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Celtis sinensis Pers. (Ulmaceae) naturalised in northern South Africa and keys to distinguish between *Celtis* species commonly cultivated in urban environments

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Background: Alien *Celtis* species are commonly cultivated in South Africa. They are easily confused with indigenous *C. africana* Burm.f. and are often erroneously traded as such. *Celtis australis* L. is a declared alien invasive tree. *Celtis sinensis* Pers. is not, but has become conspicuous in urban open spaces.

Objectives: This study investigates the extent to which *C. sinensis* has become naturalised, constructs keys to distinguish between indigenous and cultivated *Celtis* species, and provides a descriptive treatment of *C. sinensis*.

Methods: Land-cover types colonised by *C. sinensis* were randomly sampled with 16 belt transects. Woody species were identified, counted and height measured to determine the population structure. *C. africana* and the three alien *Celtis* species were cultivated for 2 years and compared morphologically.

Results: *Celtis sinensis*, *Ligustrum lucidum* and *Melia azedarach* were found to be alien species, most abundant in urban areas. The population structure of *C. sinensis* corresponds to that of the declared invasive alien, *M. azedarach*. Although *C. africana* occurs naturally, it is not regularly cultivated. This is ascribed to erroneous plantings because of its resemblance to juvenile plants of *C. sinensis*. Keys are provided to identify *Celtis* species based on leaf shape and margin, and drupe characters.

Conclusion: *Celtis sinensis* is naturalised in central South Africa, especially in urban open spaces and beginning to colonise natural areas. It is flagged as a species with invasive potential. Characteristics of the leaves and fruits allow for accurate identification of indigenous and alien *Celtis* species, both as juvenile or adult trees.

Introduction

Invasive organisms are considered to be one of the most important threats to biodiversity worldwide (Vitousek et al. 1997) and costs South Africa millions of rands annually to control (Le Maitre et al. 2002). Southern Africa's current concerns with invasive plants were already predicted in the 1960s and the 1970s (Stirton 1978; Wild 1961), fully recognised and documented in the 1980s (Henderson et al. 1987; Wells et al. 1986) and flagged, and their invasiveness categorised, since the 1990s (Henderson 2001; Henderson & Cilliers 2002).

Urban areas are seed pools for potentially invasive alien plants, as these species are cultivated as garden subjects in mass and propagules escape from there to become naturalised in natural areas, but especially along disturbed water courses and roadsides (Horvitz et al. 2014; Kalwij et al. 2008). Naturalised species are capable of reproducing and spreading without direct assistance by people, and the most aggressive species become invaders capable of penetrating and replacing indigenous vegetation and threatening indigenous biodiversity (Ndhlovu, Milton & Esler 2016). Hence, the number of species becoming invasive increases annually (Seebens et al. 2017) and threatens agricultural productivity, water resources and natural ecosystems, with temperate agricultural or urban sites among the areas most invaded by alien plants (Lonsdale 1999).

Although *C. australis* L. and *C. occidentalis* L. have been included in South Africa's NEM:BA list of invasive species as Category 3 (Department of Environmental Affairs 2014), *C. sinensis* Pers. is generally considered to be naturalised, but not invasive (Henderson 2001). In cities of the northern provinces of South Africa, *C. sinensis* is the preferred tree for street plantings and is a regular feature in domestic gardens, parks and parking lots because of its dense foliage, fast growth rate and ability to withstand the harsh winters on the Highveld (Lubbe, Siebert & Cilliers 2011).

Phytosociological studies of urban areas conducted in the 1990s hardly reported any individuals of *C. sinensis* (Cilliers & Bredenkamp 1999), and subsequently, it was highlighted as an emerging invader by Mgidi et al. (2007). In recent years, *C. sinensis* (which originates from China, Japan and Korea) has become very conspicuous in urban open spaces, roadsides and riparian areas on the Highveld. *Celtis sinensis* also poses a major threat to the indigenous *C. africana* Burm.f., as it and the closely related *C. australis* hybridise readily with the former in Gauteng (Glen & Van Wyk 2016). In a study by Whittemore and Townsend (2007) on the hybridisation potential of *Celtis* species, *C. sinensis* was one of the species that tested positive for this ability. Buck and Bidlack (1998) found that data sets of morphological and isozymic data demonstrate congruity among *Celtis* species, which is ascribable to hybridisation.

Three of the eight African *Celtis* species are indigenous to southern Africa, namely the widespread *C. africana* (white stinkwood), *C. gomphophylla* Baker (false white stinkwood) in the Eastern Cape and KwaZulu-Natal, and *C. mildbraedii* Engl. (Natal white stinkwood) in KwaZulu-Natal and Swaziland (Pooley 1997). Three alien *Celtis* species from temperate regions are commonly cultivated in South Africa (Kuruneri-Chitepo & Shackleton 2011; Lubbe et al. 2011; Molebatsi, Siebert & Cilliers 2013), namely *C. australis* (nettle tree) from southern Europe and western Asia, *C. occidentalis* (hackberry) from northern USA and Canada, and *C. sinensis* (Chinese nettle tree), all of which are easily confused with *C. africana* in the juvenile stage. *Celtis sinensis* is especially cultivated extensively in urban environments, as it is readily available from nurseries where it is sold as 'stinkwood', creating the impression that it is the indigenous *C. africana* because of morphological similarities.

