CITRUS TRIFOLIATA (RUTACEAE): REVIEW OF BIOLOGY AND DISTRIBUTION IN THE USA

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Citrus trifoliata (aka Poncirus trifoliata, trifoliate orange) has become an aggressive colonizer in the southeastern USA, spreading from plantings as a horticultural novelty and use as a hedge. Its currently known naturalized distribution apparently has resulted from many independent introductions from widely dispersed plantings. Seed set is primarily apomictic and the plants are successful in a variety of habitats, in ruderal habits and disturbed communities as well as in intact natural communities from closed canopy bottomlands to open, upland woods. Trifoliate orange is native to southeastern China and Korea. It was introduced into the USA in the early 1800's but apparently was not widely planted until the late 1800's and early 1900's and was not documented as naturalizing until about 1910.

Citrus trifoliata L. (trifoliate orange, hardy orange, Chinese bitter orange, mock orange, winter hardy bitter lemon, Japanese bitter lemon) is a deciduous shrub or small tree relatively common in the southeastern USA. The species is native to eastern Asia and has become naturalized in the USA in many habitats, including ruderal sites as well as intact natural commmunities. It has often been grown as a dense hedge and as a horticultural curiosity because of its green stems and stout green thorns (stipular spines), large, white, fragrant flowers, and often prolific production of persistent, golf-ball sized orange fruits that mature in September and October. The fruit peels are sometimes used for marmalade, but the fruits are intensely sour or bitter. "Don Shadow, a nurseryman in Tennessee, has a recipe for poncirus-ade: Take a barrel of water, a barrel of sugar, and add one sour fruit (Klingaman 2007).

Trifoliate orange is native to temperate China and Korea (Fig. 1; WHO 1998; Dianxiang & Mabberly 2008; Fang et al. 2011). The first known description of it in China and reference to its use as a rootstock occurs in the oldest known book on the orange, *Chü Lu* (Yen-Chih 1178). And in China, particularly, dried fruits of trifoliate orange have many medicinal uses (Duke & Ayensu 1985; PFAF 2014). Perhaps because of its uses in medicine and as a grafting rootstock, it was early cultivated in Japan (see below). Recent floristic treatments for Japan (e.g., Ohwi 1965; Walker 1976; Ohba 1999; Yamashita 2013) have not explicitly described it as naturalized there — Ohba (1999) noted only this: "Widely cultivated for hedges, stock for *Citrus*, and for medicine." — but André (1885) noted that it grew spontaneously in Japanese woods and that it had earlier been found there by Siebold and Burger and by Savatier.

Trifoliate orange also is known to be naturalized in Australia and Europe (Randall 2011) as well as the Kashmir Valley of northern India (Aslam et al. 2010). It is included in the Flora of Pakistan (Din & Ghazanfar 1980) but noted there to be "usually cultivated as an ornamental."

Variants

"The trifoliolate orange shows surprisingly few [horticultural] variations considering that it has been grown in China for thousands of years and in Japan since at least the eighth century" (Swingle & Reece 1967). A mutant with flattened and contorted stems, curved spines, and linear leaves (Flying Dragon, *Poncirus trifoliata* var. *monstrosa*) is popular in horticulture and was introduced into the USA from Japan in 1915. It is a dwarf variety usually cultivated as a potted plant and also used as rootstock especially for other potted *Citrus* varieties (Koskinen 2011).

