Ptelea trifoliata var. trifoliata

Wafer-ash

Rutaceae



Ptelea trifoliata var. trifoliata by J. S. Dodds, 2014

Ptelea trifoliata var. trifoliata Rare Plant Profile

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

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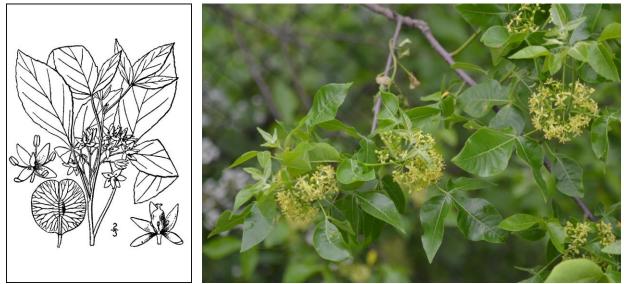
March, 2025

For: New Jersey Department of Environmental Protection Office of Natural Lands Management New Jersey Natural Heritage Program natlands@dep.nj.gov

This report should be cited as follows: Dodds, Jill S. 2025. *Ptelea trifoliata* var. *trifoliata* Rare Plant Profile. New Jersey Department of Environmental Protection, State Parks, Forests & Historic Sites, Forests & Natural Lands, Office of Natural Lands Management, New Jersey Natural Heritage Program, Trenton, NJ. 19 pp.

Life History

Ptelea trifoliata var. *trifoliata* (Wafer-ash) is a small tree or multi-stemmed shrub in the rue family. *Ptelea trifoliata* includes numerous poorly-defined subordinate taxa but only one occurs in New Jersey (see Synonyms and Taxonomy section). The species does not spread clonally (Ambrose et al. 1985), although basal root sprouts may occasionally develop (Brizicky 1962). A high turnover in *P. trifoliata* populations suggests that individual plants are not long-lived (Ambrose et al. 1985). Fully grown plants may range from 3.5–8 meters in height and attain a maximum trunk diameter of 15 cm. The bark of young trunks is smooth, chestnut-colored, and sprinkled with horizontal lenticels but with age it can become ridged and duller brown. The long-stemmed leaves are divided into three stalkless, ovate, acute-tipped leaflets. *P. trifoliata* var. *trifoliata* leaflets are smooth and their margins are entire or somewhat wavy. The flowers develop in clusters and they may have 3–5 sepals and petals, although 4 is typical. The indehiscent, conspicuously-winged fruits are nearly circular and 20–25 mm in diameter. (See Small 1901, Britton and Brown 1913, Fernald 1950, Bailey 1962, Gleason and Cronquist 1991, Morgenson 2002).



Left: Britton and Brown 1913, courtesy USDA NRCS 2025a. Right: Joseph Kurtz, 2018.

Ptelea trifoliata is primarily dioecious, meaning that the male and female flowers occur on separate plants. The flowers on female plants have reduced stamens and their anthers do not produce pollen. Male plants tend to generate more numerous and showier inflorescences—their flowers have fertile anthers, and pistils are present but they generally remain small. However about 3% of male *P. trifoliata* plants produce a few functional bisexual flowers that can develop fruit (Ambrose et al. 1985).

Plants in the Rutaceae usually have cavities or glands that secrete volatile oils (Brizicky 1962). All parts of *Ptelea trifoliata* are distinctly aromatic, including the roots, foliage, flowers, and fruit. The glands in the leaves are located just below the epidermis, and large cells in the fruits typically contain one large globule of oil and several smaller ones (Bigelow 1894). Bailey (1960) characterized the odor of *P. trifoliata* roots as strong and bitter. Mickelbart et al. (2013)

noted that the smell of the fruits was reminiscent of hops (*Humulus*) while that of the flowers was sweeter and more pleasant, although Genders (1977) suggested that the blooms and foliage also had overtones of hops. Different scents are produced by male and female flowers. In a blind test, a panel of judges convened by Talcott Stewart et al. (2022a) described the aroma of staminate flowers as damp-earthy, spicy, and sweet and that of pistillate flowers as light, fresh, grassy, and pleasant. Comparative analyses of the chemical constituents of male and female *P*. *trifoliata* flowers have found that they contain a similar array of compounds but the components are present in different proportions (Setzer and Satyal 2019, Talcott Stewart et al. 2022a).



