

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

GUY L. NESOM
2925 Hartwood Drive
Fort Worth, Texas 76109
www.guynesom.com

ABSTRACT

Citrus trifoliata (aka *Poncirus trifoliata*, trifoliolate 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. Trifoliolate 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. (trifoliolate 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 communities. 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).

Trifoliolate 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 trifoliolate 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.

Trifoliolate 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).

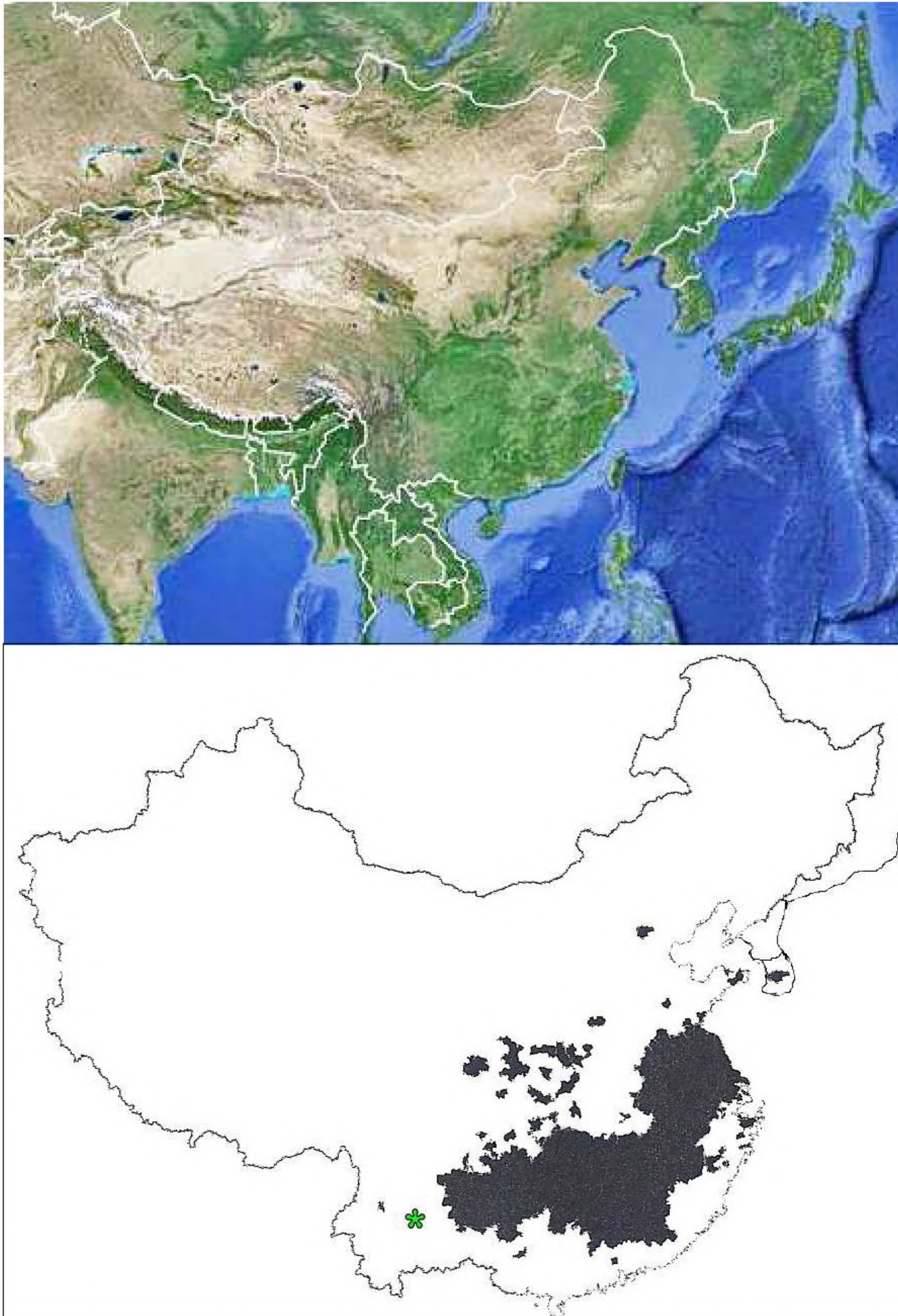


Figure 1. Distribution of *Citrus trifoliata* in China and Korea. Some of the area may represent naturalized occurrence. Top: southeastern Asia, from Google Maps. Bottom: Outline of species distribution in China, from Fang et al. (2011), with South Korea added. Green star shows location of *Poncirus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