This article investigates the extent to which *C. sinensis* has become naturalised in urban open spaces and surrounding agricultural areas in the central part of northern South Africa. *Celtis sinensis* is not a declared alien invasive tree in South Africa, and this article compares its population data with that of an indigenous (*C. africana)* and declared alien tree species (*Melia azedarach* L.) from similar urban and agricultural environments in the Tlokwe Municipal area. A key is provided to distinguish between the indigenous and cultivated *Celtis* species of northern South Africa, and a simple key for quick identification of juvenile *Celtis* individuals sold at nurseries. A taxonomic treatment of *C. sinensis* is provided for the species to be officially included in the southern African flora as naturalised.

Material and methods

Distribution and population data

Distribution records were obtained from the National Museum in Bloemfontein (NMB), National Herbarium in Pretoria (PRE), H.G.W.J. Schweickerdt Herbarium (PRU), A.P. Goossens Herbarium (PUC) and the South African Plant Invaders Atlas database (Henderson 1998).

Cultivation records of trees were extracted from a garden database comprising frequency data for 256 gardens surveyed in Ganyesa, Potchefstroom and Roodepoort (Davoren et al. 2016). Three land-cover types (riparian, rangelands and urban open space) were identified within a 60 km radius of Potchefstroom, and 16 belt transects per land-cover were sampled. Transects were 50 m × 5 m, and every woody species within each transect was identified up to species level, counted and the height measured with a clinometer. Land-cover type data were supplemented with frequency data from 16 belt transects from domestic gardens (Davoren et al. 2016) and included in the study for comparative purposes.

Height class distributions were compiled for each species. Sturge's rule was applied (Scott 2009) to determine the size-class distribution and frequency intervals for the population graphs. Stability between successive size classes was determined with quotient analysis (Botha, Witkowski & Shackleton 2004). The likelihood that any two trees within a population originate from the same size-class was assessed by Simpson's Index of Dominance (SDI) (Venter & Witkowski 2010). Permutation Index (PI) was calculated for each species to calculate the degree of deviation from a monotonic decline or from an inverse-J curve (Wiegand et al. 2000).

Juvenile morphology

Seeds were collected from correctly identified *C. africana, C. australis, C. occidentalis* and *C. sinensis* in the field and germinated at the North-West University Botanical Garden. Plants were maintained under identical nursery conditions for 3 years in terms of watering, fertiliser additions and percentage shade. The length and width of the petiole, leaf and fruit of six plants per species were measured (plants < 1.5 m in height).

Results and discussion

Cultivation and naturalisation patterns

Celtis sinensis occurs as a garden subject throughout South Africa and is one of the ten most widely cultivated species in our sample of Highveld gardens (third overall, Table 1). It is also very popular as a street tree. *Celtis sinensis* is the only alien tree in the top five that is not a fruit tree, suggesting that its popularity lies elsewhere, probably its hardiness, fast growth, dense shade, resistance to pollution and being deciduous (letting the sun through in the winter) (Glen & Van Wyk 2016). These are also the characteristics that make *Vachellia karroo* a popular indigenous garden subject (Joffe 2001; Table 1). It is important to note that the indigenous *C. africana* is less popular as a garden subject compared to *C. sinensis* (Table 1).

Celtis sinensis is more popular as a garden subject than all but one declared alien invasive species, namely *Morus alba* (Table 1).

TABLE 1: Ten most frequently recorded tree species during a survey of 256 gardens on the Highveld

Species	Family	Gardens (%)	Invasive category
Prunus persica†	Rosaceae	59	None
Morus alba†	Moraceae	39	3
Celtis sinensis†	Ulmaceae	28	None
Vachellia karroo	Fabaceae	27	-
Prunus armeniaca†	Rosaceae	24	None
Ziziphus mucronata	Rhamnaceae	21	-
Melia azedarach†	Meliaceae	17	3
Lagerstroemia indica†	Lythraceae	16	None
Celtis africana	Ulmaceae	14	-
Robinia pseudoacacia†	Fabaceae	13	1b

Source: Davoren, E., Siebert, S.J., Cilliers, S.S. & Du Toit, M.J., 2016, 'Influence of socioeconomic status on design of Batswana home gardens and associated plant diversity patterns in northern South Africa', *Landscape and Ecological Engineering* 12, 129–139. https://doi.org/10.1007/s11355-015-0279-x

†, denotes alien species. Invasive categories are according to NEM:BA (Department of Environmental Affairs 2014).

TABLE 2: Ten tree species most frequently recorded during the survey of 48 transects (garden data excluded).

Species	Family	Transects (%)	Invasive category
Searsia pyroides	Anacardiaceae	49	-
Vachellia karroo	Fabaceae	41	-
Celtis africana	Ulmaceae	39	-
Melia azedarach†	Meliaceae	32	3
Searsia lancea	Anacardiaceae	27	-
Gymnosporia buxifolia	Celastraceae	25	-
Celtis sinensis†	Ulmaceae	22	None
Ziziphus mucronata	Rhamnaceae	20	-
Ehretia rigida	Boraginaceae	19	-
Ligustrum lucidum†	Oleaceae	18	1b

†, denotes alien species. Invasive categories are according to NEM:BA (Department of Environmental Affairs 2014).

