

Research Article

First record of the alien plant species *Cucurbita foetidissima* Kunth (Cucurbitaceae) in Bulgaria

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Abstract

Cucurbita foetidissima is a native plant species found in the central and southwestern United States, as well as from northern to central Mexico. It is a perennial trailing vine, with large fleshy tap root (tuber) and one to many long prostrate and climbing stems. The aim of the present article is to report *C. foetidissima* for the first time for Bulgaria as a naturalised alien species and to provide some biosystematic, chorological and ecological data from the Bulgarian population. The species is found in the Thracian Lowland, in and near the town of Sadovo, and occupies a total area of about 3 ha. The chromosome number and genome size of the species are reported here for the first time based on Bulgarian accessions and they are in line with earlier data from the native distribution range of the taxon. *Cucurbita foetidissima* grows mainly in man-disturbed habitats. It blooms and fructifies abundantly and the fruits have numerous seeds. It is supposed to be dispersed mainly by debris and waste associated with human activities but other dispersal modes are also possible. The species easily forms dense overgrowths mainly on the earth's surface, but also climbs on the surrounding plants, thus competing with them for sunlight, water, and nutrients. It also changes the structure and composition of plant communities. Thus, it can be inferred that *C. foetidissima* is locally invasive.

Key words: Bulgarian flora, chromosome number, distribution, genome size, naturalised alien species

Introduction

Cucurbitaceae Juss. is a family with mainly tropical and subtropical distribution, consisting of 15 tribes (Schaefer and Renner 2011a) and containing 95–97 genera with about 940–980 species depending on the taxonomic concept (Schaefer and Renner 2011a, b; Christenhusz and Byng 2016). The number of genera and species most probably will change following future taxonomic revisions (Ebert et al. 2021). Cucurbitaceae species are mainly herbaceous annual or perennial climbers and woody lianas (Schaefer and Renner 2011a, b). After Solanaceae, it is the second largest vegetable and fruit yielding family in the world, with great importance in the food economy of many tropical countries (Bhowmick and Jha 2015).

The genus *Cucurbita* L. is native to the New World, but has been introduced and cultivated in the Old World since the 1500s (Whitaker 1947; Paris 1989, 2001); it comprises the squash, zucchini, gourd and pumpkin and belongs to the tribe Cucurbiteae Ser., as described by Schaefer and Renner (2011a, b). It is one of the world's most widely cultivated crops (Paris 2001). Whitaker and Bemis (1975) recorded altogether 27 *Cucurbita* species, but the genus is now thought to comprise 10 wild and five cultivated species (Ebert et al. 2021).

Combined archaeological, phylogenetic and molecular data have revealed early origins for *Cucurbita* crops, with the oldest initial domestication of *C. pepo* L. subsp. *pepo* occurring in Mexico up to 8 000–10 000 years ago (Chomicki et al. 2020). Wild *Cucurbita* species have their main centre of diversity in Mexico (Khoury et al. 2020), however, the highly diverse cultivated *Cucurbita* species are grown worldwide for their edible fruits or seeds (Ebert et al. 2021). The cultivated species include the major globally valuable crops *C. argyrosperma* C. Huber, *C. ficifolia* Bouché, *C. maxima* Duchesne, *C. moschata* Duchesne, and *C. pepo* (Chomicki et al. 2020; Khoury et al. 2020).

There are no native species of *Cucurbita* in Europe, but in many European countries several taxa like *C. ficifolia*, *C. maxima*, *C. moschata*, and *C. pepo* are widely cultivated (see more details in Henning et al. 2017+). In many cases, these species have escaped from cultivation and are casual or naturalised aliens, some of them growing far away from any vegetable crops (Henning et al. 2017+; Juan et al. 2023). All of the above-mentioned representatives of *Cucurbita*, except *C. ficifolia*, are cultivated in Bulgaria (Jordanov and Andreev 1979).

The aim of the present article is to report *C. foetidissima* Kunth as a newly naturalised alien species in the Bulgarian flora and to provide data about its main distinguishing morphological features, distribution, habitats, chromosome number, genome size, alien and invasive status in Bulgaria. To our knowledge, this is the first documented record of this species in Europe growing wild, albeit in an urban and agricultural environment.