A number of selections of *Citrus trifoliata* were identified 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 trifoliolate 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] trifoliolate orange rootstock at different sites ranged from 10 to 14 feet tall. Comparable trees on Pomeroy [large-flowered] trifoliolate 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 trifoliolate 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 trifoliolate orange had been grown outside in Jamaica Plain, Massachusetts, 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, trifoliolate orange is reported to naturalize in eastern Pennsylvania but not further north into New York.

Because of its hardiness, trifoliolate 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 trifoliolate orange rootstocks. Trifoliolate orange therefore may not be a consistently freeze hardy rootstock."

Trifoliolate 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 Trifoliolate rootstocks: Flying Dragon (a dwarfing rootstock), Large Flower Trifoliolate (a semi-dwarfing rootstock), and the vigorous Swingle.

Among *Citrus* species, trifoliolate 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 trifoliolate orange seeds develop from apomictic embryos. Ferguson et al. (2004) noted that "In one report, seed

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 — trifoliolate 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. Trifoliolate orange also reproduces by basal sprouting and root suckers.

Plants of trifoliolate 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. Trifoliolate 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

Trifoliolate 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 vesicles 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 trifoliolate 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*) = citrusquats; 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.

(101)

145 Silver striped willow leaved orange	} Citrus, <i>salicifolia</i> var.	§ 5
146 Myrtle leaved do.	----- <i>myrtifolia</i>	
147 Bergamot do.	----- <i>aromatica</i>	
148 St. Salvador sweet do.	----- <i>pyriformis</i>	
149 Red cored Malta sweet do.	----- <i>sanguineus</i>	
150 China sweet do.	----- <i>sinensis</i>	
151 ----- curled leaved do.	----- <i>humile</i>	
152 ----- mandarin do.	----- <i>nobilis</i>	5
153 ----- cherry size do.	----- <i>minor</i>	
154 Tangiers do.	----- <i>tanjierano</i>	5
155 Three leaved do.	----- <i>trifoliata</i>	
156 Turkish do.	----- <i>lunata</i>	
157 Violet begarade do.	----- <i>violacea</i>	
158 Horned begarade do.	----- <i>cornuta</i>	
159 Forbidden fruit do.	----- <i>Adami</i>	
160 Shaddock, monstrous fruit	----- <i>decumana</i>	
161 Lisbon lemon	----- <i>limon</i>	
162 Imperial do.	----- <i>var.</i>	
163 Pear shaped do.	----- <i>pyriformis</i>	
164 Red fruited lemon of Ponsino	} ----- <i>sanguineus</i>	
165 Gold striped do.	----- <i>aureo striato</i>	5
166 Monstrous lemon	----- <i>v. tuberosa</i>	
167 Madeira citron	----- <i>medica</i>	
168 Palermo solid do.	----- <i>var.</i>	
169 Cedra do.	----- <i>cedra</i>	
170 West-India lime	----- <i>limonella</i>	
Orange, Lemon, Citron, Shaddock, and Lime Trees,		
<i>one year inoculated, (except those noted)</i>		2 50
<i>Ditto two years do.</i>		3
<i>Ditto three years do in a bearing state</i>		3 50

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.

Origin in the USA and distribution

Trifoliolate 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, trifoliolate 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).

Trifoliolate 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 trifoliolate 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, trifoliolate 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 trifoliolate 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 trifoliolate orange, probably first year.