The survey of land-cover types (urban open space, riparian areas and rangelands) revealed that *M. alba*, despite its wide cultivation, was not the most common alien of non-cultivated areas, but instead *C. sinensis*, *Ligustrum lucidum* and *Melia azedarach* were recorded more frequently (Table 2). *Celtis sinensis* and *M. azedarach* were the only alien trees in both the top ten lists for most frequently cultivated (Table 1) and naturally occurring (Table 2) species. *Melia azedarach* is a declared invasive alien and is no longer available in the nursery trade because of its weedy nature and public awareness (Henderson 2007).

Celtis africana, one of the only three indigenous tree species that naturally occur more frequently than *M. azedarach* and one of the five tree species found more frequently than *C. sinensis,* is commonly found across all the sampled land-cover types (Table 2). *Celtis africana* is not common in gardens because of *C. sinensis* being most available from nurseries. *Celtis africana* is very common in natural areas, with > 60% of the surveyed population recorded from rangeland, hills and ridges (Figure 1). *Melia azedarach* is also not commonly cultivated and is most commonly found in urban open space (> 40% of the population). More than 60% of the recorded *C. sinensis* individuals were from gardens, with the rest found in urban open space, riparian areas and rangelands in descending order (Figure 1). *Celtis sinensis* is definitely spreading from urban

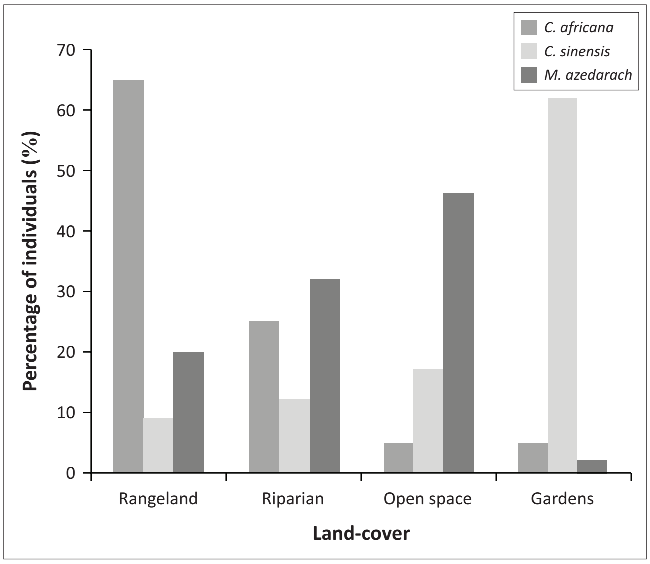


FIGURE 1: Percentage of total number of recorded individuals of *Celtis sinensis* across land-cover types compared to a co-occurring indigenous relative (*Celtis africana*) and an invasive alien (*Melia azedarach*).

areas outward, typically following the predicted pathway along watercourses and roads (Milton & Dean 1998). This adaptability can be ascribed to its ability to withstand heavy winter frosts, fleshy fruits that are prone to bird dispersal and lack of competition in a predominantly treeless Highveld landscape.

Population structure

Limited variation in the quotient (0.2–0.8) is indicative of a stable population for *C. africana* (Figure 2a) (Botha et al. 2004; Shackleton 1993). The fluctuating quotient for *C. sinensis* (0.1–1.2) is interpreted as instability within the height classes of the specific population probably because of erratic colonisation and survival events (Figure 2b). However, the comparatively little variation (0–0.8) detected for *M. azedarach* indicates that the population structure is stable because of the longer time it has had to establish since naturalisation (Figure 2c).

None of the populations had SDI values below 0.1, revealing that size frequency is steeper than would be expected from an exponentially declining population (Botha et al. 2004). In this case, the two *Celtis* species have the same SDI (0.66) and lower than *M. azedarach* (0.86). In all three cases, this is an indication that individuals are not evenly distributed among the size classes, but this needs to be considered with PI values that are based on the assumption that an ideal undisturbed population should represent a monotonic decline (PI = 0). This is typical for *C. africana*, but not for *C. sinensis* (PI = 4) and *M. azedarach* (PI = 2), which have discontinuous populations, where larger individuals show a higher frequency than a previous size-class (Botha et al. 2004; Venter & Witkowski 2010).

Overall, the population structure of *C. sinensis* is most similar to that of the invader (*M. azedarach*) and not the related, indigenous species (*C. africana)*. The *C. sinensis* population

