

Nelumbo lutea

American Lotus

Nelumbonaceae



Nelumbo lutea by J. S. Dodds, 2023

***Nelumbo lutea* Rare Plant Profile**

New Jersey Department of Environmental Protection
State Parks, Forests & Historic Sites
State Forest Fire Service & Forestry
Office of Natural Lands Management
New Jersey Natural Heritage Program

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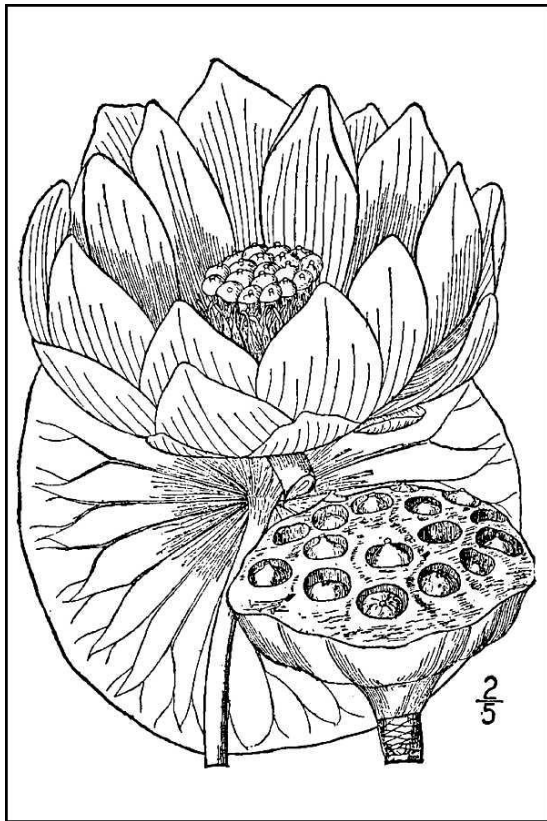
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Life History

Nelumbo lutea (American Lotus) is a distinctive colonial aquatic plant in the lotus-lily family. The family (Nelumbonaceae) only contains two extant species in a single genus (Wiersema 2020). Both species can be found in New Jersey, although *N. lutea* is native to North America while *N. nucifera* (Sacred Lotus) is not. The extant *Nelumbo* species arise from an ancient clade and have been referred to as 'living fossils' (Sanderson and Doyle 2001, Yang et al. 2014). Early classifications included *Nelumbo* in the waterlily family (Nymphaeaceae) but the families were soon separated on the basis of differences in leaf and fruit morphology and growth habits. However, Nelumbonaceae was still thought to be associated with the basal angiosperm families (Cabombaceae, Nymphaeaceae) until fairly recently. The lotus-lily family has an embryological feature that is more common in gymnosperms than angiosperms (Meeuse and Ott 1962) and an aerenchyma formation typical of aquatic monocots and basal angiosperms (Seago et al. 2005), but its pollen development and root structure support separation from the basal angiosperm families (Kreunen and Osborn 1999, Seago 2002). Molecular analyses indicate that *Nelumbo* is more closely related to *Platanus* than it is to *Nymphaea* (Sanderson and Doyle 2001).



Left: Britton and Brown 1913, courtesy USDA NRCS 2023a. Right: W. H. Fitch, 1840.

Nelumbo lutea has two kinds of rhizomes, slender ones that lie near the substrate surface and larger, tubiferous ones that usually extend farther into the soil. While examining a New Jersey population, Heritage (1895) noted that the large tubers were 8–28 cm long and resembled bananas in shape but their color was creamy white and they were marked with purplish dots. Fibrous roots are produced at the nodes of the rhizomes and the leaves arise directly from the

rhizomes on long petioles. Floating leaves may be present, particularly in young or deeply rooted colonies, but the majority of leaves are held well above the surface of the water on erect stems. *N. lutea* leaves are large (up to 6 dm in diameter) and the petioles are attached to the undersides near the middle of the blade. Schaffner (1910) observed that the leaves had a light-colored marking at the center reminiscent of a beetle. Both emergent and floating leaves have a water-repellent surface. Lotus flowers are very showy, rising above the leaves on long, axillary stalks and bearing 14–30 tepals that become progressively larger (up to 13 cm) and more petal-like near the center of the flower. The tepals of *N. lutea* are pale yellow while those of *N. nucifera* are pink to white. White-flowered populations of *N. lutea* are occasionally encountered, including one in southern New Jersey (Schuyler 1980). Each flower has 100–200 stamens surrounding a large gynoecium consisting of numerous pistils embedded in a cup-like receptacle, and each stamen has a hook-like tip extending beyond the anthers. Detailed descriptions of the gynoecium and pollen grains are available from Van Leeuwen (1963) and Banks et al. (2007), respectively. As the fruits develop, *N. lutea* sheds its anthers and all but the outermost tepals. The nutlike fruits are retained in the receptacle which expands and dries into a structure which has been described as top-shaped and likened in appearance to a watering-can spout or a showerhead (York 1904, Stack 1909, Nelson 2016). The two species of *Nelumbo* can also be distinguished by fruit shape—the fruits of *N. lutea* are nearly round while those of *N. nucifera* are ovoid. (See Britton and Brown 1913, Hall and Penfound 1944, Fernald 1950, Fassett 1957, USDA 1971, Gleason and Cronquist 1991, Tiner 2009, Wiersema 2020).



N. lutea in northern New Jersey on July 22, 2014, J. S. Dodds.

While engaged in mapping the aquatic vegetation of Lake Erie, Ghioca-Robrecht et al. (2008) observed that multi-season imagery was needed to identify *N. lutea* beds because the plants disappeared in the fall and reemerged in the spring. Late in the growing season, *Nelumbo* rhizomes form swollen storage tubers (Wiersema 2020). Buds for the following year's growth were evident on tubers collected in southern New Jersey during November and December of 1894 (Heritage 1895). Once the new leaves develop, clonal reproduction continues throughout the growing season. Stack (1909) indicated that *N. lutea* leaves turned "a peculiar bluish green" color as the season advanced. Throughout its range, American Lotus may flower from May through September (Schneider and Buchanan 1980, Weakley et al. 2022) although in New Jersey blooming usually starts during late July (Stone 1911, Hough 1983). The initiation of flowering may be delayed in years that follow severe winters. Flower buds start to form underwater but quickly emerge on the elongating petioles (Schneider and Buchanan 1980) and pollen

development begins when the floral buds reach a certain stage. A detailed description of pollen development was recorded by Farr (1922). The plants in a *N. lutea* colony do not flower simultaneously, and those flowering earliest have relatively short peduncles but the stalks of later-blooming plants become progressively longer (Hall and Penfound 1944). Flowers that bloom toward the end of the season are often incompletely fertilized and produce fewer seeds (Ainslie 1922). After an individual flower begins to bloom it will open and close for several days in succession (Smyth 1898): Taylor (1927) observed that the process lasted for 3–6 days depending on the weather. The tepals begin to fall off within a day or two (Sohmer 1975) and four days after they are all shed the floral receptacle bends 45 degrees and faces eastward (Hall and Penfound 1944). As the fruits develop the peduncle continues to bend, eventually reaching a 90 degree angle, but it straightens out at maturity. When the growing season comes to a close the leaves and petioles drop to the water surface, ultimately sinking and decaying (Ainslie 1922).