Left: Jacques Ranger, 2020. <u>Right</u>: Steve Hurst, courtesy USDA NRCS 2025b.

Ptelea trifoliata var. *trifoliata* may bloom from April through July and the fruits can mature from June through October. The process begins earlier in the southern part of the species' range and later to the north (Stone 1911, Robertson 1929, Rhoads and Block 2007, Weakley et al. 2024, Brinkman et al. undated). The leaves usually remains bright green throughout the growing season but turn yellow-green in the fall prior to being discarded. The fruits often persist on the branches well beyond leaf-off, which can help to identify the species in the winter (Foerste 1892, Ambrose et al. 1985, Morgenson 2002, Leopold 2005).

Pollinator Dynamics

Because *Ptelea trifoliata* is dioecious, cross-fertilization is needed for fruit development. Both the male and female flowers produce nectar and they are highly attractive to insects. The pollinators of *P. trifoliata* are unusually diverse: They include a wide variety of bees, wasps, and flies as well as an assortment of butterflies, moths, and beetles (Robertson 1896 & 1929, Brizicky 1962, Ambrose et al. 1985, Stubbs et al. 1992, Hilty 2020, Talcott Stewart et al. 2022b). Wafer-ash is a critical nectar resource for the Juniper Hairstreak (*Callophrys gryneus*) in Ontario, where the butterfly is declining (Denomme-Brown and Otis 2012).

Fruit set in an Iowa population of *Ptelea trifoliata* was drastically reduced when the flowers were enclosed in mesh bags, demonstrating that pollination was dependent on insects that were too large to fit through the 600 µm holes in the covers (Talcott Stewart et al. 2022b). Ambrose et al. (1985) suggested that wind might occasionally facilitate *P. trifoliata* pollination if male and female plants were growing in close proximity but the contribution was likely to be negligible. The possibility of self-fertilization in the occasional bisexual flowers does not appear to have been ruled out.

Seed Dispersal and Establishment

The majority of *Ptelea trifoliata* fruits contain a single seed but in roughly a fifth of them two or more seeds develop. The fruits (samaras) are adapted for wind dispersal although many do not travel far from the maternal plants: Foerste (1892) noted that they could often be found on the ground directly below the trees. Once the samaras have fallen from a tree additional movement may be hampered by their size and weight, but on smooth surfaces like snow, ice, or sand the wind can carry them farther with relative ease. Fruits that land on water-borne chunks of ice or debris may be dispersed over longer distances by the currents. Multi-seeded fruits have the potential to establish new populations that include both male and female plants (Ambrose et al. 1985).

Ptelea trifoliata seeds are dormant at the time of dispersal and the fruits contain chemicals that inhibit germination. They will not sprout until they have been exposed to a period of cool temperatures and the fruit has broken down. As a result of the dual requirements the seeds are typically ready to sprout in the spring when conditions are optimal for seedling development. Propagules that fail to germinate in the spring do not do so during the hot, dry months of summer, but they remain viable and can form a seed bank (McLeod 1974, McLeod and Murphy 1977a).

Ptelea trifoliata seedlings are particularly sensitive during their first year because their ability to survive depends on whether the roots can grow long enough to obtain sufficient water, but survival rates can improve dramatically in second-year seedlings (McLeod 1974, McLeod and Murphy 1977b). Seedling growth is also enhanced by nutrient availability. In shifting substrates such as sand dunes, *P. trifoliata* seedlings may develop adventitious roots that aid in their stabilization (McLeod and Murphy 1983). Seedling establishment rates are high in most populations (Ambrose et al. 1985). Ciosek et al. (2015) identified *P. trifoliata* as a potentially invasive species in Poland because it has such a great capacity to reproduce and establish when conditions are favorable. Like other members of the Rutaceae, *Ptelea trifoliata* forms arbuscular mycorrhizae (Appelhans et al. 2008). It is not clear whether fungal associations are required for seedling establishment although it appears that they would be advantageous.