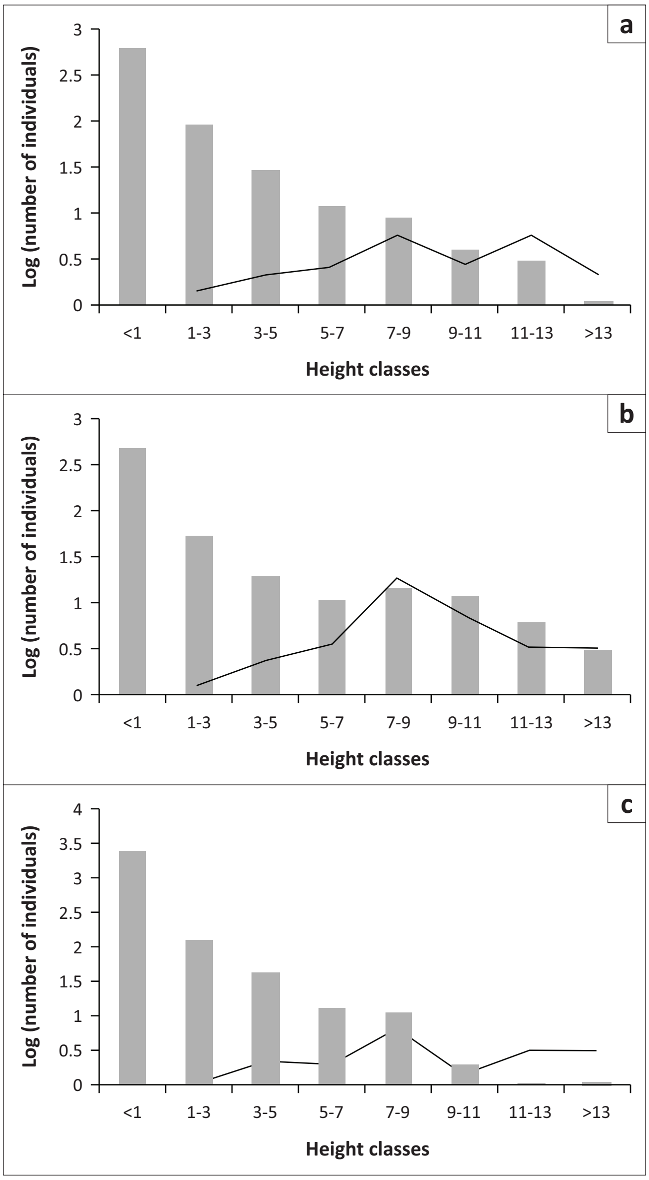


FIGURE 2: Height classes (log transformed) and quotient analyses (solid black line) of (a) *Celtis africana*, (b) *Celtis sinensis* and (c) *Melia azedarach*.

has more individuals than *C. africana* in the taller height classes, which is indicative of successful establishment, and the high numbers of saplings show the ability to reproduce (Table 3). This is an indication that *C. sinensis* is successfully increasing by reproducing and establishing in the environment. In the urban open spaces, one can argue that the seeds are originating from cultivated individuals or garden refuge; however, the fact that it also occurs in rangelands and riparian areas in agricultural areas indicates that it can reproduce independently and that it has acquired a successful dispersal vector.

Taxonomic treatment

Celtis sinensis Pers., Syn. Pl. 1: 292 (1805); Spach, Ann. Sci. Nat., Bot. ser 2:t.16: 37 (1841); Benth., Fl. Hongk.: 324 (1861); Schltr., Bot. Jahrb. Syst. 36: 33 (1905). *Celtis tetrandra* Roxb. subsp. *sinensis* (Pers.) Y.C.Tang, Acta Phytotax. Sin. 17: 51 (1979). Type: Specimen cultivated in Cel's garden, *Persoon* (herbarium not designated).

Celtis sinensis Willd., *nom. illeg.*

Sponia sinensis Decne., *nom. inval.*

Celtis willdenowiana Roem. & Schult., Syst. Veg. 6: 306 (1820). *Sponia willdenowiana* (Roem. & Schult.) G. Don, Hort. Brit., 3: 610 (1839). Type: China, *Willdenow, s.n.* (B, holo.).

Celtis japonica Planch. in Prodr. 17: 172 (1873). *Celtis sinensis* Pers. var. *japonica* (Planch.) Nakai, Bot. Mag. Tokyo 28: (264) (1914). Type: Japan. Nagasaki. *Oldham 722* (MPU, P, syn.); Yokohama, *Maximowicz, s.n.* (P, syn.); Japan, *Wright, s.n.* (P, syn.); China, Macao, *Callery 20* (P, syn.).

Celtis nervosa Hemsl., J. Linn. Soc., Bot. 26(177): 450 (1894). Type: Taiwan, Apes Hills, *Playfair 458* (K, holo.).

Celtis bodinieri H. Lév., Repert. Spec. Nov. Regni Veg. 13: 265 (1914). Type: China, *Bodinier 1633, 2587* (E, A, syn.).

Celtis cercidifolia C.K. Schneid., Pl. Wilson 3(2): 276 (1916). Type: China, Ichang, *Henry 2262* (A, holo.; GH, NY, iso.).

Celtis labilis C.K. Schneid., Pl. Wilson 3(2): 267 (1916). Type: China, Hubei, Changyang Xian, *Wilson 444* (A, holo.; GH, K, CAS, iso.).

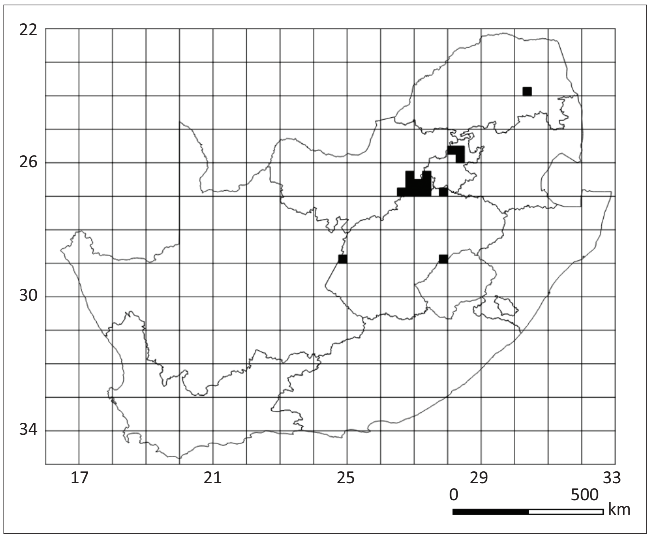
Celtis hunanensis Hand.-Mazz., Anz. Akad. Wiss. Wien, Math.-Naturwiss. Kl., 59(7): 53 (1922). Type: China, Hunan, Lengshuijiang, *Handel-Mazzetti 11968* (WU, holo.; A, iso.).