Materials and methods

Data were collected during fieldwork carried out in 2021–2024 in and near the town of Sadovo, Plovdiv district. The herbarium specimens gathered were deposited in the Herbarium of the Institute of Biodiversity and Ecosystem Research (SOM) [herbarium acronym according to Thiers (2024+)]. Information on general species distribution was based on data from Sánchez de la Vega et al. (2019), Khoury et al. (2020), Mejía-Morales et al. (2021), and Plants of the World Online (POWO 2024). Abbreviations of author names of taxa follow Brummitt and Powell (1992), with additions available from the continuously updated International Plant Names Index

(IPNI 2024) and POWO (2024). The morphological description was based mainly on own observations during the fieldwork and on the collected plant material, and compared with the data in relevant specialised sources (e.g., Teppner 2004; Nesom 2015; Butterwick 2016; SEINet Portal Network 2024; etc.). Data on the size and state of the population, and on habitats were based on authors' observations in the field.

The genome size of *C. foetidissima* from the Bulgarian accessions was measured by CyFlow SL Green flow cytometer (PARTEC, Germany), equipped with a green (532 nm) solid-state laser. Fresh leaves from plants obtained from seeds and cultivated in a greenhouse were used. *Solanum pseudocapsicum* (2C = 2.59 pg, Temsch et al. 2022) was applied as an internal standard. The plant material was treated with the extraction and staining kit "CyStain® PI Absolute P" (SYSMEX) following the protocol prescribed by the manufacturer. The samples were then measured at a rate of 10–20 nuclei per second, with a total of 5 000 nuclei per run. Five replicates were done for each sample and only measurements with CV below 5% were taken into account.

For karyological studies, fruits were collected from the natural accessions in the town of Sadovo and seeds were sown in the Cytotaxonomic Laboratory of the Institute of Biodiversity and Ecosystem Research (IBER-BAS). Root-tips were pretreated with 0.01% colchicine for 30 min, fixed in ethanol:glacial acetic acid (3:1) for 2 h at room temperature, and then stored for 24 h in a refrigerator. Hydrolysis was conducted in 1N HCl at 60 °C for 15 min. Then, the root-tips were transferred in HCl:ethyl ether (1:1) for 10 min at 60 °C, washed in distilled water and stained with haematoxylin after Gomori (Melander and Wingstrand 1953) for 30–40 min at 60 °C. Finally, root-tips were squashed in 45% acetic acid. Chromosome plates were photographed using a Nikon ECLIPSE 50i microscope equipped with a Nikon DS-5Mc digital camera. The chromosome numbers were compared with data in the Chromosome Counts Database (CCDB, version 1.66, <http://ccdb.tau.ac.il/>) (Rice et al. 2015), the Index to Plant Chromosome Numbers (IPCN, <http://legacy.tropicos.org/Project/IPCN>) (Goldblatt and Lowry 2011), and other available literature sources.

For testing seed germination, ripe fruits were collected from the field and left for about three months at room temperature in a laboratory. Later, 50 seeds were obtained from two fruits and seeded in a tray with commercially available universal soil (neutral pH). The tray was kept at room temperature (about 18–20 °C) in the Lab and watered regularly to maintain moderate soil moisture. The obtained seedlings were counted and the percentage of seed germination was determined on this basis.

Results and discussion

In September 2021, a large patch of an unidentified *Cucurbita* species was noticed in the town of Sadovo in Bulgaria. A thorough search of the town and its surrounding areas revealed several additional subpopulations, some