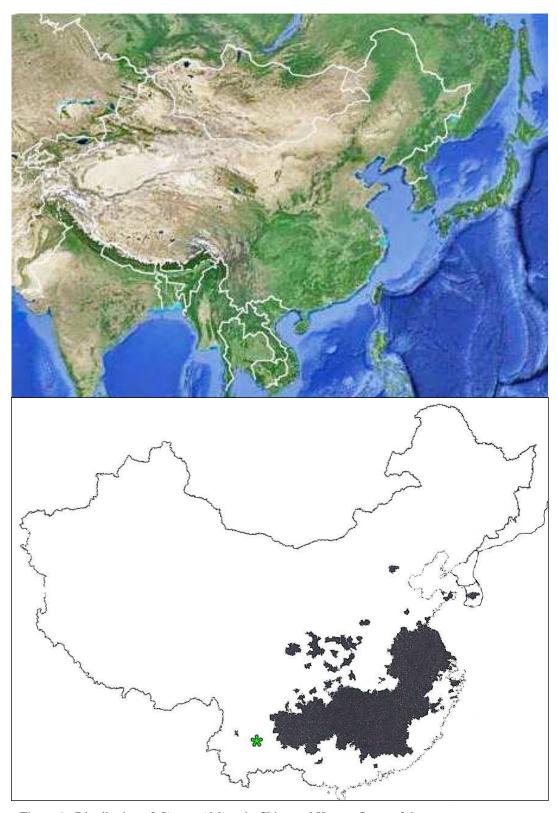


Figure 1. Distribution of *Citrus trifoliata* in China and Korea. Some of the area may represent naturalized occurrence. Top: southeastern Asia, from Google Maps. Bottom: Outline of species distribution in China, from Fang et al. (2011), with South Korea added. Green star shows location of *Poncirus polyandra* — Yunnan Province, Kunming Prefecture, Fumin County.

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A number of selections of Citrus trifoliata were identifed by Shannon et al. (1960) based on differences in origin, growth habit, and leaf or flower morphology, but these traits are significantly influenced by environmental conditions. Two groups, however, have been generally recognized with respect to flower size. In California, smaller-flowered plants become dormant earlier, which may be associated with greater cold resistance when used as a rootstock. Smaller-flowered selections of trifoliate orange also are less vigorous than larger-flowered types and are more bushy (Koskinen 2011). "In California, where dwarfing citrus rootstocks have been widely used, 8-to-12-year-old navel and Valencia oranges, Minneola tangelos, and Dancy tangerines on Rubidoux [small-flowered] trifoliate orange rootstock at different sites ranged from 10 to 14 feet tall. Comparable trees on Pomeroy [large-flowered] trifoliate rootstock were predicted to be 15%-20% taller, about 12 to 17 feet (Ferguson et al. 2004). In Japan, the larger-flowered forms also are considered to be more dwarfing (Bitters 1964).

Most modern accessions of trifoliate orange in the USA apparently have originated from early-imported lines by mutation or self-pollination. Based on polymorphic ISSR markers, Fang et al. (1997) found that 48 accessions clustered in four major groups, with most accessions falling into 2 groups — one group (24 accessions) included all large-flowered selections, the other (20 accessions) all small-flowered selections, including the Flying Dragon and a tetraploid (see below). One of the smaller groups was distinct in its loss of diversity and is perhaps derived from the small-flowered group. The other small group included accessions recently introduced from China.

Hardiness and associated use as a rootstock

Citrus trifoliata is said to survive temperatures as low as -13° F in Missouri (Porter 1972) and 3° F in Georgia (Ferguson et al. 2004). Edgar Anderson (1932) reported that a plant of trifoliate orange had been grown outside in Jamaica Plain, Massachussetts, and had regularly fruited — it was cultivated by Alfred Rehder in a protected place in a corner by the north wall of his home. Anderson also noted that plants had occasionally been seen growing without protection as far north as New York City. As mapped below, however, trifoliate orange is reported to naturalize in eastern Pennsylvania but not further north into New York.

Because of its hardiness, trifoliate orange has been used as a rootstock for grafting other species and varieties of Citrus and as a parent of novel cold-hardy varieties. Ferguson et al. (2004) noted, however, that "In north Florida, unseasonably warm temperatures higher than 70° F day/50° F night ... can reduce the freeze hardiness of trifoliate orange rootstocks. Trifoliate orange therefore may not be a consistently freeze hardy rootstock."

Trifoliate orange has long been the most important rootstock in Japan, primarily for satsuma mandarins, and is increasingly being employed in Australia, California, and Argentina (Koskinen 2011). A Florida nursery (JF&E 2014) currently uses three Trifoliate rootstocks: Flying Dragon (a dwarfing rootstock), Large Flower Trifoliate (a semi-dwarfing rootstook), and the vigorous Swingle.

Among Citrus species, trifoliate orange is the only one deciduous, which is significant in maintaining winter dormancy when used as a rootstock for other species. This also accounts for the more northern and temperate natural range of the species and perhaps for why it does not naturalize in warmer, more tropical climates.