When growing *Ptelea trifoliata* in controlled conditions, recommendations include pre-soaking the fruits, removing the seed coats, and exposing the seeds to cold temperatures for 3-4 months (Dreesen and Harrington 1997, Leopold 2005, Talcott and Graves 2020). In some varieties *of P. trifoliata* germination can be improved if the cold stratification is preceded by an equivalent

period of warm, moist stratification (Morgenson 2002). The species can also be propagated vegetatively using techniques like layering, grafting, or budding (Brinkman et al. undated).

<u>Habitat</u>

Ptelea trifoliata can grow in an assortment of mesic habitats ranging from sea level to elevations of 1000 meters or more (Bailey 1962). The species can occur over a variety of substrates although it does best in soils that are fertile and moist but well-drained (Leopold 2005, Ciosek et al. 2015). However, populations have also been documented in xeric habitats (Ambrose et al. 1985, Majure 2007). Typical habitats in New Jersey include rocky hillsides and alluvial riverbanks (Stone 1911, Hough 1983, NJNHP 2024). *P. trifoliata* utilizes similar habitats in other parts of its range, but it has also been recorded on sandy lake shores and in glades, barrens, prairies, or old fields (Bailey 1962, Van Auken et al. 1979, Klotz and Walck 1993, Kirk 1994, Rhoads and Block 2007, Weakley et al. 2024).

Ptelea trifoliata can tolerate a variety of light conditions, although it does poorly in deep shade (Leopold 2005, Mickelbart et al. 2013). Weakley et al. (2024) assigned the species a heliophily rank of 6 on a scale from 1 (shade obligate) to 9 (sun obligate). Ciosek et al. (2015) observed that *P. trifoliata* was more frequent along woodland edges than in forest interiors. The rate of photosynthesis in Wafer-ash leaves rises in response to higher levels of light (Van Auken 2021). When growing in shaded locations, *P. trifoliata* can increase carbon capture by developing larger leaves, but the production of flowers and fruits is nevertheless reduced (Ambrose et al. 1985, Morgenson 2002).

Sufficient light is needed for seedling development. Ambrose et al. (1985) observed that *Ptelea trifoliata* seedlings were absent from heavily shaded locations or sites with a dense vegetative cover and surmised that periodic disturbances along shorelines created favorable germination sites. In Poland the rapid spread of *P. trifoliata* along the edges of forest has been attributed to the availability of both abundant light and patches of bare soil (Ciosek et al. 2015).

Wetland Indicator Status

The U. S. Army Corps of Engineers divided the country into a number of regions for use with the National Wetlands Plant List and portions of New Jersey fall into three different regions (Figure 1). *Ptelea trifoliata* has more than one wetland indicator status within the state. In the Eastern Mountains and Piedmont region it is a facultative species, meaning that it occurs in both wetlands and nonwetlands. In other parts of the state *P. trifoliata* is a facultative upland species, meaning that it usually occurs in nonwetlands but may occur in wetlands (U. S. Army Corps of Engineers 2022).

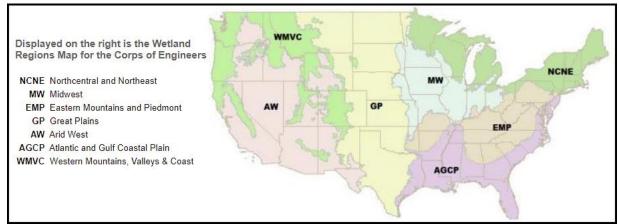


Figure 1. Mainland U. S. wetland regions, adapted from U. S. Army Corps of Engineers (2022).

USDA Plants Code (USDA, NRCS 2025c)

The USDA lists the New Jersey form as *Ptelea trifoliata* ssp. *trifoliata* var. *trifoliata*, code PTTRT2.

Coefficient of Conservancy (Walz et al. 2020)

CoC = 7. 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

Ptelea trifoliata var. *trifoliata* is native in parts of the central and eastern United States and Canada, although occurrences in some districts along the edges of its natural range are apparently adventive. Seeds collected in colonial America during the early 1700s were cultivated in Europe, where the species remained popular as a garden shrub for nearly two centuries (Bailey 1960, 1962). Since then, *P. trifoliata* has naturalized in a number of European counties (POWO 2025) and it was recently documented in Russia (Tokhtar et al. 2017). The map in Figure 2 depicts the extent of the variety in Canada and the United States.