Throughout its history *N. lutea* has been both revered and reviled, and even now a quick internet search will turn up an assortment of articles either touting its merits or suggesting mechanisms for its destruction. Many indigenous people utilized the starchy tubers and nuts of *N. lutea* as a food source and at least one tribe viewed the species as sacred and followed strict ceremonial procedures for its collection (Swan 2010). The colonists were more enchanted by the plant's appearance. John Bartram first viewed *N. lutea* in New Jersey in 1750 and made numerous attempts to establish the species in a pond on his property before finally meeting with success: He later packed some tubers in a barrel along with a couple of bullfrogs and shipped them to the king of England for the royal gardens (Fry 1997). Barton (1818) was equally taken with the lotus, remarking that "*There is not surely in North America any plant comparable to this for grandeur, simplicity and beauty.*" Taylor (1927) called it "the queen of the wild flowers" and expressed the wish that every state should have a bed of *N. lutea*.

Heritage (1895) cited *Nelumbo lutea* as evidence of the perfection of divine creation but one of the features that most impressed him was the species' ability to proliferate clonally, which is the same quality that has made the lotus a target for eradication in many locations. Hall and Penfound (1944) described the vegetative reproduction rate of *N. lutea* as "phenomenal" and estimated an average expansion area of 14 meters in a growing season, Martin et al. (1957) indicated that expansion rates of up to 75 meters per year had been reported, and an Ohio colony observed by Bouchard and Mitsch (2005) doubled in size over the course of a single year. It is no wonder, then, that *N. lutea* has also been identified as weedy, problematic, invasive, or noxious—particularly in places where it interferes with small boat navigation, fishing, or other recreational activities in aquatic settings (eg. Cheshier et al. undated, USDA 1971, Sayre 2004, Burkalova and Karatayey 2007).

Pollinator Dynamics

N. lutea flowers are pollinated by diurnal insects. Each flower blooms for several days in succession, opening in the morning and closing in the afternoon. Reported opening times range from 5:00–10:00 a.m. and may vary depending on location, day length, and cloud cover. Typical closing time is around 2:00 p.m., and by late afternoon the flowers are as tightly shut as unopened buds (Smyth 1898, Sohmer and Sefton 1978, Schneider and Buchanan 1980). On the

first day that *N. lutea* flowers bloom the tepals do not fully expand so only the top of the receptacle and the stigmas are exposed. At that point the anthers have not yet dehisced and their hooked tips prevent visitors from attempting to reach the pollen (Robertson 1889, Sohmer and Sefton 1978, Schneider and Buchanan 1980). The receptive stigmas secrete a mucilaginous fluid that emits a heavy, sweet odor on the first day but a less intense scent on subsequent days (York 1904, Schneider and Buchanan 1980). According to Genders (1977) the fragrance of *N. nucifera* is even stronger than that of *N. lutea*. Anther dehiscence begins on the second or third day of blooming, after which time the stigmas harden and are no longer receptive to pollen (Sohmer and Sefton 1978, Schneider and Buchanan 1980).

In addition to producing a strong scent the flowers of *Nelumbo lutea* are thermogenic, so the temperature inside the flowers can be as much as 6°C higher than that of the surrounding air (Schneider and Buchanan 1980). The higher floral temperatures are attractive to beetles seeking a warm place to spend the night and the warmth also helps to disperse the floral fragrance that draws in other pollinators (Dieringer et al. 2014). Thermogenesis is often associated with beetle pollination, as are food bodies such as the starchy anther tips noted in *N. lutea*. Beetles are frequent visitors to lotus flowers and numerous species have been documented on *N. lutea*, but the flowers are also regularly visited by an assortment of bees and flies (Keeler 1917, Sohmer and Sefton 1978, Schneider and Buchanan 1980, Dieringer et al. 2014, Bernhardt 2000).

The principal pollinators observed on *N. lutea* by Robertson (1889) were Andrenid bees and Syrphid flies. Several bee species, including *Lasioglossum nelumbonis*, *L. nymphaearum*, and *Hylaeus nelumbonis*, have been reported as specialists on lotus and waterlily flowers (Hilty 2020), although according to Fowler (2016) the bees are restricted to wetland habitats but forage on a wide variety of plants. Many other kinds of bees have been observed on *N. lutea* flowers including honeybees (*Apis mellifera*) and various species of *Agapostemon*, *Augochlorella*, *Ceratina*, *Dialictus*, *Halictus*, *Hylaeus*, and *Lasioglossum* (Sohmer and Sefton 1978, Stubbs et al. 1992, Hilty 2020). However, Robertson (1889) noted that when bumblebees (*Bombus* spp.) visited the flowers they generally departed rapidly without collecting pollen. While bees have frequently been identified as the most important pollinators of *N. lutea*, that may vary among populations, in some locations beetles have been found to be of greater or equal importance (Schneider and Buchanan 1980, Dieringer et al. 2014). In places where gnats or flies are also abundant they usually carry smaller quantities of pollen (Schneider and Buchanan 1980). Sohmer and Sefton (1978) inferred that *N. lutea* was originally reliant on beetles for fertilization but the role had gradually been usurped by more generalist insects, and similar conclusions were reached by Li et al. (2009) after studying the pollinators of *N. nucifera*.

Seed Dispersal and Establishment

The nutlike fruits of *Nelumbo lutea* are single-seeded (Wiersema 2020). An individual flower typically produces 9–30 fruits, although Schneider and Buchanan (1980) occasionally observed receptacles with fewer carpels, particularly in stressful habitats. Ainslie (1922) reported that intact pods held an average of 17 fruits. The fruits are initially green and fill the cavities of the receptacle but as they mature they turn dark brown, later changing to purple as they dehydrate and shrink to about a third of their original size (Hall and Penfound 1944). Loose fruits may be

dispersed into the water near the parent plants as the stems decay (Ainslie 1922) or the receptacles may remain afloat with the seeds intact. Pods containing viable propagules have been found floating in water bodies as long as a year after dispersal (Hall and Penfound 1944).