Biology

Poncirus and its close relatives Fortunella and Citrus reticulata are facultatively apomictic (Garcia-Lor et al. 2013), seed production described as through adventitious embryony (Solntseva 1983), the seeds polyembryonic, containing both sexual and apomictic embryos (Fang et al. 1997). Khan and Roose (1988) observed that about 80-90% of seedlings from open-pollinated trifoliate orange seeds develop from apomictic embryos. Ferguson et al. (2004) noted that "In one report, seed

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from Flying Dragon trees grown in four different locations produced between 0% and 75% zygotic [of sexual origin] seedlings. Researchers also found that the percentage of Flying Dragon [asexual and sexual] seedlings fluctuated greatly from year to year on the same tree." Self-compatibility facilitates production of sexual embryos.

Ability of solitary plants to reproduce has been confirmed by field observations — trifoliate orange was noted to be "apparently self-seeding" at an old farmhouse site in Polk Co., Texas (21 Mar 1957, Traverse 321, BRIT); Serviss (2014) also observed that it can set fruit without cross pollination.

Seed dispersal is described in various literature as through birds and other animals, but "seedlings will germinate from rotten fruits without dispersal or mechanical breach of the pericarp" (Serviss 2014). Where the species forms dense colonies, at least a significant portion of the recruitment is through seeds (Serviss, pers. comm.). One recent internet observer reported that fruits produced an average of 30 seeds. Trifoliate orange also reproduces by basal sprouting and root suckers.

Plants of trifoliate orange in England are described as relatively short-lived, deteriorating after about 25 years (Davis 1990), but at the Missouri Botanical Garden (St. Louis, Missouri), some individuals apparently reached almost 50 years in age (Porter 1972), limited in age by the cold winters. Individuals can reach 4-5 feet tall in 10 years and ultimately can grow to about 12 feet. Various internet nursery sites and discussions apparently have observed even more vigorous growth, reporting that it can grow up to 8–10 feet tall, rarely to 20 feet, and can reach 6 feet in 3 years. Trifoliate orange has been reported to begin flowering and fruiting when 3-4 years old or as late as 10–12 years old. Seedlings and a sapling are shown in Figures 4 and 5.

A tetraploid (2n = 36) of *Citrus trifoliata* was discovered in Jiangsu Province in 1974 (Chen & Liang 1989; Chen & Song 1989). It is faster-growing than the diploids and has thicker stems and smaller and more irregularly shaped fruits, and the seeds are fewer and with reduced viability.

Poncirus polyandra from Yunnan Province

A second trifoliolate species has recently been described from Yunnan Province: Poncirus polyandra S.Q. Ding et al. (Ding et al. 1984). It is thought to be extinct in the wild — the only living plants are cultivated in several localities with reproduction monitored by botanists at the Kunming Institute of Botany (GONGxun 2013). Pang et al. (2007) and Li et al. (2010) found evidence confirming the distinction of P. polyandra from P. trifoliata and its independent origin (without an indication that *P. trifoliata* was involved in hybrid parentage of *P. polyandra*).

Phylogenetic and taxonomic position of the genus

Trifoliate orange has been treated in *Poncirus*, apart from *Citrus*, differing from the latter in its cold-hardiness, discontinuous pith (as transverse plates), deciduous, 3-foliolate leaves, flowers borne on old wood in early spring rather than on shoots of the season, basally free stamens, densely pubescent fruits, and pulp vescicles containing oily drops and having hair-like appendages (Bailey 1949, p. 609). Recent molecular studies, however, have generally indicated that *Poncirus* evolved from within the larger evolutionary nexus of Citrus (Araújo et al. 2003; Bayer et al. 2008; Penjor et al. 2013; Garcia-Lor et al. 2013), thus trifoliate orange is the more appropriately identified within the genus Citrus. Barkley et al. (2006) found that Fortunella clusters within Citrus but that Poncirus is sister to Citrus. Li et al. (2010) also found Poncirus sister to Citrus but species of Fortunella were not included in their analysis. Within Citrus sensu lato, the closest relatives of Poncirus are Citrus reticulata and species of Fortunella (Garcia-Lor et al. 2013).