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

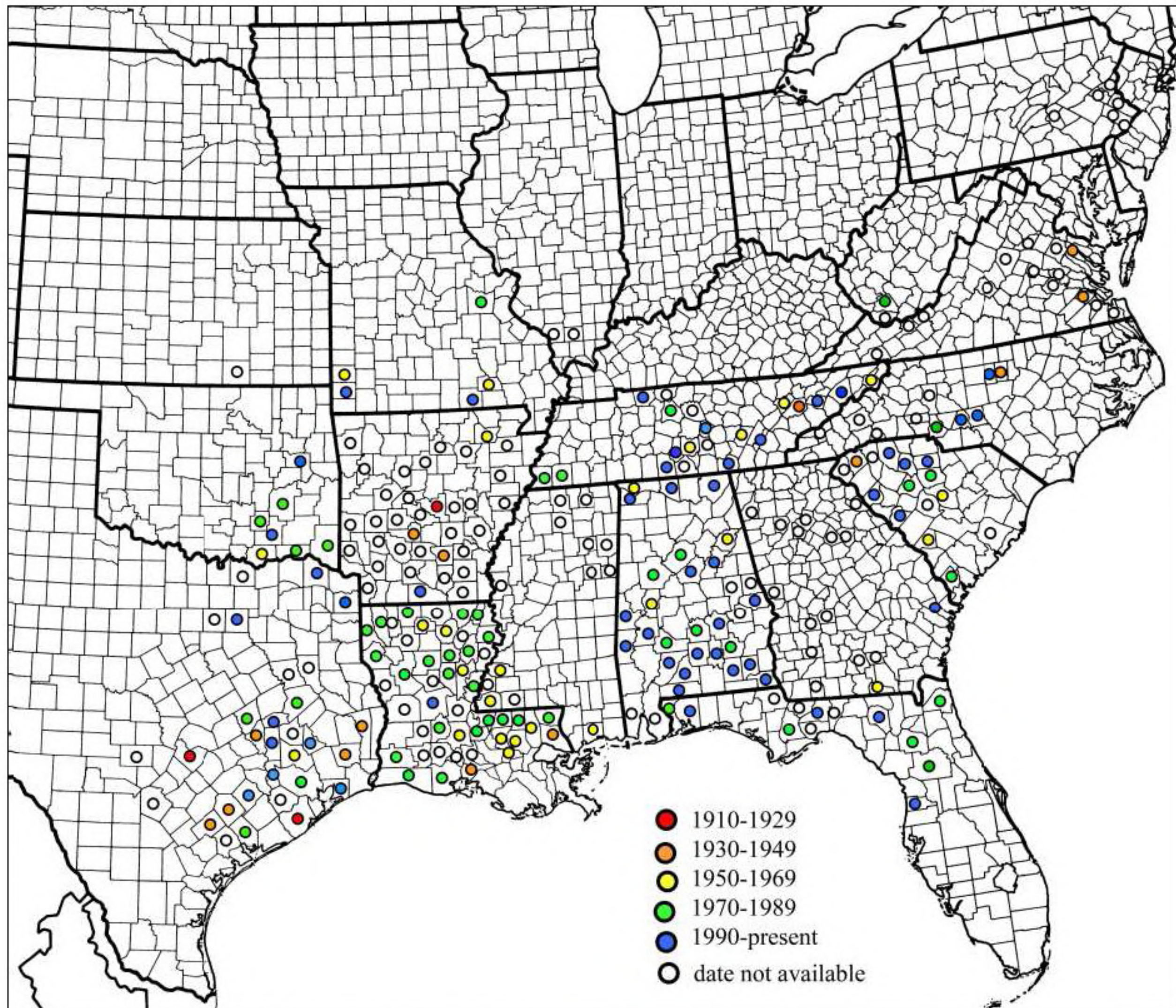


Figure 6. Distribution of *Citrus trifoliata* in the USA, with indication of time of naturalization. Dates are first collection for the county (see Appendix). The scattered locations of older collections suggests that the species has spread from multiple introductions. Concentration of 'green' in Louisiana 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).