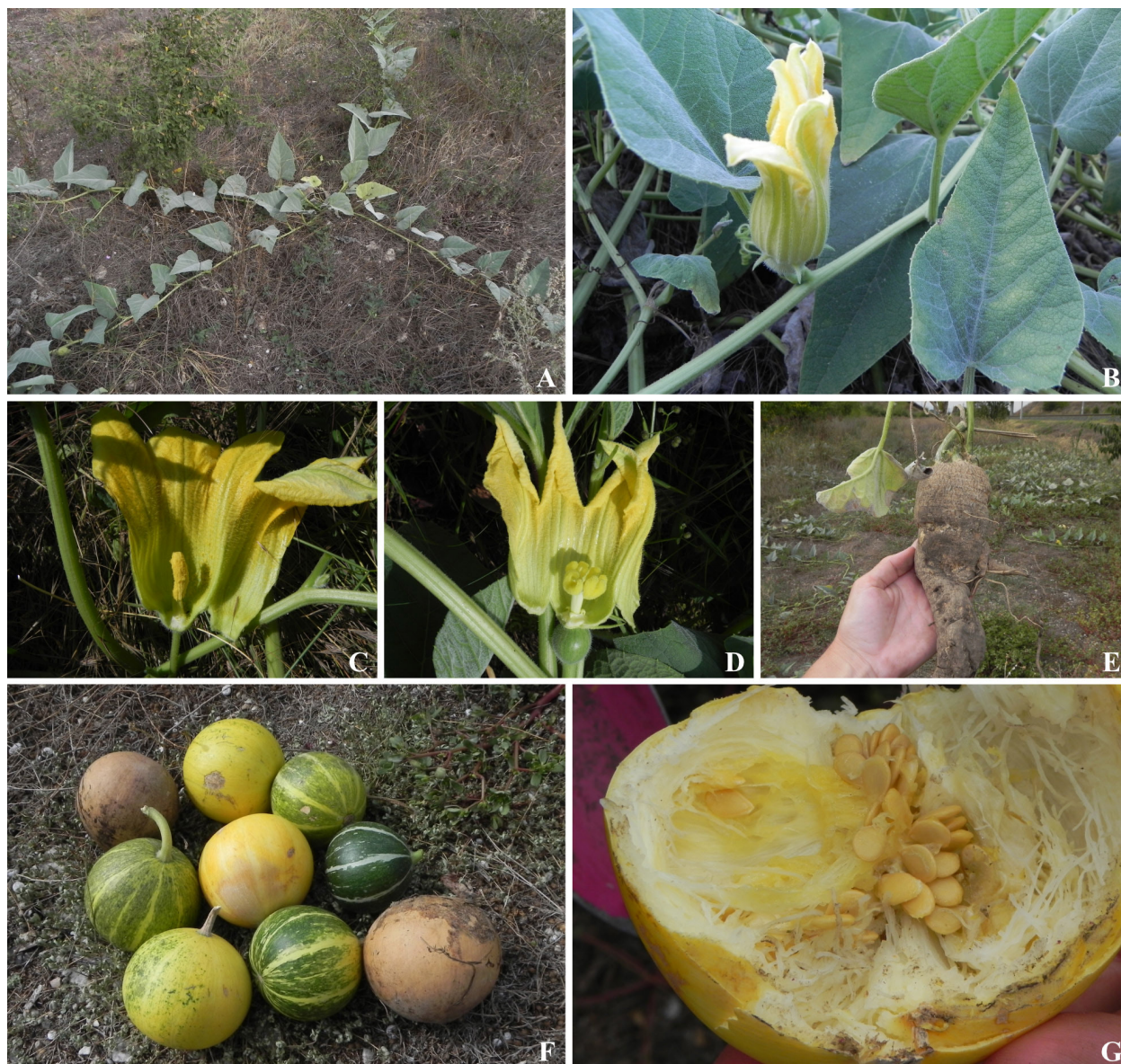


Figure 1. *Cucurbita foetidissima* Kunth. A, one individual with four stems appearing from its tap root; B, close-up view of a flower and leaves; C, male (staminate) flower; D, female (pistillate) flower; E, tap root; F, gourds at different stages of maturity (two of them last-year); G, interior view of a fruit, with the seeds and pulp exposed (Photographs A, E, F, G, 18 September 2021; B, 16 September 2021; C, D, 05 June 2024). Photos by Daniella Ivanova.

of which were rather large. After consulting the relevant literature, the plant was identified as *Cucurbita foetidissima*. The site was revisited in November 2021, September 2022, and June 2024 in order to gather more information on the species.

Taxonomy

***Cucurbita foetidissima* Kunth, Nov. Gen. Sp. [H.B.K.] 2: 123 (1817)
(Figure 1)**

Syn.: *Pepo foetidissima* (Kunth) Britton

Plants perennial, trailing or climbing vines, forming sizeable dense patches, sometimes over several square metres, slightly foul-smelling. Tap root large, elongated, fleshy, tuberous. Stems one to many per individual, coarse,