Figure 2. *Citrus triptera* Desf. (= *C. trifoliata*), from Andre (1885).

Trifoliate orange freely hybridizes with other *Citrus* species and was used in the USDA citrus breeding program, beginning in Florida in 1897 and continuing for several decades. This work produced a series of hybrids — (X kumquats (*Fortunella*) = citrumquats; X sweet oranges = citranges; X pummelos = citrumelos; X mandarins = citrandarins; X lemons = citremons; and X sour oranges = citradias) (Swingle & Reece 1967).

- Citrus trifoliata L., Sp. Pl. ed. 2, 1101. 1763. *Poncirus trifoliata* (L.) Raf., Sylva Tellur. 143. 1838. *Bilacus trifoliata* (L.) Kuntze, Revis. Gen. Pl. 1: 99. 1891. TYPE: Protologue: "Habitat in Japonia." LECTOTYPE (designated by W.T. Swingle in Webber & Batchelor (ed.), *Citrus Industry* 1: 368. 1943): "*Karatats banna*" in Kaempfer, Amoen. Exot. Fasc., 801, 802. 1712.
- Citrus triptera Desf., Tabl. École Bot., ed. 3 (Cat. Pl. Horti Paris.), 406. 1829.

 Authorship of Citrus triptera often has been attributed to Ed. André (1885; see Fig. 2), but André himself appeared to recognize that C. triptera Desf. was the correct form of the name; in synonymy of that, he cited Citrus trifoliata L. and Citrus trifolia Thunb.
- Citrus trifoliata var. monstrosa T. Itô, Encycl. Jap. (Nippon Hyakka Daijiten) 2: 1056. 1909. Poncirus trifoliata var. monstrosa (T. Ito) Swingle in Bailey, Stand. Cycl. Hort. 5: 2952. 1916.

145 Silver striped willow	Citrus, salicifolia var.	85
leaved orange	175.53	
146 Myrtle leaved do.	myrtifolia 	
147 Bergamot do.		
148 St. Salvador sweet do.		
149 Red cored Malta sweet	singuincus	
150 China sweet do		dill street
151 ——— curled leaved do. 152 ——— mandarin do.	——— nobilis	5
153 —— cherry size do.	minor	
154 Tangiers do.	tanjierano	5
155 Three leaved do.	trifoliata	(53)
156 Turkish do.	lunata	
157 Violet begarade do.	violacea	
158 Horned begarade do.		
159 Forbidden fruit do.	Adami	
160 Shaddock, monstrous fr	uit decumana	
161 Lisbon lemon	limon	
162 Imperial do.		
163 Pear shaped do.	pyriformis	
164 Red fruited lemon of	} sanguineus	
Ponsino		4
165 Gold striped do.	aureo striato	5
166 Monstrous lemon 167 Madeira citron	v. tuberosa	
168 Palermo solid do.	medica	
169 Cedra do.	cedra	
170 West-India lime	limonella	
TIO Mesemble time	IIII Olicini.	

Figure 3. Listing of Citrus trifoliata in William Prince's 1823 "Catalogue of fruit and ornamental trees and plants, bulbous flower roots, green-house plants, &c. &c., cultivated at the Linnaean Botanic Garden" in Flushing, New York.

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Origin in the USA and distribution

Trifoliate orange was listed in William Prince's catalog (Prince 1823, Fig. 3, as Citrus trifoliata) of his Linnaean Botanic Garden in Flushing, New York, which sold many hundreds of woody and herbaceous species.

The species apparently was little noticed until it assumed a significant role in the U.S. Department of Agriculture citrus breeding program, as noted above. In 1869 William Saunders, (first botanist to be hired by the U.S.D.A. immediately upon its establishment in 1862) "was endeavoring to secure a hardy type of Japanese orange, and the trees froze in transit from San Francisco to Washington, but the stocks survived, and these proved to be the now well-known P. trifoliata. He enlisted the aid of the late Prof. P.J. Berckmans of Augusta, Georgia, in the work of saving the perpetuating this stock" (Brackett 1919, p. 1595).

In Texas, trifoliate orange was advertised as a hedge plant in the 1894 catalog of the Pearfield Nursery in Frelsburg (Colorado Co.) but was already in use for hedges at least by 1869 in Navasota (Grimes Co.) (Welch & Grant 2011).