Lacoul and Freedman (2006) cited *N. lutea* as an example of a species that is dispersed by zoochory, which occurs when animals consume the fruits and defecate viable seeds. The most frequent use of *N. lutea* seeds is by waterfowl: reported consumers include Wood Ducks (*Aix sponsa*), other dabbling ducks in the genus *Anas* (mallards, shovelers, and teal), and Canada Geese (*Branta canadensis*) (McAtee 1917, Martin et al. 1957, Hilty 2020). Although *N. lutea* seeds usually comprise a very small portion of a duck's diet they can be considerably more important in some locations (McAtee 1917, Bellrose 1941, Fassett 1957, Nelson 2016). Wood ducks and teal have been known to utilize them extensively in late summer before the seed coats have hardened (Low and Bellrose 1944, Martin et al. 1957). Ducks were noted as the apparent source of a newly established *N. lutea* population observed by Pierce (1910). American Lotus seeds have also been found in the stomach contents and feces of crocodilians, suggesting the possibility of reptilian dispersal in southern parts of the plant's range (Platt et al. 2013).

Human distribution has also played a significant role in establishment of the two *Nelumbo* species at new locations both within and beyond their native ranges. Many parts of *Nelumbo lutea* are edible—including young leaves, stems, fruits, and tubers—and the species has been used for both food and medicine by many native tribes (Havard 1895, Hood 1910, Saunders 1920, Swan 2010, Orozco-Obando and Gettys 2014). *N. lutea* was cultivated by indigenous Americans along the shores of the Tennessee and Cumberland Rivers (Keeler 1917) and that probably also occurred at some other locations. After the European settlement of North America *N. nucifera* was introduced on the continent and *N. lutea* was grown by the colonists for a variety of purposes including water gardens, the attraction of waterfowl on game preserves, and use of the dried fruits in winter bouquets or cemetery wreaths (Taylor 1927, Jones 1928). *N. lutea* is still cultivated commercially for water gardens, food, herbal medicines and decorative dried seed capsules (e.g., Kane et al. 1988). People's fascination with lotus plants has led to the development of numerous cultivars featuring an array of colors and scents (Genders 1977, Yang et al. 2014), and hybrids from crosses between *N. lutea* and *N. nucifera* are also readily available on market (Orozco-Obando and Gettys 2014).

Natural occurrences along rivers or in tidal areas may commence with the deposition of tubers carried downstream by floodwaters following storm events but the initiation of populations in upstream areas or inland water bodies is likely to be dependent on the seeds. *N. lutea* is notoriously difficult to establish from seed because once the fruits have fully developed and shrunk enough to permit their release from the receptacles they have a tough coat that is impervious to water. American Lotus seeds that were experimentally maintained in water for periods of 18 months (Jones 1928) or two years (Shaw 1929) showed no signs of germination. It is likely that the species can persist in the seed bank for a very long time; Ohga (1926) successfully germinated *N. nucifera* seeds that were estimated to be over 200 years old. In order for *N. lutea* seeds to sprout, the seed coat must be breached. The embryos are not dormant and germination can then occur rapidly afterwards (Jones 1928, Shaw 1929, Hall and Penfound 1944). Researchers have successfully used files, sandpaper, acids, or heated water to weaken the seed coats (eg. Ohga 1926, Taylor 1927, Sayre 2004, Ryon et al. 2013). Hall and Penfound

(1944) discovered that if *N. lutea* fruits were taken from the receptacle while still at their maximum size they could germinate in water but they still sprouted more quickly and more frequently if the coats were removed. Research has shown that cold or freezing temperatures do not weaken the seed coats enough to permit germination (DeGroft and Francko 1966), although it is possible that bacterial action could wear them away over a very long period of time (Shaw 1929). The necessary scarification is probably most often achieved by passage through an animal's digestive system (Ryon et al. 2013).

When *N. lutea* seedlings emerge in aquatic settings they initially float on the surface until they reach the water's edge where they can become anchored. The species first produces four small leaves and a rhizome that has rootlets at the nodes and forms a tuber. The early leaves die back quickly and the young plants enter a resting stage that lasts for several weeks. The brief respite is followed by a period of rapid enlargement as the rhizome develops and forms leaves and roots at the nodes. The average growth rate during that time is 2.5 cm per day although rates as high as 12 cm per day have been recorded. However, infrequent seedling development and a high degree of vegetative proliferation suggest that sexual reproduction probably contributes little to the maintenance of extant *N. lutea* populations (Meyer 1930, Hall and Penfound 1944).

Habitat

N. lutea usually occurs in quiet waters at elevations within 0–400 meters of sea level (Wiersema 2020). Reported habitats include ponds, pools, lakes, marshes, swamps, estuaries, sinkholes, sluggish streams, and the margins of slow rivers. The species can also grow in artificial wetland sites associated with dams or reservoirs (Taylor 1915, Hall and Penfound 1944, USDA 1971, Hough 1983, Rhoads and Block 2007, Hilty 2020, Weakley et al. 2022). Tidally influenced habitats may be in fresh or slightly brackish waters (Tiner 2009). One unusual occurrence reported by Hall and Penfound (1944) was situated in water over two meters deep where the plants were occasionally exposed to severe wave action.

Within the noted habitats, *N. lutea* may be found on muddy shorelines, periodically exposed mudflats, or in shallow water (Fassett 1957, Carle et al. 2015). The initial length of the petioles is determined by water level, so the leaves may appear to be floating when the water is high but are held well above the surface or substrate when water levels drop (Wheeler 1900, Detmers 1910, Hall and Penfound 1944, Martin et al. 1957). Deppe and Lathrop (1993) reported that the growth of *N. lutea* reached the greatest density at depths of a meter or less, and the average depth of lotus beds studied by Ghioca-Robrecht et al. (2008) was 51 cm (range 20–80 cm). Artificial impoundments along the upper portion of the Mississippi River were found to support different vegetation communities depending on environmental characteristics such as inundation depth and duration, system productivity, and water clarity. The community where *N. lutea* was prevalent occurred in sites that had relatively shallow water, low water clarity, and variable productivity (Larson et al. 2022).