The USDA PLANTS Database (2025c) shows records of *Ptelea trifoliata* in eight New Jersey counties: Burlington, Hudson, Hunterdon, Mercer, Middlesex, Morris, Somerset, and Warren (Figure 3). There is also a record from Bergen County (NJNHP 2024). The data include historic observations and do not reflect the current distribution of the species.

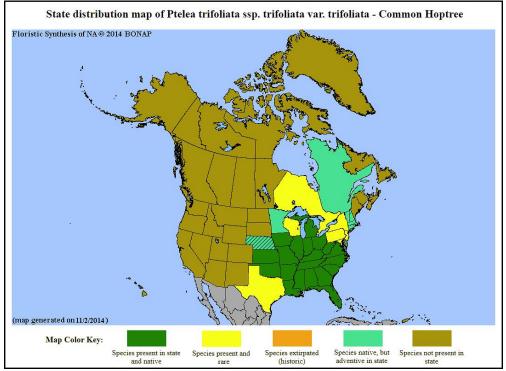


Figure 2. Distribution of P. trifoliata ssp. trifoliata var. trifoliata in North America, adapted from BONAP (Kartesz 2015).

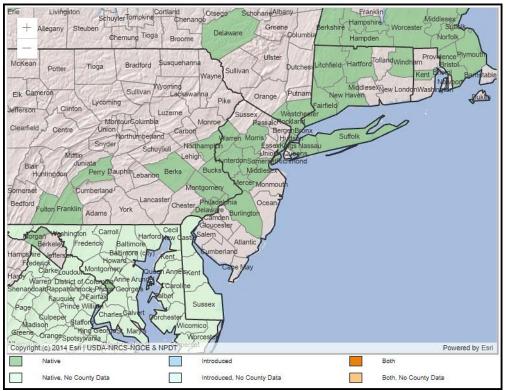


Figure 3. County records of *P. trifoliata ssp. trifoliata var. trifoliata in New Jersey and vicinity (USDA NRCS 2025c).*

Conservation Status

Ptelea trifoliata var. *trifoliata* is considered globally secure. The G5T5 rank means the variety has a very low risk of extinction or collapse due to a very extensive range, abundant populations or occurrences, and little to no concern from declines or threats (NatureServe 2025). The map below (Figure 4) illustrates the conservation status of *Ptelea trifoliata* var. *trifoliata* in the United States. *P. trifoliata* is also listed as threatened in Canada, where native occurrences are restricted to Ontario, but that status is not displayed on the map because it was identified as a subspecies rather than a variety by COSEWIC (2015). *P. trifoliata* var. *trifoliata* has not been ranked in the majority of the states where it occurs. However, the variety is vulnerable (moderate risk of extinction) in three states, imperiled (high risk of extinction) in two states, and critically imperiled (very high risk of extinction) in one state.

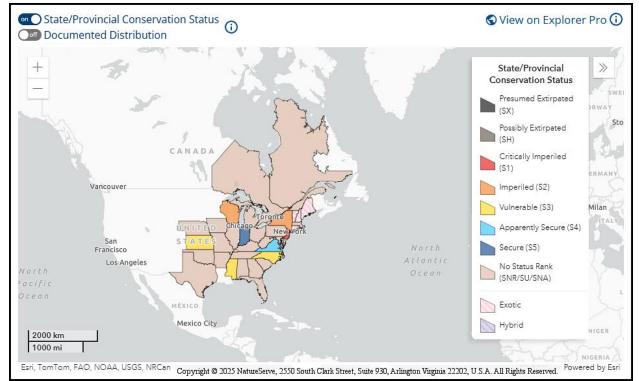


Figure 4. Conservation status of P. trifoliata var. trifoliata in the United States (NatureServe 2025).

New Jersey is the one state where *Ptelea trifoliata* var. *trifoliata* is critically imperiled (NJNHP 2024). 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. *Ptelea trifoliata* 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 *P. trifoliata* 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).