Celtis sinensis Pers. var. *japonica* Planch. forma *purpurascens* Nakai, Fl. Sylv. Kor. 19: 66 (1932). Type: Keinan, Mt. Mirokusan peninsulae Tôei, *Nakai 11029* (TI, holo.).

Description: Deciduous tree up to 20 m tall; bark smooth, grey; branchlets flexuose, brown or pale grey-brown, covered in lenticels, pubescent, sometimes glabrescent late in the season; winter buds brown, 1 mm–3 mm long, glabrous. *Leaves* alternate, with stipules linear to lanceolate, 3 mm–5 mm long, fugacious; petioles 3 mm–10 mm long, pubescent, adaxial with a broad and shallow furrow; leaf blade ovate to ovate lanceolate or obliquely ovate, 30 mm–100 mm × 35 mm–60 mm; apex acute to shortly acuminate; base rounded, obtuse, obliquely truncate, asymmetrical, with three main veins; margin subentire to crenate in upper half, teeth 0–16 on each side, lower margin entire; thickly papery; adaxial surface glossy dark green, glabrous or becomes scabrous with age; abaxial surface light green, glabrous or puberulent. *Flowers* inconspicuous, male or bisexual; pedicles 4 mm–12 mm long; greenish. Bisexual flowers 1–3 in axils near the tip of the branch; perianth ± 2 mm long, stamens 4; ovary 1.5 mm–3.0 mm long, stigma hairy, divided into two, whitish. Male flowers fascicled. *Fruit* a drupe, 1(–3) per axil, globose

TABLE 3: Number of individuals > 1.5 m and saplings (< 1.5 m) of *C. sinensis* compared to a co-occurring indigenous relative and an invasive alien across land-cover types.

Land-cover types	*Celtis africana*		Saplings	*Celtis sinensis*		Saplings	*Melia azedarach*		Saplings
	Adults	Stems per hectare		Adults	Stems per hectare		Adults	Stems per hectare	
Gardens	7	18	34	58	145	300	12	30	43
Open space	11	28	30	31	78	72	125	313	1146
Riparian	27	68	165	17	43	64	27	68	846
Rangeland	105	263	398	14	35	56	39	98	511
Total	**150**	**-**	**627**	**120**	**-**	**492**	**203**	**-**	**2546**



Source: E. van Rensburg, National Museum, Bloemfontein

FIGURE 3: Distribution map of *Celtis sinensis* in South Africa based on herbarium specimens and records from the South African Plant Invaders Atlas database.

or ovoid, 5–7(–8) mm in diameter, green when immature turning yellow to reddish-brown when mature, becoming brown and wrinkled with age; stone white, sub-globose, surface texture reticulately foveolate.

Etymology: *Celtis* is a classical Latin name for the unrelated African species, *Ziziphus lotus* L., and *sinensis* indicates that the species originates from China (Clarke & Charters 2016; Glen 2004).

Common names used for the tree in South Africa include Chinese nettle tree, Japanese hackberry, *Chinese netelboom* (Afr), *po shu* (Chinese), *modutu* (Setswana), *lesika*, *mohatlakgomo*, *mogatakgomo* (Sesotho). The Tswana name, *modutu*, means boredom and loneliness, suggesting that the dense shade of this tree is sought by people feeling bored.

Distribution: *Celtis sinensis* occurs on the Highveld of central South Africa (Figure 3) as a garden subject and has become naturalised in urban open spaces and riparian areas. It is generally sparsely distributed, but can form dense infestations in riparian areas and on roadsides. It is gradually colonising natural areas such as rangelands.

Phenology: Small, greenish flowers are present for a brief period during early spring. Fruits are produced in summer, but dried fruit can be present on the trees till late autumn.

Dispersal: *Celtis sinensis* reproduces with seeds, but also produces suckers. Its fleshy seeds are usually dispersed by animals (birds and bats) and by water run-off, or are dumped in urban open space as garden waste.

Diagnostic characters

Most *Celtis* species exhibit juvenile leaf morphology (Whittemore & Townsend 2007) and long persistence thereof, which is different from the adult leaf morphology and makes it difficult to distinguish between young plants of *C. africana*, *C. australis*, *C. occidentalis* and *C. sinensis*. The shape and size of the leaves, number of teeth on the toothed margin, the extent to which the teeth extend along the margin to the leaf base, petiole length and the colour and size of the drupe show enough variability to distinguish between species in their juvenile state.

Celtis sinensis has dark green, ovate leaves (30 mm–100 mm × 35 mm–60 mm) that are glossy above and softly hairy underneath. The leaves of *C. australis* are ovate-elliptic (50 mm–120 mm × 15 mm–35 mm), dark green and rough on the upper surface, but the lower surface is a lighter green and minutely hairy. *Celtis africana* leaves are ovate (15 mm–100 mm × 10 mm–50 mm), very hairy on both surfaces and dark green when young, but adult leaves are dull green. *Celtis occidentalis* leaves are broadly ovate to cordate (60 mm–130 mm × 40–80 mm), darker green and glossy above and softly hairy underneath.