N. lutea is most likely to be found in sites with an organic-rich clay substrate (Meyer 1930, Lacoul and Freedman 2006). Meyer (1930) observed that *N. lutea* plants grew more rapidly in acidic conditions but could also develop normally in sites with a high pH. Francko (1986)

reported that the species could assimilate carbon via photosynthesis around 50 times faster in water with a pH of 4.5 than in water with a pH of 8.5. The fact that *N. lutea* plants are also capable of rapid development in neutral or alkaline waters may be attributable to abundant endosperm in the seeds and the ability of elongating petioles to function as photosynthetic structures in young plants (Francko 1886, Al Hamdani and Francko 1992).

Dense stands of *N. lutea* are sometimes nearly monotypic but that is not always the case. Detmers (1910) observed that the American Lotus at an Ohio site co-occurred with *Persicaria amphibia* in deeper waters while in the shallower areas it shared the habitat with other plants, particularly *Stuckenia pectinata*. Whyte et al. (2008) described a site in a section of Lake Erie where *Nelumbo* and *Nymphaea odorata* were growing together and were sometimes interspersed with submersed plants such as *Potamogeton* spp. and *Ceratophyllum demersum*. Shivers et al. (2018) indicated that *N. lutea* sometimes occurred in mixed communities of floating and submergent aquatic plants in southwestern Georgia, and Larson et al. (2022) noted that several submersed species were present in lotus-dominated beds along the upper Mississippi River. In some locations *Nelumbo lutea* can be a significant component of a community classified as a *Nymphaea odorata*—*Nuphar* spp. Permanently Flooded Temperate Herbaceous Alliance, co-occurring with submersed aquatic species such as *Cabomba caroliniana* or *Heteranthera dubia*. *N. lutea* is also one of the herbaceous species that may be found in the tidal sediments of *Acer rubrum*—*Fraxinus pennsylvanica* Tidal Woodlands. Associates include *Acorus calamus*, *Cinna arundinacea*, *Impatiens capensis*, *Mikania scandens*, *Peltandra virginica*, *Sagittaria latifolia*, and *Zizania aquatica* (Breden et al. 2001). *Brasenia schreberi*, *Nuphar advena*, and *Nymphaea odorata* were noted as growing amongst the *N. lutea* plants at one New Jersey site in the 1870s (Porter 1878) and both *Nuphar* and *Nymphaea* continued to be associated with the occurrence in 2020, along with *Potamogeton* and *Ranunculus* species (NJNHP 2022).

Extensive areas dominated by *N. lutea* sometimes influence or alter the communities where they occur. For example, Styles et al. (2021) found that dense stands of the plant could help reduce wave size and bottom stress in intermittently flooded sections of a Louisiana delta, resulting in conditions that promoted sediment accumulation. The preponderance of *N. lutea* in some other locations raised concerns as to whether the lotus released biochemicals that inhibited the establishment or development of nearby plant species. Vance and Francko (1997) examined a colleague's theory that *N. lutea* was allelopathic but found no significant impacts on the growth of the tested species resulted from interactions with either intact lotus plants or derived extracts. Following the rapid expansion of *N. lutea* at a Pennsylvania site, Turner et al. (2010) investigated the species' potential effects on water quality. They found that significant oxygen depletion occurred in the immediate vicinity of the plants as the season progressed, reaching a state of persistent hypoxia with the potential to have a negative impact on fish or other aquatic fauna late in the summer. However the effects did not extend far from the *N. lutea* plants, as no significant depletion was recorded by a sensor located 10 meters beyond the outer edge of the bed. Some positive effects on water quality were reported following phytoremediation research conducted by Reddy et al. (2015), whose work showed that *N. lutea* effectively reduced nearly all of the toxic effects of effluent from the sugar industry at a significant level. *N. lutea* beds are generally beneficial to wildlife in multiple ways. In addition to serving as a food supply for animals that consume the nuts and tubers (Fassett 1957, Hilty 2020), the stands may be utilized by nesting Pied-billed Grebes (*Podilymbus podiceps*) (Lee et al. 2008) and are a preferred roosting habitat

for Wood Ducks during August and September (Thompson and Baldassarre 1988). The decomposing leaves of *N. lutea* are also an important food source for a wide variety of macroinvertebrates, which in turn nourish species that are higher on the food chain (Smock and Stoneburner 1980). *N. lutea* has been identified as an ideal native plant for use in constructed and restored wetlands because it is generally perceived as having high ecological value for fish and wildlife (Ryon et al. 2013, Orozco-Obando and Gettys 2014, Larson et al. 2022).

Wetland Indicator Status

Nelumbo lutea is an obligate wetland species, meaning that it almost always occurs in wetlands (U. S. Army Corps of Engineers 2020).

USDA Plants Code (USDA, NRCS 2023b)

NELU

Coefficient of Conservancy (Walz et al. 2020)

CoC = 8. Criteria for a value of 6 to 8: Native with a narrow range of ecological tolerances and typically associated with a stable community (Faber-Langendoen 2018).

Distribution and Range

The native range of *Nelumbo lutea* extends from the southern edge of Ontario south through parts of Mexico, Central America, and the West Indies (USDA 1971, Wiersema 2020, Weakley et al. 2022). The northern end of South America (Columbia) is sometimes included in descriptions of the species' range (Sayre 2004, POWO 2023). The map in Figure 1 depicts the extent of *N. lutea* in the United States and Canada.

Some sources view New England as part of *Nelumbo lutea*'s native range but others do not. Nearly 200 years ago Rafinesque (1830) explained "*As it is scarce in the Atlantic states it is said to have been planted in some ponds by the Indians*" and Havard (1895) later noted that some eastern populations were "*so far out of its range as to lead to the general supposition that the Indians brought it and naturalized it in those local habitats.*" Many subsequent authors repeated the idea but most simultaneously acknowledged it as theoretical (e.g., Keeler 1917, Saunders 1920, Wiersema 2020). However, recent studies of plant use and dispersal by indigenous people have not turned up any evidence that *N. lutea* was introduced or cultivated in the northeast, although documentation of the plant's use and cultivation by tribes in the midwest and Great Lakes region is plentiful (MacDougall 2003, McKnight 2004, Sayre 2004, Messner 2011). The occurrence of disjunct populations might just as easily be attributable to waterfowl. In some instances the introduction of *N. lutea* at particular sites in the northeastern states has been traced back to post-colonial landowners rather than early inhabitants.