Ptelea trifoliata has always been rare in New Jersey. The species was documented at two sites in the state during the 1880s and a third location was added near the beginning of the 1900s (Britton 1889, Stone 1911, Taylor 1915). By the mid-1990s the original populations had not been seen for more than fifty years, although several new occurrences had been documented (Hough 1983). *P. trifoliata* has been listed as endangered in New Jersey since 1990 (NJONLM 1990). Four populations are currently ranked as historical and four others are thought to be extant. A population that was identified as extant by Breden et al. (2006) has since been extirpated. On a brighter note, recent monitoring of two of the extant *P. trifoliata* occurrences found greater numbers of individuals than those recorded during the prior site visits (NJNHP 2024).

Threats

One New Jersey population of *Ptelea trifoliata* was destroyed by maintenance activities conducted along a corridor associated with a footpath. Although the last remaining tree resprouted several times it eventually succumbed after repeated cutting. Other populations in the state currently face threats from habitat loss and fragmentation, all-terrain vehicle traffic, and the proliferation of invasive flora (NJNHP 2024), which are among the top challenges faced by many other native plants in New Jersey. The spread of invasive species is likely to cause a particular problem for *P. trifoliata* by limiting the availability of suitable germination sites for seedling establishment. Similar threats have been reported in other parts of the species' range (McLeod and Murphy 1983, COSEWIC 2015).

As previously noted, *Ptelea trifoliata* attracts a wide variety of pollinators, and the plants are also utilized by to a broad array of herbivorous insects. Alkaloids present in the sap and foliage can be a deterrent to some would-be consumers but others have adapted to tolerate, or even benefit from, the compounds. *Enchenopa binotata*—a treehopper complex that includes a number of yet-to-be described species with different host plant affiliations—is one example. The nymphs of six *E. binotata* species were tested by Kiss (1984) and only one type was able to feed on *P. trifoliata*. That treehopper is often found on Wafer-ash leaf petioles. The insect's exudate (honeydew) contains the same alkaloids that occur in the plant (Kiss 1984, McNett and Cocroft 2008). Another example is a western grasshopper (*Schistocerca emarginata*) that can utilize two food plants during its juvenile stage. The grasshoppers that preferentially consume *P. trifoliata* become unpalatable to predators, but they quickly lose their toxicity if they switch to another food source (Sword 1999 & 2001, Sword and Dopman 1999, Dopman et al. 2002).

Some of the insects that are capable of feeding on *Ptelea trifoliata* can cause significant harm to the trees while other have a relatively low impact. Young trees may be seriously damaged by the twig-boring Hoptree Barkbeetle (*Phloeotribus scabricollis*), and herbivory by larvae of the Hoptree Leaf-roller Moth (*Agonopterix pteleae*) can result in extensive defoliation. The Hop-tree Ermine Moth (*Prays atomocella*) exclusively feeds inside developing *P. trifoliata* shoots (COSEWIC 2015, BugGuide 2025). *Ptelea trifoliata* has been identified as a larval food plant of two swallowtail butterflies (*Papilio cresphontes* and *P. glaucus*) but recent studies have indicated that the butterflies preferentially utilize alternative woody species (*Zanthoxylum* and *Liriodendron*, respectively) when they are available (Scriber 1972, Scriber and Dowell 1991,

Mercader et al. 2008, Fadamiro et al. 2010). Webster (1922) observed numerous leafhoppers (*Empoasca flavescens*) feeding on the foliage of *Ptelea trifoliata* and noted that their activity resulted in patches of necrotic tissue in the leaves. However the leafhoppers are a generalist species that uses multiple hosts, and their eggs are parasitized by a fairy wasp (*Anagrus spiritus*) which probably keeps their abundance in check. A number of other species in the Rutaceae are threatened by an introduced psyllid (*Diaphorina citri*) that is the vector of a serious plant pathogen but the insects do not appear to pose a threat to *Ptelea* (Setamou et al. 2016).