ACKNOWLEDGEMENTS

I'm grateful to Bill Carr for stimulating this article by his observation (pers. comm.) that *Poncirus* has become a damaging invasive in southeast Texas and to Bret Serviss for comments on the species in Arkansas. Dave Boufford provided notes on earlier GH collections and the following provided information for specific states: Dennis Bell – Louisiana; Amy Buthod – Oklahoma; Carol Ann McCormick – North Carolina; Gene Wofford – Tennessee; and George Yatskievych – Missouri. Various online herbarium databases provided useful information: FLA, FLAS, LSU, MISS, South Carolina Atlas, TAMU, and USF. Personal study was done on site at BRIT-SMU-VDB and TEX-LL. NLU specimens shown in Figures 4 and 5 are from the developing digital database of Louisiana plants, courtesy of Dennis Bell at NLU.

LITERATURE CITED

- Ahles, H.E. 1968. Rutaceae. Pp. 652–654, in A.E. Radford, H.E. Ahles, and C.R. Bell. *Manual of the Vascular Flora of the Carolinas*. Univ. of North Carolina Press, Chapel Hill.
- Anderson, E. 1932. Growing oranges in Boston. *Bull. Popular Inf.*, ser. 3, 6: 45–47.
- André, E. 1885. *Citrus triptera*. *Rev. Hort.* 57: 516–518.
- Araújo, E.F. de, L.P. de Queiroz, and M.A. Machado. 2003. What is *Citrus*? Taxonomic implications from a study of cp-DNA evolution in the tribe Citreae (Rutaceae subfamily Aurantioideae). *Org. Div. Evol.* 3: 55–62.
- Aslam, S., K. Ahmad Ganaie, A.Q. John, and G.H. Dar. 2010. Family Rutaceae in Kashmir Himalyas: *Poncirus trifoliata* (L.) Raf. – A new record for flora of Kashmir, India. *Acad. Arena* 2: 40–41.
- Bailey, L.H. 1949. *Manual of Cultivated Plants* (rev. ed.). MacMillan Co., New York.
- Bailey, L.H., E.Z. Bailey, and the L.H. Bailey Hortatorium. 1976. *Poncirus*. Pp. 275–276, in *Hortus Third: A Concise Dictionary of Plants Cultivated in the United States and Canada*. Macmillan Co., New York.
- Barkley, N.A., M.L. Roose, R.R. Kruger, and C. Federici. 2006. Assessing genetic diversity and population structure in a citrus germplasm collection utilizing simple sequence repeat markers (SSRs). *Theoret. Appl. Genet.* 112: 1519–1531.
- Bayer, R.J., D.J. Mabberley, C. Morton, C.H. Miller, I.K. Sharma, B.E. Pfeil, S. Rich, R. Hitchcock, and S. Sykes. 2008. A molecular phylogeny of the orange subfamily (Rutaceae: Aurantioideae) using nine cpDNA sequences. *Amer. J. Bot.* 96: 668–685.
<<http://www.amjbot.org/content/96/3/668.full>>
- Bitters, W.P. 1964. *Citrus* rootstocks and nursery practices in Japan. *Calif. Citrog.* 49: 205–210.
- Brackett, G.B. 1919. William Saunders. Pp. 1594–1595, in L.H. Bailey. *The Standard Cyclopedia of Horticulture* (ed. 3), Vol. III. MacMillan Co., New York.
- Chen, Q.Y. and G.L. Liang. 1989. Study on the karyotype of *Poncirus*. *Acta Bot. Yunnan.* 11: 103–106.
- Chen, Q.Y. and N.J. Song. 1989. A tetraploid *Poncirus trifoliata* cv. Guan Yun No. 1. *Acta Hort. Sin.* 16: 78–80.
- Correll, D.S. and M.C. Johnston. 1970. *Manual of the Vascular Plants of Texas*. Texas Research Foundation, Renner, Texas.
- Davis, B. 1990. *The Gardener's Illustrated Encyclopedia of Climbers and Wall Shrubs*. Viking, London.
- Dianxiang, Z. and D.J. Mabberly. 2008. *Citrus* (Rutaceae). *Fl. China* 11: 90–96.
- Din, H.-U. and S.A. Ghazanfar. 1980. Flora of Pakistan. 132. Rutaceae. Department of Botany, Univ. of Karachi, Karachi.
- Ding S., X. Zhang, Z. Bao, and M. Liang. 1984. A new species of *Poncirus* from China. *Acta Bot. Yunnan.* 6: 292–293.
- Duke, J.A. and E.S. Ayensu. 1985. *Medicinal Plants of China*, Vols. 1 and 2. Reference Publications, Algonac, Michigan.