The most conspicuous character by which juvenile plants of *C. sinensis* can be distinguished from *C. africana*, *C. australis* and *C. occidentalis* is the extent to which leaf margin is serrated (Figure 4). This variability is also contained in the adult leaf morphology. *Celtis sinensis* leaves are only toothed in the upper third towards the apex and have 8–16 teeth per side on the leaf margin. The leaf margin of *C. africana* is toothed more than two-thirds from the apex to the leaf base and generally has 14–22 teeth per side. *Celtis australis* has more than 20 teeth per side, and the margin is nearly completely toothed from the apex to near the base. *Celtis occidentalis* is also completely toothed down to the leaf base and commonly has 30–40 teeth per side.

The petiole length ranges from 3 mm to 7 mm for *C. africana*, from 3 mm to 10 mm for *C. occidentalis* and from 5 mm to 15 mm for both *C. sinensis* and *C. australis*.

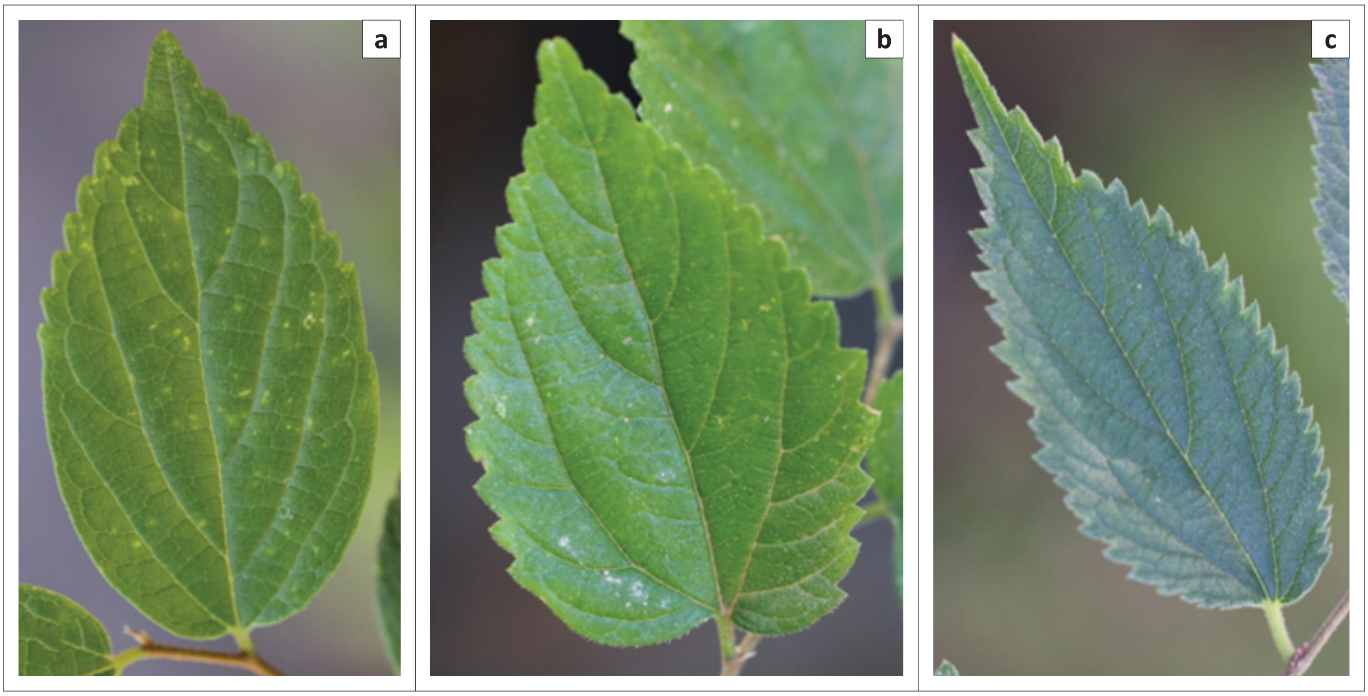


FIGURE 4: Sapling leaves of commonly sold 'stinkwood' trees at nurseries: (a) *Celtis sinensis* (× 2.5), (b) *Celtis africana* (× 2.5) and (c) *Celtis australis* (× 1.5).

FIGURE 5: Fruit of (a) *Celtis sinensis* (× 1.8), (b) *Celtis africana* (× 2.4) and (c) *Celtis australis* (× 2).

Fruit morphology and colour are also variable (Figure 5), but not a character of value to distinguish between saplings. Fruit of *C. sinensis* are glabrous and an ovoid (5 mm–8 mm) drupe, dark orange in colour and presented on short, stout stalks (4 mm–6 mm). *Celtis australis* fruit (10 mm–12 mm) are also ovoid and hairless, yellow-white turning purple-black when ripe and presented on long stalks (12 mm–14 mm). *Celtis africana* fruit (4 mm–6 mm) are ovoid and glabrous, yellow turning brown and presented on long thin stalks (12 mm–14 mm). *Celtis occidentalis* has obovate or subglobose and dark orange fruit (8 mm–11 mm) turning purple-black when ripe and presented on long stalks.

Celtis sinensis is easily distinguishable from the indigenous *C. gomphophylla* and *C. mildbreadii* in that the leaf apex of *C. gomphophylla* is elongated into a distinct drip tip, which is almost a third of the leaf length, and from *C. mildbraedii*, which has a symmetric leaf base (apex of *C. sinensis* is elongated, but not into a distinctive drip tip, and the leaf base is asymmetrical).