Ptelea trifoliata is also susceptible to a rust fungus, *Puccinia windsoriae*. Like many rusts, *P. windsoriae* uses alternate hosts in order to complete its life cycle—in this case the primary alternate host is *Tridens flavus* (Arthur 1900 & 1903, Anderson and Anderson 1919, Mains 1933, Thurston and White 1933). Warren (1898) also reported an occurrence of the rust on *Muhlenbergia racemosa. Puccinia* is an especially destructive genus and many of the rusts can bring about severe losses in the host plants (Avasthi et al. 2023). Plants that are already stressed by other factors are particularly likely to experience reduced reproduction or increased mortality (Kranz 1990).

<u>Climate Change Vulnerability</u>

Information from the references cited in this profile was used to evaluate the vulnerability of New Jersey's *Ptelea trifoliata* var. *trifoliata* populations to climate change. The species was assigned a rank from NatureServe's Climate Change Vulnerability Index using the associated tool (Version 3.02) to estimate its exposure, sensitivity, and adaptive capacity to changing climactic conditions in accordance with the guidelines described by Young et al. (2016) and the state climactic computations by Ring et al. (2013). Based on available data *P. trifoliata* was assessed as Moderately Vulnerable, meaning that it is likely to show some decrease in abundance or range extent in New Jersey by 2050.

Changing climactic conditions in New Jersey are resulting in higher temperatures, more frequent and intense precipitation events, and increasing periods of drought (Hill et al. 2020). *Ptelea trifoliata* is most likely to be sensitive to excessive heat or drought during the establishment phase when soil moisture is critical (McLeod and Murphy 1977b, 1983). Mature *P. trifoliata* var. *trifoliata* trees with well-developed root systems can be relatively resistant to droughts, and they can minimize water loss by shedding their leaves during dry periods and producing new ones if conditions improve later in the season (Mickelbart et al. 2013, Peterson and Graves 2013). The species appears to be less tolerant of extended flooding, although brief floods along waterways following storms could create favorable microsites for seedlings. Existing threats from invasive plants are likely to increase as the climate continues to warm (Bellard et al. 2013, Salva and Bradley 2023).

Because *Ptelea trifoliata* can utilize a broad range of pollinators and is able to spread rapidly under the right conditions the species may establish at new locations if old ones become unsuitable (Talcott Stewart et al. 2022b). A comparison of *P. trifoliata*'s distribution during two periods (1959–1999 and 2000–2018) suggests that a northward range shift is already underway (Wilson et al. 2021).

Management Summary and Recommendations

The management of extant *Ptelea trifoliata* populations in New Jersey should focus on maintaining favorable habitat conditions for reproduction, germination, and the growth of young plants. Actions to be considered at the various sites may include selective removal of canopy trees to encourage flower and fruit development, invasive species control, or the creation of microsites featuring bare soil and abundant light to promote seedling establishment. One occurrence in the state has not been monitored since 1995 so an updated assessment is recommended to assess the population status, identify current threats, and determine site-specific management needs. Searches for extant *P. trioliata* plants should also be carried out at four historical sites where suitable habitat still exists (NJNHP 2024).

Synonyms and Taxonomy

The accepted botanical name of the species is *Ptelea trifoliata* L. var. *trifoliata* (NJNHP 2024, Weakley et al. 2024, ITIS 2025, NatureServe 2025). *Ptelea trifoliata* is a variable species and botanists have taken an assortment of approaches to delineating subordinate taxa, some of which remain poorly differentiated and display overlapping or intermediate characteristics that may be more indicative of a continuum (Bailey 1962, Skornia et al. 2015). The results of transplantation experiments indicated that regional differences are attributable to genetic variation rather than local environmental factors (Bailey et al. 1970). The form that occurs in New Jersey is consistent with the original species description and no other named varieties occur in the state. Equivalent names utilized by sources in this text include *P. trifoliata* ssp. *trifoliata* (POWO 2025) and *P. trifoliata* ssp. *trifoliata* var. *trifoliata* Kartesz 2015, USDA NRCS 2025). Two synonyms on which most sources agree are listed below, along with some common names.

Botanical Synonyms

Ptelea microcarpa Small Ptelea serrata Small

Common Names

Wafer-ash Common Hoptree Three-leaved Hop-tree Stinking Ash

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