- Fang, D. 1993. Intra- and intergeneric relationships of *Poncirus polyandra*: Investigation by leaf isozymes. *J. Wuhan Bot. Res.* 11: 34–40.
- Fang, D.Q., M.L. Roose, R.R. Krueger, and C.T. Federici. 1997. Fingerprinting trifoliolate orange germ plasm accessions with isozymes, RFLPs, and inter-simple sequence repeat markers. *Theor. Appl. Genet.* 95: 211–219.
- Fang, J., Z. Wang, and Z. Tang (eds.). 2011. *Atlas of Woody Plants in China: Distribution and Climate*. Vols. 1 and 2. Higher Education Press, Beijing.
- Ferguson, J.J., J. Chaparro, and T.M. Spann. 2004 (revised 2010). Dwarfing and freeze hardiness potential of trifoliolate orange rootstocks. Fact Sheet HS982. Horticultural Sciences Dept., Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, Univ. of Florida. <<http://edis.ifas.ufl.edu/hs221>>
- Fernald, M.L. 1950. *Gray's Manual of Botany* (ed. 8). American Book Co., New York.
- Garcia-Lor, A., F. Curk, H. Snoussi-Trifa, R. Morillon, G. Ancillo, F. Luro, L. Navarro, and P. Ollitrault. 2013. A nuclear phylogenetic analysis: SNPs, indels and SSRs deliver new insights into the relationships in the 'true citrus fruit trees' group (Citrinae, Rutaceae) and the origin of cultivated species. *Ann. Bot.* 111: 1–19.
- GONGxun. 2013. The *ex situ* conservation of *Poncirus polyandra* has been successfully achieved in Kunming Institute of Botany. Kunming Institute of Botany, Chinese Academy of Sciences. <http://english.kib.cas.cn/rh/rp/201301/t20130128_98591.html>
- Hodgson, R.W. 1967. Horticultural varieties of *Citrus*. Pp. 431–591, in Reuther, W., H.J. Webber, and L.D. Batchelor (eds.). *The Citrus Industry* (rev. ed.). Vol. I. Division of Agricultural Sciences, Univ. of California, Berkeley. <<http://websites.lib.ucr.edu/agnic/webber/Vol1/Vol1TP.html>>
- JF&E. 2014. Just Fruits and Exotics. 30 Saint Frances St., Crawfordville, Florida. <<http://www.justfruitsandexotics.com/Citrus.htm>>
- Khan, I.A. and M.L. Roose. 1988. Frequency and characteristics of nucellar and zygotic seedlings in three cultivars of trifoliolate orange. *J. Amer. Soc. Hort. Sci.* 113 :105–110.
- Klingaman, G. 2007. *Poncirus trifoliata*, Plant of the week. Univ. of Arkansas Division of Agriculture, Cooperative Extension Service. Extension News - 9 Feb 2007.
- Koskinen, J. 2011 [last update]. Citrus Pages. A comprehensively illustrated *Citrus* website with descriptions and uses of over 400 varieties of *Citrus*. <<http://users.kymp.net/citruspages/home.html>>
- Li, X., R. Xie, Z. Lu, and Z. Zhou. 2010. The origin of cultivated *Citrus* as inferred from internal transcribed spacer and chloroplast DNA sequence and amplified fragment length polymorphism fingerprints. *J. Amer. Soc. Hort. Sci.* 135: 341–350.
- Mohr, C. 1901. Plant Life of Alabama. *Contr. U.S. Natl. Herb.* 6: 1–921.
- Ohba, H. 1999. Rutaceae. In K. Iwatsuki, D.E. Boufford, and H. Ohba (eds.). *Flora of Japan*, Vol. 2c. UHBS, Devon, United Kingdom.
- Ohwi, J. (F.G. Meyer and E.H. Walker, eds.). 1965. *Flora of Japan* (rev. ed.). Smithsonian Institution, Washington, D.C.
- Pang, X.-M., C.-G. Hu, and X.-X. Deng. 2007. Phylogenetic relationships within *Citrus* and its related genera as inferred from AFLP markers. *Genet. Resources Crop Evol.* 54: 429–436.
- Penjor, T., M. Yamamoto, M. Uehara, M. Ide, N. Matsumoto, R. Matsumoto, and Y. Nagano. 2013. Phylogenetic relationships of *Citrus* and its relatives based on matK gene sequences. *PLoS ONE* 8(4): e62574. doi:10.1371/journal.pone.0062574
- Porter, D.M. 1972. The hardiest of Oranges. *Missouri Bot. Gard. Bull.* 60(3): 19–21.
- Prince, W. 1823. *Catalogue of fruit and ornamental trees and plants, bulbous flower roots, greenhouse plants, &c. &c., cultivated at the Linnaean Botanic Garden, William Prince, Proprietor, Flushing, Long Island, near New York*. Swords, New York.
- Randall, R. 2011. *Global Compendium of Weeds*. Last update 16 November 2011. <<http://www.hear.org/gcw/>>