trailing, long (often to several m), radiate, 5–15 mm in diameter, sulcate, with stout, stiff, spreading or curved hairs and variously pubescent with curved and appressed hairs. Tendrils emerging from the stem just below the leaf petiole, thick, stout, hirsute, usually 3–7-branched, mostly coiled into a head at apex of stalk that is 4–6 cm long. Leaves alternate along the stems and generally pointing upward, on relatively long thick scabrous stalks (3–12 cm long); leaf blades coarse and thick, greyish-green above and greyish beneath, triangular-ovate, narrowly triangular, triangular-acuminate to triangular-lanceolate or long triangular, longer than wide, 10–35 cm long, 8–30 cm wide, unlobed; base cordate, hastate-cordate to nearly truncate, apex mostly acute and mucronate, margins irregularly and finely dentate; prominently veined, the upper surfaces densely scabrous with soft silver-grey hairs, the lower surfaces similar but often greyer, more densely scabrous. Flowers large, born solitary at the vine nodes in the leaf axils, opening early in the day, male (staminate) and female (pistillate) (gynodioecy reported from native American populations, see Winsor et al. 2000); sepals 5, green, united at the base, narrow and pointed at the tips, much shorter than the petals; petals 5, pale or golden yellow, united into a campanulate to cylindric-campanulate corolla; corolla with spreading or curved hairs, with long tube and long, recurved, apiculate lobes. Fruit peduncles 5-ribbed, hardened, woody. Fruits (gourds) predominantly dark green, but yellowish to orange-yellow at full maturity, with 6–8 main cream-white longitudinal stripes, oblong-globose, globose to depressed-globose, 5–10 cm in diameter, smooth, the rind thin, hard-shelled, the flesh yellowish-white, fibrous, bitter. Seeds numerous, ovate, 7.1–8.2 mm long, 4.5–5.2 mm wide, tan, cream, yellowish or bright ochre-coloured, without a differentiated margin, surface smooth.

Flowering from the end of May to September. Fruiting from August to November.

Reproduction: sexually (by seeds) or vegetative propagation via adventitious roots at the nodes, which produce separate plants after the vines die back. Under suitable environmental conditions, with adequate moisture and at the right stage of growth, any node on the vine can form an adventitious root; as a result, large clonal populations can be propagated and sustained through asexual reproduction (Bemis et al. 1978a). However, no rooting at the nodes of the vines has been observed in Bulgaria yet, although it is probable.

Chromosome number

As far as is known, most if not all *Cucurbita* species have a uniform complement of 20 pairs of chromosomes (see the Chromosome Counts Database and the Index to Plant Chromosome Numbers; references in Olvera-Vazquez et al. 2019). The chromosome number of *C. foetidissima* collected in Bulgaria is $2n = 40$ (Figure 2). This is the first count for the species from Bulgaria. The chromosomes are small, with no easily distinguishable

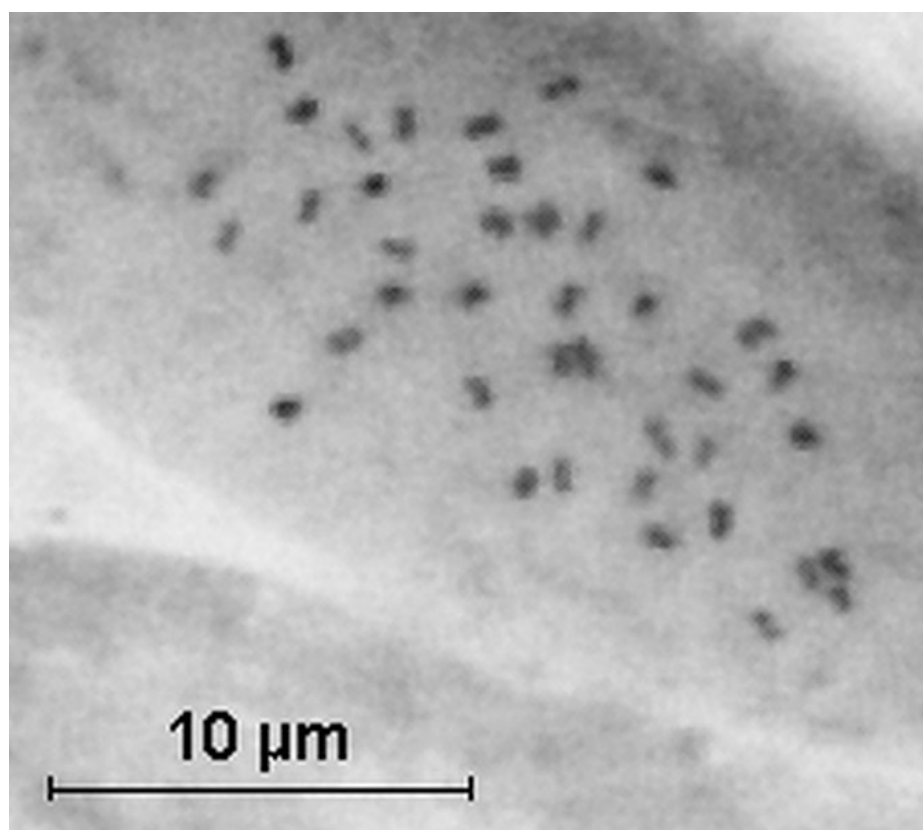


Figure 2. Metaphase plate in somatic cell of *Cucurbita foetidissima* Kunth from the Bulgarian accession showing $2n = 40$ chromosomes. Photo by Daniella Ivanova