Key to juvenile plants commonly sold at nurseries

1A. Lamina margin predominantly entire to dentate or serrate in apical third with < 17 teeth per side... *C. sinensis*

1B. Lamina margin predominantly dentate or serrate from apex to basal third, > 16 teeth per side... 2

2A. Lamina margin predominantly with > 20 teeth per side, lamina apex acute to caudate... 3

2B. Lamina margin rarely with > 20 teeth per side, lamina apex predominantly acute to acuminate... *C. africana*

3A. Lamina ovate lanceolate to broadly ovate, lamina length and width 1.5:1.... *C. occidentalis*

3B. Lamina predominantly ovate lanceolate, lamina length and width 2:1 to 3:1.... *C. australis*

Key to adult specimens of *Celtis* in South Africa

1A. Leaf apex elongate into a distinct drip tip, up to one-third of the leaf length … 2

1B. Leaf apex elongate pointed, but not into a distinct drip tip … 3

2A. Margin of leaf entire, base slightly asymmetric, leaf covered in minute and stiff hairs giving it a roughish feel; drupe conical-ovoid, 5 mm in diameter, mature fruit dark yellowish; distributed in KwaZulu-Natal and Eastern Cape in lowland and upland forests … *C. gomphophylla*

2B. Margin of leaf sharply serrated from base to apex or along the upper two-thirds of the leaf, base strongly asymmetric, leaf covered in spreading hairs giving it a velvety feel; drupe subglobose to pyriform, 10 mm–12 mm in diameter, mature fruit dark brown almost black; distributed mainly in urban areas throughout South Africa … *C. australis*

3A. Leaf base cuneate and symmetric; fruit ovoid-ellipsoid, mature fruit red; distributed in Swaziland and KwaZulu-Natal in isolated patches of lowland forests… *C. mildbreadii*

3B. Leaf base rounded to cuneate or cordate and asymmetric; fruit globose or subglobose, mature fruit yellow to orange, brown or purplish … 4

4A. Margin of leaf subentire to crenate along upper half of leaf, glossy dark green, ovate to ovate-elliptic, adaxial surface glabrous, but with hairs abaxially scattered along major veins and tufted in vein axils, leaf has a leathery, smooth surface; fruit 5 mm–8 mm in diameter; distributed mainly in urban areas throughout South Africa … *C. sinensis*

4B. Margin of leaf serrated along upper two-thirds of the leaf; dark green on both surfaces or paler beneath, narrowly to broadly ovate; velvety or roughish surface... 5

5A. Leaves broadly to narrowly ovate to ovate-elliptic, dark green in colour, sparingly to densely covered with hairs, leaf has a velvety surface; fruit 4 mm–6 mm in diameter; distributed throughout South Africa in all forests types, mesic savanna and wooded grassland … *C. africana*

5B. Leaves ovate lanceolate to broadly ovate, dark green above, paler beneath, rough on the upper surface, smooth below; fruit 8 mm–11 mm in diameter; distributed mainly in urban areas throughout South Africa … *C. occidentalis*

Conclusion

Celtis sinensis is commonly cultivated on the Highveld of central South Africa as a garden subject or street tree and is naturalised in urban open spaces and riparian areas. It is colonising rangelands of agricultural areas and should therefore be considered as a potential invasive species. It shows a similar population structure and dispersal corridors as the declared invasive, *M. azedarach*. Vegetative characters of the leaves and fruits distinguish accurately between indigenous and alien *Celtis* species, both for juvenile and adult trees. The findings of this study will sensitise the horticultural industry to the potential invasive threat of *C. sinensis* and will inform the public on how to ascertain that white stinkwood purchased from nurseries are indeed *C. africana*.

Specimens examined

Celtis africana

SOUTH AFRICA. NORTH-WEST. – **2526** (Zeerust): Grasfontein, Lichtenburg, red sand, (–CC), 08 December 1929, *Sutton 297* (PRE). **2626** (Klerksdorp): Renovaal, Klerksdorp, (–DD), 04 June 1975, *De Feijter 232* (PUC). **2627** (Potchefstroom): North-West University, Potchefstroom, fence along botanical garden, (–CA), 11 October 2007, *Siebert 3426*; central town, roadside, Potchefstroom, (–CA), 18 November 2008, *Lubbe & Siebert* 128 (PUC); North-West University, Potchefstroom, next to Totius Hall, (–CA), 07 February 2017, *Komape 642* (PUC).

GAUTENG. – **2527** (Rustenburg): Uitkomst, Rustenburg, upper dam of Dunnungkamp, (–DD), 23 September 1970, *Coetzee 259* (PUC). **2528** (Pretoria): Groenkloof, Pretoria, (–CA), 17 September 1904, *Burtt-Davy 1980* (PRE); between Beestekraal and Vaalkop, Pretoria, at the bottom of hill, (–DC), 26 March 1978, *Engelbrecht 2* (PRU). **2627** (Potchefstroom): Sterkfontein Caves, Isaac Stegmann Nature Reserve, Krugersdorp, (–BA), 06 September 1974, *Mogg 36196* (PRE).