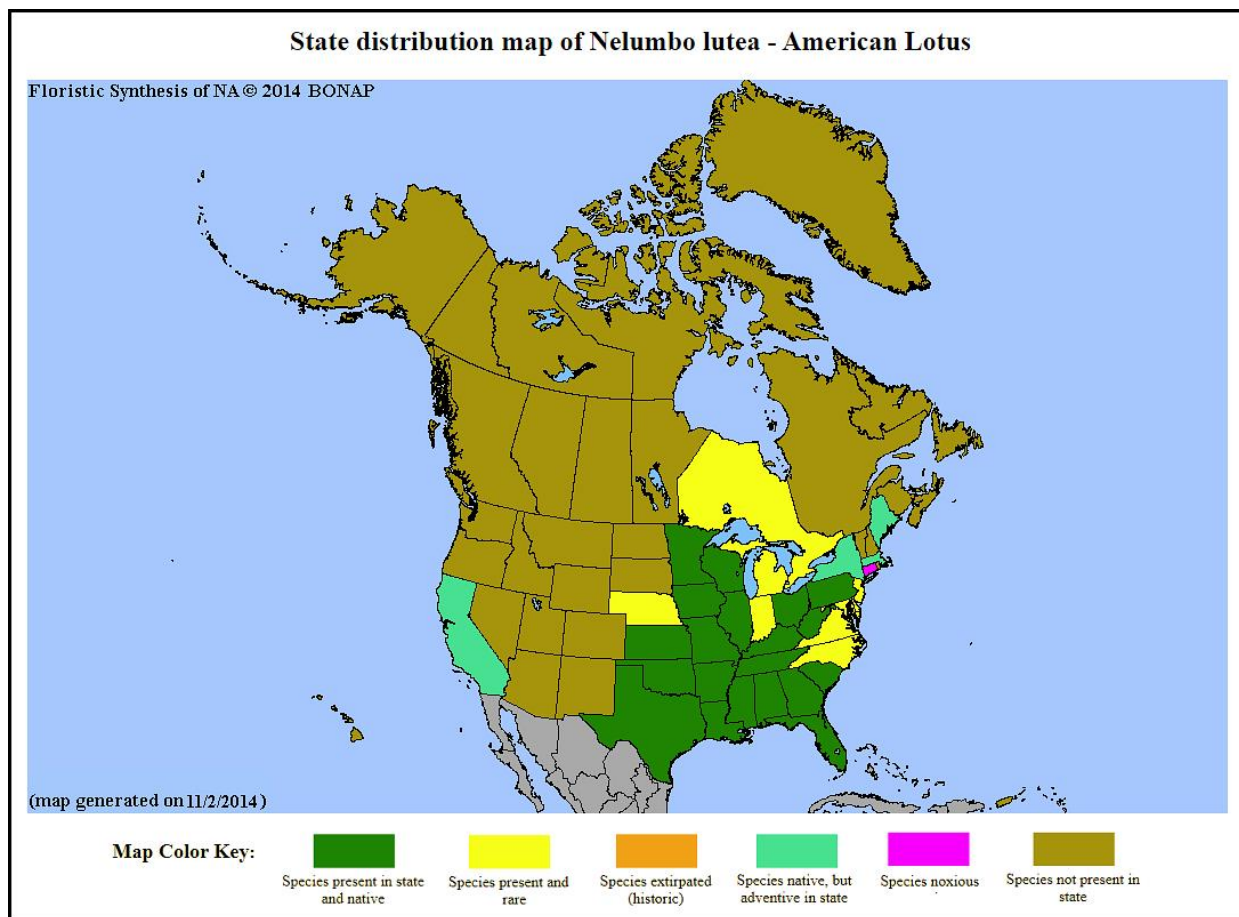


Figure 1. Distribution of *N. lutea* in the United States and Canada, adapted from BONAP (Kartesz 2015).

N. lutea is not broadly established throughout the northeastern United States, although there is a growing concern that it may become more widespread in that region. Angelo and Boufford (2010) reported a limited distribution of the species in three New England states: Maine, Massachusetts, and Connecticut. American Lotus is currently considered adventive in those states (Figure 1) and also in Vermont where it was recently collected (Gilman 2022). In 2017 *N. lutea* was documented in Rhode Island and planting it in that state is now prohibited (RIDEM 2018). In Connecticut *N. lutea* was determined to be Potentially Invasive and its sale, importation, relocation, or cultivation is now banned in the state (CTIPC 2004, 2018). In Maine *N. lutea* is categorized as Severely Invasive but the list has an advisory function rather than a regulatory one (MENAP 2019). Massachusetts occurrences were referred to as probable introductions or escapes by Hellquist and Crow (1984), although Hellquist and Barre (2002) described it as native and aggressive. When threatened and endangered species programs were still in the early phases of establishment *N. lutea* was listed as Endangered in New York (Nelson 1980), but the lotus is now considered adventive in that state too although at least one extant population may have become established naturally (Werier et al. 2023). A similar shift in thinking has occurred in Pennsylvania, where *N. lutea* was previously classified as rare but is now viewed as nonnative and invasive (PADCNR 2018).

N. lutea is accepted as a native species in New Jersey. McKnight (2004) found no references to the plant's use by the Delaware Indians prior to their westward migration, when they entered regions where *N. lutea* was more common. However there is archaeobotanical evidence of lotus seeds at several sites in the region, and a few starch grains identified as originating from *N. lutea* were found on pottery shards recovered from a layer of New Jersey sediments dating back more than a millennium (Messner 2011). The discoveries indicated that *N. lutea* was at least occasionally consumed by indigenous people in the state, so the lack of data documenting usage of *N. lutea* in the northeast may be due to the species' rarity and general unavailability (McKnight 2004). Like many other native plants, *N. lutea* was probably utilized locally where it was obtainable but there is no evidence that the species was cultivated in New Jersey prior to European colonization.

Early floras in the state clearly distinguished between occurrences that were planted—such as one in Bergen County, and native—such as those in Salem and Sussex counties (Britton 1889, Taylor 1915, Fairbrothers and Hough 1973). Fairbrothers and Hough added an Essex County population to the list of native occurrences, and Hough (1983) later noted that some of the colonies known from Burlington and Camden counties had been planted. Only eight of the sites where *N. lutea* has been documented in the state have been recognized as natural occurrences (NJNHP 2022).