morphology. The earliest published diploid chromosome count for this species appears to be that of McKay (1930), who reported $2n = 42$. According to Fedorov (1969), however, a year later MacKay published the number $2n = 40$ (McKay 1931, sec. Fedorov 1969). Since then, no other data on the chromosome number of *C. foetidissima* have been found by us in the literature.

Genome size

Genome sizes are known in 11 species of *Cucurbita* (see Plant DNA C Value database, Leitch et al. 2019). In contrast to the uniform chromosome number, there are differences between genome sizes within the genus, with 1C values ranging from 0.34 pg to 0.54 pg (Leitch et al. 2019). The PI determined genome size (2C) of *C. foetidissima* was reported to be 0.686 pg (1C = 0.34 pg), and that determined by DAPI was 0.586 pg (Šiško et al. 2003). In our study we used PI staining protocol and obtained results that are very similar to those already published. Three plants were measured and the obtained values varied in the range $2C = 0.656\text{--}0.658$ pg (1C = 0.33 pg).

Seed germination

The purpose of the seed germination experiments was solely to confirm that under Bulgarian conditions, mature fruits have viable seeds that can ensure the self-sustenance of the naturalised population. For this reason,

no repeated experiments were performed with different soil types or with seeds that had been dormant for different periods. Field observations suggested that the propagation, spread and self-sustenance of the Bulgarian population occur through seed propagation. So, we wanted to make sure that there was a sufficient percentage of viable seeds to ensure this process. The results showed that out of the 50 seeds sown, a total of 28 seeds germinated during the second and third weeks after sowing. The seedlings were kept for two months to ensure that they were viable and developing well. All seedlings survived and grew at approximately the same rate. This shows that 56% of the sown seeds germinated and produced viable seedlings, which, considering the huge number of seeds in each fruit, is sufficient to ensure seed propagation and self-sustainability of the population in Bulgaria.

Distribution in Bulgaria

Bulgaria: Thracian Lowland floristic region, in and near the town of Sadovo, generally in its W and SW parts, at 150–160 m a.s.l.

A list of exact localities and dates of visits is provided: Thracian Lowland floristic region: Sadovo town, Plovdiv district, a large stand in an abandoned arable land W of the town, 150 m, 42.13270N, 24.92747E, 16 September 2021, 12 November 2021, 25 September 2022, and 05 June 2024 (obs.); loc. *ibid.*, wasteland in the NW part of the town, near a dump-site, 150 m, 42.13771N, 24.93300E, 18 September 2021 (obs.); loc. *ibid.*, along the road and on the banks of a canal in the SW part of the town, 150 m, 42.13013N, 24.93153E, 16 September 2021, 25 September 2022, and 05 June 2024 (obs.); loc. *ibid.*, abandoned terrains in the SW part of the town, 150–160 m, 42.12991N, 24.92914E, 12 November 2021 (obs.); loc. *ibid.*, 42.13021N, 24.92816E, 12 November 2021 (obs.); loc. *ibid.*, 42.13108N, 24.92790E, 12 November 2021 (obs.); loc. *ibid.*, 42.12973N, 24.92280E, 12 November 2021 (obs.); loc. *ibid.*, in ruderalised grassland along the railway SW of the town, 150 m, 42.12936N, 24.93144E, 18 September 2021 (SOM); loc. *ibid.*, on boundary strips along arable fields, roads and railways and in the peripheries of arable lands SW of the town, 42.12653N, 24.92562E, 12 November 2021 (obs.) and 05 June 2024 (SOM); loc. *ibid.*, 42.12831N, 24.92651E, 12 November 2021 (obs.); loc. *ibid.*, around abandoned building nearby the railway, 160 m, 42.13096N, 24.93682E, 12 November 2021 and 05 June 2024 (obs.).