Trifoliate orange was not included in any floristic accounts prior to 1900 or by Mohr (1901), Small (1903), or Small (1913). Perhaps the earliest published notice of its naturalization was Small (1933): "Woods and hammocks, Coastal Plain, Fla. to Tex. and Ga." Fernald (1950) observed that it was "Much used in the South for hedges, esc. to borders of woods, etc., Fla. to Tex. n. to e. Va." Even by 1968, it evidently was not known to be abundantly naturalized — Ahles (1968) noted that it was "Frequently cultivated, persistent about old home sites, less frequently escaped to thickets; Orange Co., N.C., Barnwell, Chester, Spartanburg cos., S.C. [Va., Miss.]."

Some of the oldest collections of naturalized plants mapped on Figure 6 are from areas close to large cities or universities, where plants presumably had been earlier cultivated: e.g., Travis Co., Texas (Austin, Univ. Texas); Pulaski Co., Arkansas (city of Little Rock); Knox Co., Tennessee (Knoxville, Univ. Tennessee); Pickens Co., South Carolina (Clemson Univ.). The oldest collections I have seen that reflect naturalizations are from Texas: Brazoria Co. (1910, TEX) and Travis Co. (1911, TEX).

"Large colonies [of trifoliate orange] are often observed in places where it is naturalized, and dense populations can be essentially impenetrable." In Arkansas, it is "capable of forming dense, thorny thickets which displace native plant species" (Serviss 2014). In the USA it grows in a wide range of habits, apparently on a correspondingly wide array of substrates. At least in southern Arkansas (Brett Serviss, pers. comm.) and in Walker Co., Texas (pers. observ.), it is an aggressive colonizer in bottomlands. In Fort Bend and Colorado counties, Texas, "it sometimes is the absolute dominant in the shrub layer of woodland mottes, especially those on sandy loam and dominated by whichever live oak entity is present" (Bill Carr, pers. comm.).

"When used as a rootstock, trifoliate orange can produce a standard-sized tree, about 15 feet tall, on clay and loamy soils and on shallow soils, but does not develop a deep or widely ranging root system and consequently is not drought tolerant. On deep, sandy, ridge soils, trees on trifoliate orange do not grow rapidly, making it a good candidate for close plantings with irrigation. It is poorly adapted to saline or calcareous conditions but is useful under wet conditions because of resistance to *Phytophthora* foot rot" (Ferguson et al. 2004).



Figure 4. Seedlings of trifoliate orange, probably first year.



Figure 5. Sapling of trifoliate orange, probably 2-3 years old.

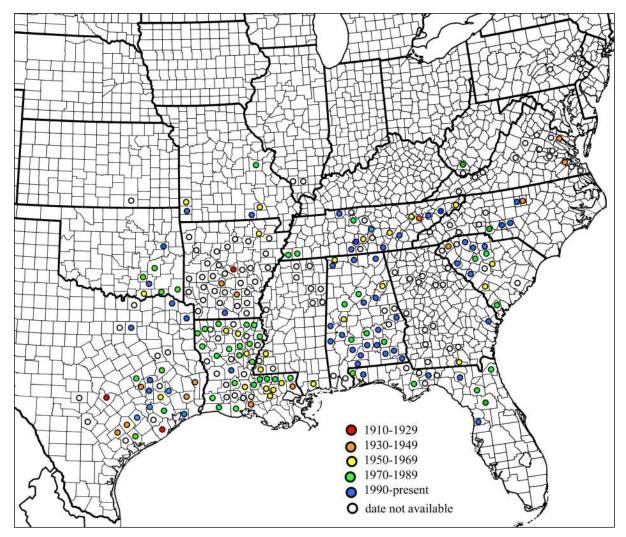


Figure 6. Distribution of Citrus trifoliata in the USA, with indication of time of naturalization. Dates are first collection for the county (see Appendix). The scattered locations of older collections suggests that the species has spread from multiple introductions. Concentration of 'green' in Louisiana and 'blue' in Alabama may reflect intensity of collecting programs, thus naturalizations probably were somewhat earlier. Undated records are from various sources and, because of incomplete or ambiguous label data, some may reflect persistent plantings rather than naturalized plants.