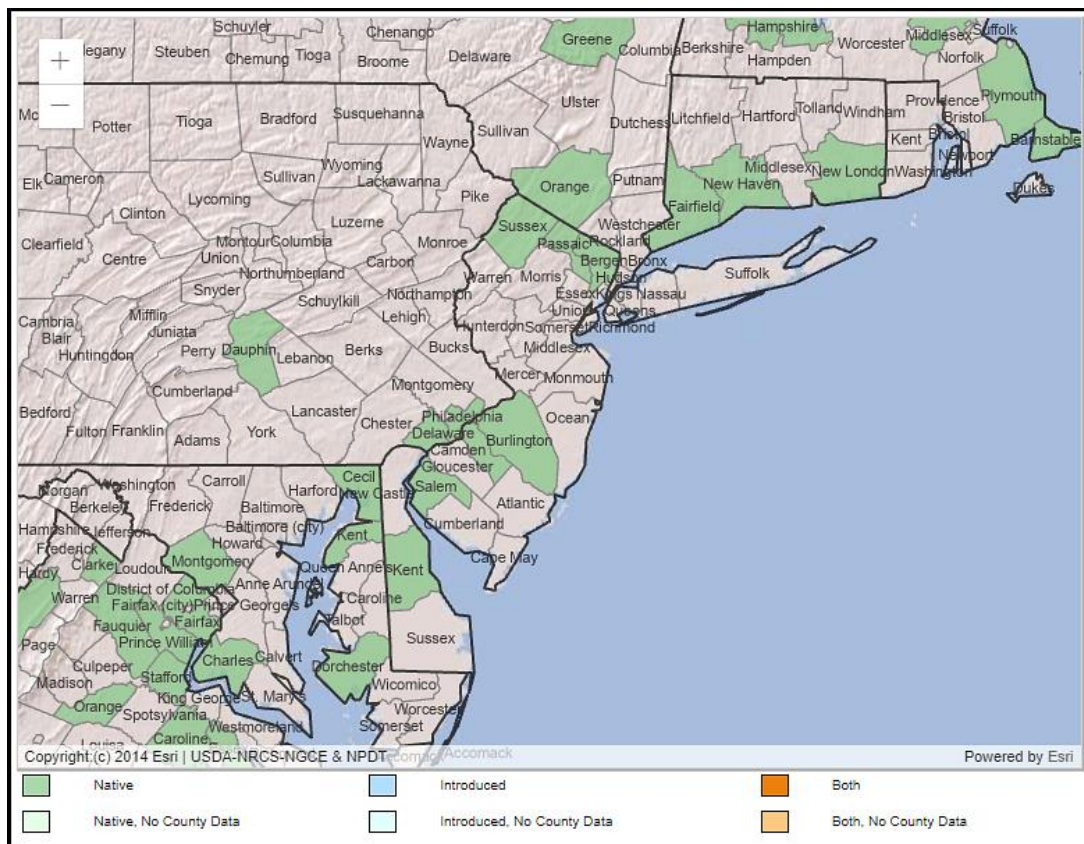


Figure 2. County records of *N. lutea* in New Jersey and vicinity (USDA NRCS 2023b). The USDA PLANTS Database (2023b) shows records of *N. lutea* in six New Jersey counties: Bergen, Burlington, Camden, Passaic, Salem, and Sussex (Figure 2 above). The data include historic observations and do not reflect the current distribution of the species.

Conservation Status

N. lutea is apparently secure at a global scale. The G4 rank means the species is at fairly low risk of extinction or collapse due to an extensive range and/or many populations or occurrences, although there is some cause for concern as a result of recent local declines, threats, or other factors (NatureServe 2023). The map below (Figure 3) illustrates the conservation status of *N. lutea* in the United States and Canada. *N. lutea* is vulnerable (moderate risk of extinction) in three states, imperiled (high risk of extinction) in four states and Ontario, and critically imperiled (very high risk of extinction) in two states. As previously mentioned, *N. lutea* is not currently accepted as native in New York, Pennsylvania, or most of New England. In other parts of the United States where it occurs the species is apparently secure or unranked.

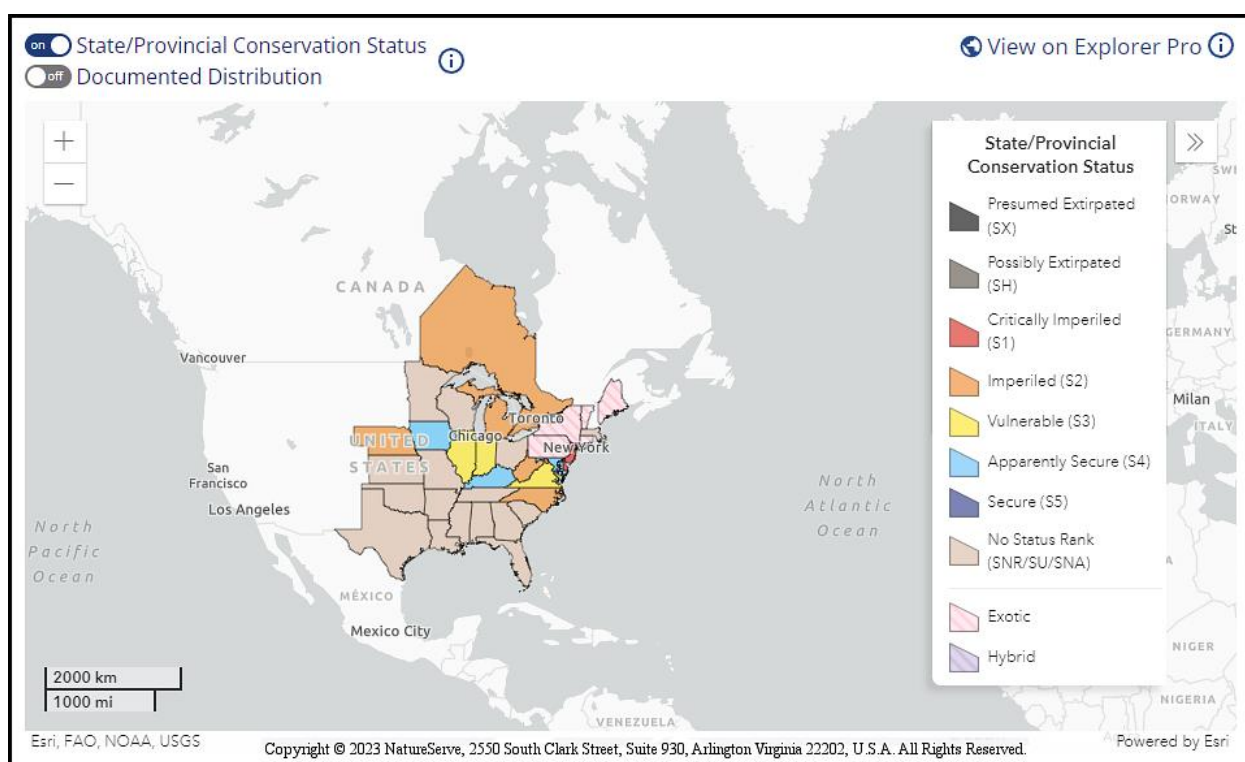


Figure 3. Conservation status of *N. lutea* in the United States and Canada (NatureServe 2023).