- Serviss, B.E. 2014. Non-Native Woody Plants of Arkansas. Website, Henderson State University, Arkadelphia, Arkansas. <<http://www.hsu.edu/interior2.aspx?id=4476>>
- Shannon, L.M., E.F. Frolich, and S.H. Cameron. 1960. Characteristics of *Poncirus trifoliata* selections. J. Rio Grande Hort. Soc. 14 :108–117.
- Small, J.K. 1903. Flora of the Southeastern States. Published by the author, New York
- Small, J.K. 1913. Flora of the Southeastern States (ed. 2). Published by the author, New York
- Small, J.K. 1933. Manual of the Southeastern Flora. Univ. of North Carolina Press, Chapel Hill.
- Solntseva, M.P. 1983. Adventivnaya embrioniya u *Poncirus trifoliata*. Pp. 268–269, in Tez. dokl. 7 Delegat. s'ezda Vses. botan. o-va, Donetsk (Leningrad). – Abstract in Ref. Zhurn., Biol., 7(2): V 424. 1984.
- Swingle, W.T. 1911. *Citrus trifoliata* in relation to citrus culture. Proc. Amer. Pomol. Soc. 32: 218–221.
- Swingle, W.T. 1914. *Citrus and Poncirus*. In C.S. Sargent. Plantae Wilsonianae 2: 141–51.
- Swingle, W.T. 1919. *Poncirus*. Pp. 2751–2752, in L.H. Bailey (ed.). The Standard Cyclopaedia of Horticulture (ed. 3), Vol. 5. MacMillan Co., New York.
<http://www.biodiversitylibrary.org/item/64402#page/360/mode/1up>
- Swingle, W.T. (rev. by P.C. Reece). 1967. The botany of *Citrus* and its wild relatives. Pp. 190–423, in W. Reuther, H.J. Webber and L.D. Batchelor (eds.). The Citrus Industry. Vol. 1. History, World Distribution, Botany, and Varieties. California Division of Agriculture Science, Univ. of California, Berkeley. <<http://websites.lib.ucr.edu/agric/webber/Vol1/Vol1TP.html>>
- Walker, E.H. 1976. Flora of Okinawa and the Southern Ryukyu Islands. Smithsonian Institution Press, Washington, D.C.
- Welch, W.C. and G. Grant. 2011. Heirloom Gardening in the South: Yesterday's Plants for Today's Gardens. Texas A & M Univ. Press, College Station.
- WHO (World Health Organization). 1998. Medicinal Plants in the Republic of Korea. Compiled by the Natural Products Research Institute, Seoul National University. WHO Regional Publications, Western Pacific Series No. 21. WHO Regional Office for the Western Pacific, Manila.
- Yamashita, J. 2013. List of naturalized plants in Japan. The Research Institute for Bioresources, Group of Wild Plant Science, Okayama University. Okayama, Japan.
<<http://www.rib.okayama-u.ac.jp/wild/>>
- Yen-Chih, H. 1178. *Chü Lu* [Monograph on the Oranges of Wen-chou, Chekiang]. English translation, M.J. Hagerty, 1923. E.J. Brill, Leiden.

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)