The apparent wide ecological amplitude suggests that differently adapted genotypes may be present. The ecological summary below for Citrus trifoliata derived from specimens examined in the current study:

Flowering (Mar-)Apr-May. Upland hardwoods, pine-hardwood, pine, beech-magnolia, and sweetgum woods, prairie openings, sandstone outcrops, hammocks over limestone, bottomlands, low pastures, streambanks and alluvial terraces, sandy floodplains, ditches, fencerows, roadsides, thickets in disturbed sites, especially in suburban areas, abandoned fields, rubbish dumps.

Many excellent photos of trifoliate orange can be found on the internet. Especially see Serviss (2014).

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APPENDIX. Citrus trifoliata: first date of collection by county (documentation for Figure 6).

Alabama - Butler (2008), Calhoun (1967), Choctaw (1997), Colbert (2004), Coffee (2006), Conecuh (2006), Crenshaw (2009), Dale (2000), Escambia (1994), Hale (1967), Houston (1994), Jackson (1998), Jefferson (1985), Lauderdale (1969), Lee (2006), Limestone (1997), Lowndes (1988), Marengo (2009), Monroe (1997), Montgomery (2011), Pike (1989), Shelby (1996), Sumter (2006), Talladega (1992), Tuscaloosa (1979), Wilcox (1973)

Arkansas - Cleveland (1941), Hot Springs (1937), Lawrence (1968), Pulaski (1925), Union (1999)

Florida - Alachua (1980), Duval (1982), Escambia (1993), Hernando (2009), Leon (2010), Liberty (1982), Marion (1975), Santa Rosa (1993), Suwanee (2000) **Georgia** - Bryan (1994), Echols (1967)

Louisiana - Ascension (1951), Bossier (1976), Caddo (1970), Calcasieu (1975), Caldwell (1973), Cameron (1977), Catahoula (1969), Claiborne (1972), Concordia (1975), DeSoto (1978), East Baton Rouge (1989), East Feliciana (1987), Evangeline (1978), Franklin (1981), Iberia (1938), LaSalle (1975), Lincoln (1969), Madison (1980), Morehouse (1977), Natchitoches (1979), Ouachita (1968), Pointe Coupee (1972), Rapides (2003), St. Helena (1971), St. Landry (1968), St. Tammany (1949), Tangipahoa (1957), Vermilion (1989), Washington (1983), West Carroll (1978), West Feliciana (1972), Winn (1981)

Mississippi - Harrison (1969), Jefferson (1966), Wilkinson (1966)

Missouri Carter (1958), Franklin (1973), Jasper (1959), Newton (2004), Oregon (2003)

North Carolina - Alamance (2011), Mecklenberg (1975), Montgomery (2000), Orange (1943), Stanly (2007)

Oklahoma - Atoka (2001), Bryan (1962), Choctaw (1989), Cleveland (cultivated), Coal (1973), McCurtain (1973), Muskogee (1994), Payne (cultivated), Pittsburgh (1973)

South Carolina - Abbeville (2000), Barnwell (1953), Chester (2003), Edgefield (1997), Fairfield (1983), Jasper (1983), Newberry (1986), Pickens (1931), Richland (1967), Spartanburg (2009), Union (1993)

Tennessee - Anderson (1966), Bedford (1965), Bledsoe (1963), Cannon (2004), Carter (1956), Davidson (1989), Fayette (1981), Giles (2004), Greene (2001), Jefferson (1991), Knox (1936), Marion (2005), Marshall (2003), Meigs (2003), Montgomery (2000), Shelby (1972)

Texas - Anderson (1964), Brazoria (1910), Brazos (1949), Chambers (1990), Dewitt (1942), Colorado (1996), Dallas (1998), Grimes (1992), Hardin (1947), Harris (1979), Houston (1979), Jackson (1982), Jasper (1948), Lavaca (1937), Madison (1998), Montgomery (1968), Red River (1993), Robertson (1979), San Jacinto (1992), Travis (1911), Victoria (1963), Waller (1993)

Virginia - Essex (1941), Spotsylvania (1939), Surry (1938)

West Virginia - Wyoming (1972)