New Jersey is one of the states where *N. lutea* is critically imperiled (NJNHP 2022). The S1 rank signifies five or fewer occurrences in the state. A species with an S1 rank is typically either restricted to specialized habitats, geographically limited to a small area of the state, or significantly reduced in number from its previous status. *N. lutea* is also listed as an endangered species (E) in New Jersey, meaning that without intervention it has a high likelihood of extinction in the state. Although the presence of endangered flora may restrict development in certain communities such as wetlands or coastal habitats, being listed does not currently provide broad statewide protection for the plants. Additional regional status codes assigned to the lotus signify that the species is eligible for protection under the jurisdictions of the Highlands Preservation Area (HL) and the New Jersey Pinelands (LP) (NJNHP 2010).

Early written records of the presence of *N. lutea* in Salem County, New Jersey date back to the mid-1700s and can be found in the correspondence of well known botanists from that era (Fry 1997). Five of New Jersey's eight native occurrences of *Nelumbo lutea* were documented with specimens collected during the late 1800s in four counties ranging across the state from Salem to Sussex (Willis 1874 and 1877, Britton 1881, Stone 1911, NJNHP 2022). However, the state's oldest record of *N. lutea* originated in Mercer—a county where the species does not appear to have been seen during the past two centuries. Dorothy Cross conducted a series of archaeological investigations in Mercer County during the mid-1900s and had the foresight to preserve some macrobotanical specimens from the sites for future research. Recent examination of the material from a 1,540-year-old sample resulted in the identification of a number of plant species, including *N. lutea* (Messner 2011).

Despite its long history in New Jersey, *N. lutea* has always been rare in the state (Taylor 1915, Fairbrothers and Hough 1973). Determination of rarity is based on consideration of multiple factors including geographic range, habitat specificity, and local population size so a species that is limited in any of those categories may be identified as rare. Consequently, a plant is categorized as rare in districts where it is known from only a few sites even if it is plentiful in the locations where it grows (Rabinowitz 1981). Heckschner (1984) observed that the lotus was generally uncommon even in the heart of its range but often extremely abundant in the places where it did occur. Referring to the distribution of *N. lutea* in New Jersey, Stone (1911) remarked that the species was "very local but abundant where found" and more than a century later that continues to be the case. Five of the eight native occurrences are ranked as historical or extirpated but the three that remain appear to be vigorous (NJNHP 2022).

Threats

Although *N. lutea* populations are often capable of rapid expansion they can also be subject to rapid decline. One well-known native occurrence in New Jersey disappeared from a site where it had previously been abundant and a similar report was made regarding an introduced population in Massachusetts—in both cases the causes of the lotus's demise were unknown (Brown 1912, Harris 1958). Whyte et al. (1997) found that individual *N. lutea* beds within a single aquatic system exhibited different patterns of growth and decline. Depending on the type and extent of local stress factors, *N. lutea* tubers may either deplete their reserves or remain dormant for a while and then re-establish a population.

N. lutea is generally tolerant of slightly fluctuating water levels or brief periods of drawdown but extensive flooding can damage or eliminate populations. Wheeler (1900) observed that rising water levels destroyed lotus leaves that had been floating on the surface while those that were held above the water survived. In some cases, the plants can extend their petioles as the water rises but at other times the water levels exceed the stems and the leaves become submerged (Spink and Rogers 1996). Acute damage to *N. lutea* plants from flooding was observed by Hall and Penfound (1944), and Martin et al. (1957) indicated that mature *N. lutea* plants could be killed if the leaves remained covered for 12 days or more. In several instances where extended inundation has triggered severe dieback in *N. lutea* populations, some beds have recovered while

others have not (McDonald 1955, Spink and Rogers 1996, Whyte et al. 1997). Fruit production may be significantly reduced following a flood (Hall and Penfound 1944) but that can also occur if water availability is limited (Schneider and Buchanan 1980). Long-term drawdowns may alter the habitat sufficiently to favor species other than *N. lutea*. At one Ohio site where water levels declined the lotus beds gradually transitioned to mixed emergent community that in turn became dominated by monotypic stands of *Phragmites australis* (Whyte et al. 2008). Gehn (2017) noted that sediment deposition resulting from shifting water levels at a Minnesota site was facilitating the establishment of Wild Rice (*Zizania aquatica*) and other emergent species in sites that *N. lutea* had previously dominated. One Florida population situated on an exposed shoreline experienced a decline after the site burned (Vogl 1973), but the lotus is unlikely to be subjected to fire under normal circumstances.

Human activities have resulted in the unintentional destruction of some *N. lutea* occurrences. Barton (1818) reported a local decrease in the species' abundance due to an unspecified habitat disturbance. A large Delaware population of *N. lutea* was lost following a "realignment" that altered the course and depth of the river associated with the occurrence (McKnight 2004), although it is not clear whether the changes resulted in higher or lower water levels at the former site of the lotus beds. River dredging was cited as the reason for the loss of a population in Washington, D. C. (Li et al. 2015). *N. lutea* populations are also intentionally destroyed by people who view the species as undesirable. For example, an evaluation of herbicides for the control of "problem plants" identified five products that have significant detrimental effects on *N. lutea* (Cheshier et al. undated).

N. lutea populations can experience extensive damage from insect activity. *Donacia hypoleuca*, a leaf beetle that utilizes *N. lutea* as a larval food plant, had such a detrimental impact on a Tennessee population observed by Steenis and Mitchell (1950) that the authors recommended investigation of the beetles as a possible means of biological control for the lotus. *Ostrinia penitalis* (American Lotus Borer) is a moth frequently—although not exclusively—associated with *N. lutea*. The larvae typically consume reproductive tissue such as floral buds and seed capsules (Chittenden 1918, Welch 1919). In a population studied by Ainslie (1922), *P. penitalis* larvae destroyed 34.7% of the seeds in affected pods but only a small proportion (5.9%) of the seeds that were produced by the entire population. However, Lotus Borer damage is likely to be exacerbated by the activity of Red-winged Blackbirds (*Agelaius phoeniceus*) as they probe the plants for moth larvae, and in some cases the combined impact can drastically reduce fertility in a lotus population (Sohmer and Sefton 1978, Schneider and Buchanan 1980). The larvae of another moth, *Bellura obliqua*, bore through the rhizomes of various aquatic plants, including *N. lutea* (Hilty 2020, BugGuide 2023). Neither moth species poses a significant threat to healthy lotus colonies.