General distribution

Cucurbita foetidissima is a native, common and widespread species in the regions from the central and southwestern United States southward to the central states of Mexico. The occurrence in the eastern USA is non-native (POWO 2024).

So far, there are no reliable reports for naturalised occurrences of *C. foetidissima* in Europe. In Austria, the species was seen in 1989 and it

was still present in 1997, in the temperate house of the Botanical Garden of the Institute of Plant Sciences of Graz University (Teppner 2004). However, it is no more grown there (Christian Berg *pers. inform.*).

POWO (2024) gives *C. foetidissima* as introduced in Germany. The record for Germany, given in the dataset of Pl@ntNet (Affouard et al. 2023), is based on human observation in September 2022, and the GPS-coordinates 49.765472N, 9.932207E actually indicate the territory of the Botanical Garden of Würzburg University.

In France, there are observations made by Midouze in August 2022 and February 2023, and published in iNaturalist (several images available; see for example <https://www.inaturalist.org/observations/194966562>) and then featured on the Global Biodiversity Information Facility, GBIF (iNaturalist contributors 2024). The GPS-coordinates 45.766799N, 0.892325W indicate Sainte-Gemme, location nearby buildings. It is not clear what the origin of this spot is. We are not aware if this finding is published in the scientific literature.

In addition to this data from Europe, it is worth mentioning a record from Australia (<https://www.gbif.org/occurrence/4850510912>). The plant seems to have been collected in the wild, however, we were unable to find any literature source providing more details for this occurrence.

Habitats and populations

In its native range, *C. foetidissima* is well adapted to desert environments and best suited to traditionally non-arable, arid or semi-arid regions (Bemis et al. 1978a; Butterwick 2016; Andres 2000). It is found in open plains, prairies, sandy or gravelly soils, dunes, gypsum hills, grasslands, along fields, and in disturbed areas, such as roadsides, railroad banks, vacant lots, wastelands, fallows and abandoned fields (DeVeaux and Shultz 1985; Nesom 2015; Butterwick 2016; Mejía-Morales et al. 2021). The species is xerophytic, tolerant of drought and high temperatures, requires little water (DeVeaux and Shultz 1985; Mejía-Morales et al. 2021), but a lot of sunlight.

In Bulgaria, the species occurs mainly in man-made or man-disturbed habitats: in abandoned arable lands or along arable fields (Figure 3A, B), near buildings, canals, dumps, along roads and railways, but it is also found in ruderalised grasslands.

Common accompanying species at the margins of arable fields were: *Aegilops cylindrica* Sm., *Bromus sterilis* L., *B. tectorum* L., *Cichorium intybus* L., *Conium maculatum* L., *Convolvulus arvensis* L., *Dasypyrum villosum* (L.) Borbás, *Galium aparine* L., *Lactuca serriola* L., *Papaver rhoeas* L., *Portulaca oleracea* L., *Prunus cerasifera* Ehrh., *Senecio vernalis* Waldst. & Kit., *Sorghum halepense* (L.) Pers., and *Tragopogon orientalis* L.

In urban environments, for example near the railway and along the streets, common accompanying species were: *Amaranthus retroflexus* L., *Ballota nigra* L., *Chondrilla juncea* L., *Cichorium intybus* L., *Convolvulus arvensis* L.,



Figure 3. *Cucurbita foetidissima* Kunth. A, B, habitat in Bulgaria (A, in abandoned arable land; B, on the boundary strip along arable field); C, D, impact of the species (C, overgrowth on the earth's surface in the large stand W of the town of Sadovo; D, stems climbing on *Sambucus nigra* L.) (Photographs A, D, 18 September 2021; B, 12 November 2021; C, drone image taken on 18 September 2021). Photos by Daniella Ivanova (A, B, D), Valeri Georgiev (C).

Crepis foetida L., *Digitaria sanguinalis* (L.) Scop., *Elymus repens* (L.) Gould, *Erigeron canadensis* L., *Lactuca serriola* L., *Malva sylvestris* L., and *Portulaca oleracea* L.

The population of *C. foetidissima* consists of many fragments located in the northwestern, western, and southwestern parts of the town, as well as in nearby western and southwestern surrounding areas. They have different sizes and different density and occupy a total area of about 3 ha. The plants bloom and fructify abundantly and the fruits contain numerous seeds.

Conservation status

Cucurbita foetidissima is globally assessed as Least Concern (Sánchez de la Vega et al. 2019). Numerous accessions are conserved in different institutions, storing genetic resources, seed or gene banks, including in several European countries (see, e.g., Sánchez de la Vega et al. 2019).