FREE STATE. – **2627** (Potchefstroom): Vredefort Dome, Parys, (–CD), January 2002, *Cilliers 3008* (PUC). **2727** (Kroonstad): Valsch River, (–CA), October 1928, *Pont 390* (PRE). **2827** (Senekal): Ferrara, Senekal, stone hills, (–AD), 18 December 1931, *Goossens 993* (PRE). **2926** (Bloemfontein): Grantsheuwel, Bloemfontein, (–AA), 21 October 1967, *Hanekom 969* (PRE);

Celtis mildbraedii

SOUTH AFRICA. KWAZULU-NATAL. – **2930** (Pietermaritzburg): Howard College, Durban, Stella Bush, (–CD), 05 November 1955, *Bayer 2* (PRE); Stella Bush, Durban, (–CD), 20 July 1969, *Strey 8785* (PRE); Inanda Mission Reserve, Matabetulu Area, just above Mzinyathi River confluence, (–DB), 10 August 1993, *Ward 12388* (PRE). **3030** (Port Shepstone): Amanzimtoti, forest in river valley, (–BB), 17 December 1966, *Ward 5905* (PRE);

Celtis gomphophylla

SOUTH AFRICA. KWAZULU-NATAL. – **2732** (Ubombo): 27 km south of Ingwavuma, Lebombo Range, Gwalaweni Forest, (–AC), 05 March 1973, *White 10431* (PRE). **2831** (Nkandla): Ngoya Forest, Zululand, next to road in forest, (–DC), 12 February 1979, *Van Wyk 2540* (PRU). **2832** (Mtubatuba): Monzi Golf Course, Mtubatuba district, Zululand, (–AD), 01 October 1976, *Jacobsen 4710* (PRE). **3030** (Port Shepstone): Vernon Crookes Nature Reserve, forest on streambank, (–BC), 10 April 1986, *Ward 9887* (PRE).

3130 (Port Edward): Fish Eagle trail, Umtamvuna Nature Reserve, forest, (–AA), 23 April 1989, *Abbott 4357* (PRU).

EASTERN CAPE. – **3129** (Port St Johns): 3 miles from Port St. Johns on road to Lusikisiki, forest, (–DA), 21 May 1970, *Jenkins 13* (PRE).

Celtis australis

SOUTH AFRICA. NORTH-WEST. – **2627** (Potchefstroom): North-West University, Potchefstroom, parking area, (–CA), 26 September 2007, *Siebert 3392* (PUC); central town, roadside, Potchefstroom, (–CA), 18 November 2008, *Lubbe & Siebert 130* (PUC); North-West University, Potchefstroom, parking area next to building G15, (–CA), 07 February 2017, *Komape 643* (PUC); Suikerbos Nature Reserve, Venterskroon, (–CC), 17 November 2011, *Komape, Mabe & Siebert 205* (PUC);

GAUTENG. – **2528** (Pretoria): Union Building, Pretoria, (–CB), 21 June 1984, *Du Plessis 75* (PRU); Elarduspark, in garden around church building, (–CD), 23 October 2012, *Van Greuning 903* (PRU).

Celtis occidentalis

CANADA. ONTARIO. – Lanark County, Elmsley, Smith's Fall, hydro park, along river on grassy banks, 22 August 1945, *Senn & Barnsley 2888* (PRU).

USA. MISSISSIPPI. – Jasper County, along small rocky streams near Webb. City, 16 October 1922, *Palmer 22313* (PRE). PENNSYLVANIA. – Crawford County, woods, along small streams near Pittsburg, 20 April 1922, *Palmer 20833* (PRE). WEST VIRGINIA. – Wirt County, top of Bonnette's hill below upper gap. About one mile up Little Kanawha River from Palestine, 02 September 1941, *Bartholomew s.n.* (PRE).

Celtis sinensis

SOUTH AFRICA. LIMPOPO. – **2330** (Tzaneen): Bonlati, Tzaneen, in mixed lowveld/bushveld, (–CD), 28 April 2002, *Prinsloo 786* (PRU).

NORTH-WEST. – **2627** (Potchefstroom): North-West University, Potchefstroom, parking area, (–CA), 19 September 2007, *Siebert 3376* (PUC); central town, Potchefstroom, roadside, (–CA), 18 November 2008, *Lubbe & Siebert 129* (PUC); Albert Luthuli Street, Potchefstroom, next to Wasgoed Stream, (–CA), 06 Oct 2011, *Komape, Mabe & Siebert 9* (PUC); North-West University, Potchefstroom, parking area next to building E4, (–CA), 07 February 2017, *Komape 644* (PUC).

GAUTENG. – **2528** (Pretoria): Salvokop residential area, Pretoria, 3rd Avenue, behind station, (–CA), 28 September 2002, *Siebert & Siebert 2031* (PRU); Elardus Park, Pretoria, planted in garden, (–CD), 23 October 2012, *Van Greuning 902* (PRU).

FREE STATE. – **2627** (Potchefstroom): Sasolburg, Plot 12, Wonderfontein Rd, (–DD), 27 September 1997, *Kroon 15291* (NMB).

CHINA. – Pai Ying Tung, Lao Shan, 14 July 1930, *Chiao 2750* (PRE); Tai Ching Kung, Lao Shan, 14 August 1930, *Chiao 29*54 (PRE).

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

S.J.S. planned and coordinated the study and wrote the manuscript. M.S. contributed to the writing of the manuscript and was responsible for the construction of the key to the indigenous and cultivated *Celtis* species and the nomenclature and description of *Celtis sinensis*. L.K. contributed tree survey data and analysed the population data. D.M.K. collected field data and contributed to the writing of the manuscript.

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