Genetic diversity has been studied in *N. lutea* using material from populations at different locations throughout the United States (Li et al. 2015, Islam et al. 2020, Lu et al. 2023). The investigations consistently found very low levels of genetic variation within individual populations but high rates of differentiation between distinct populations. The results are not surprising because the species is generally reliant on clonal growth and when the plants do reproduce sexually they are likely to be fertilized with pollen from another flower on the same genet. There is little opportunity for gene exchange between the widely scattered and often

isolated occurrences of *N. lutea*. Genetically homogenous populations are more likely to experience catastrophic losses from a single event than populations with high genetic variability (Booy et al. 2000, Hughes et al. 2008), and reduced adaptability might also increase the species' vulnerability to climate change (Jump and Peñuelas 2005).

Some of the effects of changing climactic conditions in New Jersey include higher temperatures, shifting precipitation patterns that increase the frequency and intensity of storms, droughts, and floods, and rising sea levels along the coast (Hill et al. 2020). One of the state's three extant populations of *N. lutea* is situated in a tidally influenced area that is highly susceptible to sea level rise and was affected by the storm surge associated with Superstorm Sandy in 2012 (NJ Adapt 2023). Vegetation community studies in a section of coastal Louisiana that has been subjected to a number of severe storms during the past decade indicated that *N. lutea* initially experienced significant mortality following the events but the recovery of populations varied depending on local conditions. Although some occurrences did not rebound quickly many did and *N. lutea* frequently expanded into new areas, colonizing locations with freshly deposited organic-rich sediments before other species had a chance to establish (Carle et al. 2015, Bevington et al. 2022, Li et al. 2023). On the whole, the species appeared to be quite resilient to the impacts of severe storms and associated flooding events.

Global warming may actually benefit *N. lutea* in New Jersey and elsewhere in the northeastern and north-central United States. Meyer (1930) demonstrated that lotus tubers were destroyed by freezing and suggested that winter temperatures could define the northern boundaries of the species range. Hall and Penfound (1944) noted that *N. lutea* plants in Louisiana had been described as a distinct species by one botanist due to their larger size but thought that the bigger plants were probably attributable, at least in part, to the longer growing season in the south. In controlled studies, higher temperatures have increased the growth rates of both seedlings and mature plants (Meyer 1930, Al Hamdani and Francko 1992), and Moran (1981) reported that thermal effluent in a cooling reservoir for an electric generating station accelerated the growth and enhanced the biomass of lotus plants in the discharge area. Regardless of whether *N. lutea* is native or adventive in New England the species appears to have increased its presence in the region during recent years, and the expansion may be a consequence of climate change.

Management Summary and Recommendations

Although *N. lutea* is generally long-lived, more than half of the documented populations in New Jersey have been lost, making conservation of the three that remain particularly important. Extirpated lotus populations are not readily replaced because the colonization of new sites is relatively infrequent. Since there is a strong genetic divergence among *N. lutea* populations, isolated occurrences such as those in New Jersey could serve as a significant heritable diversity resource for the species as a whole.

Little active management is currently required to preserve the extant populations of *N. lutea* in New Jersey. In fact, at one site where extensive growth of the species was perceived as a nuisance by local residents some activities were undertaken to reduce the size of the occurrence (NJNHP 2022). That particular population is the sole remaining occurrence in the state that was

documented during the 1800s and it has remained large and vigorous for at least 145 years (Porter 1878, NJNHP 2022), so the established pattern of annual monitoring should be maintained in order to assure that it continues to thrive.

If *N. lutea* becomes more widespread and abundant as the climate continues to warm, future management may require striking a balance between maintaining occurrences and controlling the spread of the species at some locations. Application of herbicides is discouraged, particularly at sites where other threatened and endangered species co-occur with *N. lutea*. Hall and Penfound (1944) pointed out that herbicides typically removed the leaves but not the tubers, recommending instead the use of a mechanized underwater weed-cutter. They noted that recurrent cutting could be used to slow the spread of *N. lutea* clones or reduce the size of existing stands. Cutting is most effective at the beginning of June—after the plants have invested much of their energy in new growth but before they spread farther into new areas or develop fruits and seeds (Hall and Penfound 1944).

Synonyms

The accepted botanical name of the species is *Nelumbo lutea* Willd. Some orthographic variants, synonyms, and common names are listed below (ITIS 2023, POWO 2023, USDA NRCS 2023b). *Nelumbo lutea* was initially described as a variety of *N. nucifera* (Linnæus 1762) but Willdenow (1799) made a clear distinction between the two in a subsequent edition of *Species Plantarum*. Another name (*Nymphaea pentapetala*) proposed by Walter in 1788 was widely used for a while and was the basis for some subsequent names, but several of Walter's descriptions were apparently based on flawed specimens so years of taxonomic arguments ensued as to how the code of botanical nomenclature should be applied in that situation (eg. Fernald 1934, Sohmer 1975, Ward 1977). The debate was resolved by the formal rejection of Walter's name, which established Willdenow as the authority (Wiersema and Reveal 1991). As Willdenow had not designated a type in his publication, Wiersema and Reveal selected a specimen collected by John Bartram in New Jersey during 1793 as the neotype.

Botanical Synonyms

Nelumbium codophyllum Raf.
Nelumbium jamaicense DC.
Nelumbium luteum Willd.
Nelumbium pentapetalum (Walter) Willd.
Nelumbium reniforme Willd.
Nelumbo nucifera ssp. *lutea* (Willd.) Borsch & Barthlott
Nelumbo nucifera var. *lutea* (Willd.) Kuntze
Nelumbo pentapetala (Walter) Fernald
Nymphaea pentapetala Walter
Cyamus flavicomus Salisb.
Cyamus luteus (Willd.) Nutt.
Cyamus mysticus Salisb.
Cyamus nelumbo Sm.

Common Names

American Lotus
Yellow Lotus
Water Chinquapin
Duck Acorns
Yonkapin

Cyamus pentapetalus (Walter) Pursh
Cyamus reniformis Pursh

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Neotype of *Nelumbo lutea* from New Jersey (Bartram 1793).