Uses

Seeds are rich in edible oil and protein, and the root system is rich in starch (Bemis et al. 1978a). *Cucurbita foetidissima* produces exceedingly large storage roots. The central tap root alone may reach 50 kg for 3–4 growing

seasons (Bemis et al. 1978b) or even up to 72 kg (Dittmer and Talley 1964). Bemis et al. (1978a) published a picture of one half of the root from a four-year-old plant grown under cultivation having a fresh weight of 45 kg and a length of 2.5 m.

Attempts have been made starting in the 1940s to cultivate some of the wild species of *Cucurbita* for use of their seeds, particularly the xerophytic species that thrive on marginal lands. Big efforts have been invested in *C. foetidissima*, but the attempts at commercial production in the USA, Mexico, Chile, Lebanon, Pakistan, and Australia, have not been successful (Andres 2000).

This plant has been used for centuries by Native American and Mexican tribes for food (after processing), as soap, shampoo, cosmetics, detergent, bleach, and insecticide (Bemis et al. 1978b; DeVeaux and Shultz 1985; Butterwick 2016; Sánchez de la Vega et al. 2019; Mejía-Morales et al. 2021). *Cucurbita foetidissima* is not used as food any more (Gry et al. 2006), but can be used for medicinal purposes (Camazine and Bye 1980; DeVeaux and Shultz 1985; Mejía-Morales et al. 2021).

Alien and invasive status

The Bulgarian population of *C. foetidissima* has persisted for many years without any human intervention and can be considered as naturalised. The exact time of introduction is not known. However, interviews with local residents indicate that the species has been present for at least 15 years. Two possible pathways of introduction may be suspected – escape from confinement (e.g., cultivation for ornamental purposes by local residents or for breeding programs in the Institute for Plant Genetic Resources “Konstantin Malkov” – Sadovo) or transport – contaminant (e.g., import of contaminated seeds of other *Cucurbita* species or other agricultural crops). Additionally, seeds of *C. foetidissima* are available for sale on the Internet. However, the present data and knowledge do not allow us to infer the exact pathway and time of introduction.

The species is supposed to be dispersed mainly by debris and waste associated with human activities. Gourds are used by some locals for decoration and vessels. Other modes of dispersal are probably agricultural machinery and the wind blowing away the seeds or dried fruits (overwintered fruits become very light). Long-distance dispersal by natural means seems to be rather unlikely. However, human-mediated long-distance dispersal is possible and likely.

Once established in a given location, the species can become locally abundant through natural regeneration. It easily forms dense stands mainly on the earth's surface, but also climbs fences, walls and other supports, as well as the near shrubs and small trees, thus competing with the latter for sunlight, water, and nutrients (Figure 3C, D). It also changes the structure

and composition of plant communities. Field observations showed that in the densest stands of the species, annual plant species prevailed with rather low cover.

Local farmers do not report any negative impact on arable land although we observed single plants or small groups of individuals growing in the periphery of the grain crops but also as far as 5 to 20 meters within the plots. However, the presence of the species in the plots means that its seeds can be transported by agricultural machinery, including over longer distances. Unsuccessful attempts have been made to destroy the mats formed by the species in one of its sites in the urban environment by burning. So far, it can be inferred that *C. foetidissima* is locally invasive and may be a potentially invasive species in Bulgaria. Monitoring is needed and, in particular, measures to confine the species to its current localities and prevent long-distance dispersal. It is worth noting that other two representatives of Cucurbitaceae – *Sicyos angulatus* L. and *Echinocystis lobata* (Michx.) Torr. & A. Gray are invasive alien plants in many European countries. The former is an invasive alien species in the Bulgarian flora, intensively spreading along the banks of the Danube River and some of its larger tributaries in Northern Bulgaria (cf. Petrova et al. 2013). The latter is less spread in Bulgaria (cf. Petrova et al. 2013), however, it is an aggressive invader in Central and Eastern Europe (cf. Kostrakiewicz-Gierałt et al. 2022).

Authors' contribution

All authors equally participated in the research conceptualisation, fieldwork and data collection, review and editing of the manuscript; VG – drone images; DI – chromosome number investigation and imaging, data analysis and interpretation, writing original draft; VV – flow cytometry measurement, seed germination, data analysis and interpretation. All authors have given approval for publication.

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