemlock-eastern white pine-hardwood	Replacement	17%	≥1,000	500	>1,000
	Surface or low	83%	210	100	>1,000
Oak (eastern dry-xeric)	Replacement	6%	128	50	100
	Mixed	16%	50	20	30
	Surface or low	78%	10	1	10
Appalachian Virginia pine	Replacement	20%	110	25	125
	Mixed	15%	145		
	Surface or low	64%	35	10	40
Appalachian oak forest (dry-mesic)	Replacement	6%	220		
	Mixed	15%	90		
	Surface or low	79%	17		
Southeast					

- Southeast Grassland
- Southeast Woodland
- Southeast Forested

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
Southeast Grassland					
Southeast Gulf Coastal Plain Blackland prairie and woodland	Replacement	22%	7		
	Mixed	78%	2.2		
Southeast Woodland					
Longleaf pine/bluestem	Replacement	3%	130		
	Surface or low	97%	4	1	5
Longleaf pine (mesic uplands)	Replacement	3%	110	40	200
	Surface or low	97%	3	1	5
Longleaf pine-Sandhills prairie	Replacement	3%	130	25	500
	Surface or low	97%	4	1	10
Southeast Forested					
Coastal Plain pine-oak-hickory	Replacement	4%	200		
	Mixed	7%	100		
	Surface or low	89%	8		
Loess bluff and plain forest	Replacement	7%	476		
	Mixed	9%	385		
	Surface or low	85%	39		
Southern floodplain	Replacement	7%	900		
	Surface or low	93%	63		

*Fire Severities—
Replacement: Any fire that causes greater than 75% top removal of a vegetation-fuel type, resulting in general replacement of existing vegetation; may or may not cause a lethal effect on the plants.
Mixed: Any fire burning more than 5% of an area that does not qualify as a replacement, surface, or low-severity fire; includes mosaic and other fires that are intermediate in effects.
Surface or low: Any fire that causes less than 25% upper layer replacement and/or removal in a vegetation-fuel class but burns 5% or more of the area [56,82].

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