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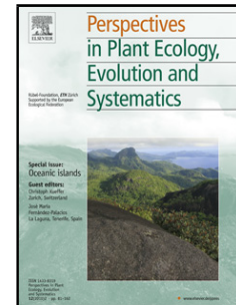
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**Biological flora of Central Europe: *Cyperus esculentus* L.**

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## Highlights

- *Cyperus esculentus* is a tuber geophyte with a high ecological plasticity and variability.
- It reproduces primarily by its underground tubers although abundant seeds are produced
- It is invasive and spreading in many Central European countries.
- It is most abundant on arable land and in ruderal habitats.
- *C. esculentus* remains difficult to control although different management strategies are available

## Abstract

This paper presents information on all aspects of the biology of *Cyperus esculentus* L. (yellow nutsedge) and deals with its taxonomy, morphology, genetic diversity, distribution, habitat requirements, ecology and life cycle, with special emphasis on uses and cultivation, history of introduction, impact and management in Europe. *C. esculentus* is a tuber geophyte and most likely originates from the Mediterranean and Southwest Asia. It is a very variable plant and four wild-type varieties are presently recognized, in addition to a cultivated form. *C. esculentus* reproduces primarily by its underground tubers, although abundant seeds are produced. In temperate climates, tubers usually sprout in late spring and the plant withers at the beginning of the winter. *C. esculentus* is only cultivated in the València region in Spain. Invasion foci emerged across Europe at the beginning of the 1980s and at present, *C. esculentus* is most abundant on arable land and in ruderal habitats, followed by riverine vegetation. In heavily infested regions of Europe, *C. esculentus* causes substantial yield losses in field crops and although different management strategies are available, *C. esculentus* remains difficult to control.

**Keywords:** invasive plant species; management; species biology; spread; yellow nutsedge

## Taxonomy and morphology

### Taxonomy

The worldwide distributed genus *Cyperus* (Monocots, Poales, Cyperaceae Juss. nom. cons.) (Stevens, 2001–2015) was established by Linnaeus (1753: 44). It is the second-largest genus in the Cyperaceae family and the most important genus of this family in the tropics (Larridon et al., 2011a). Several authors reported that it is represented by approximately 600 species (e.g. Tucker et al., 2002), while about 700 species are recorded by The Plant List (2013). However, there may be even more than 900 species (cf. Stevens, 2001–2015; WCSP, 2015). Obviously, *Cyperus* is the type genus of the family, and it is the “core taxon” of the tribe Cypereae (Larridon et al., 2011a).

The species of our interest is crucial in the nomenclature of the genus, as *C. esculentus* was designated as the type species of *Cyperus* by Britton (1907). As a consequence of this designation, *C. esculentus* is the type of subgenus *Cyperus*, as well as of both the autonym section (sect. *Cyperus*) and subsection (subsect. *Cyperus*) (Larridon et al., 2011a). However, *C. esculentus* had been designated later as the type species of subgen. *Chlorocyperus* (Rikli) Schischk. and of sect. *Esculenti* Kük., but these latter names are invalid *ipso facto* under Art. 22.2 of the ‘International Code of Nomenclature for algae, fungi, and plants’ (Melbourne Code) (McNeill et al., 2012), as indicated by Larridon et al. (2011a). For the erroneous inclusion of *C. esculentus* in a not clearly defined “sect. *Bulbosi*” by Chermezon (1922), as well as for a complete synonymy of the subgeneric taxa based on *C. esculentus*, see Larridon et al. (2011a).

Linnaeus (1753: 51) based *C. esculentus* on two polynomials by Royen (1740) and Bauhin (1623), and he reported southern France (Montpellier), Italy and the East (“Habitat Monspelii, inque Italia, Oriente”) as its native range. A type of the name was designated by Tucker (1994): the Fig. 10 of the plate 11 (sect. 8) of Morison (1699), cited by Linnaeus (1753) in the

protologue. However, a valid lectotype has already been designated the precedent year by D.A. Simpson in Jarvis et al. (1993: 41). They selected as a lectotype an illustration cited in the protologue as well, i.e. that in Bauhin (1658: 222), which has therefore priority upon Morison's plate.

The infraspecific taxonomy of *C. esculentus* was firstly studied by Boeckeler (1870) for the American forms and the cultivated *C. esculentus* (var. *sativus* Boeckeler). Later, Clarke (1884) and Britton (1886) distinguished new varieties from North America and India. Ascherson and Graebner (1902–1904) divided the species in a cultivated and a wild race. In his extensive work on Cyperaceae, Kükenthal (1936) reviewed the taxa and proposed further varieties for *C. esculentus*. A detailed account of the previous infraspecific treatments is provided by Schippers et al. (1995), who recognized a cultivated and four wild varieties. However, most of the contemporary authors do not distinguish infraspecific taxa (see section “Morphology”).

The most common synonyms of *C. esculentus* in old European literature are: *C. aureus* Ten. 1824 (nom. illeg.), *C. chrysostachys* Boeckeler 1859, *C. gracilescens* Schult. 1824, *C. gracilis* Link 1820 (nom. illeg.), *C. melanorhizus* Delile 1813, *C. nervosus* Bertol. 1819, *C. officinalis* T.Nees 1830, *C. tenoreanus* Schult. & Schult.f. 1827, and *C. tenorei* C.Presl 1826. Exhaustive lists of synonyms can be found in Schippers et al. (1995) and in WCSP (2015).

The Latin name of the genus derives from the Greek *kýpeiros* (several variants are known), indicating a kind of rush (Castroviejo, 2007). The specific adjective *esculentus* means “edible” in Latin, likely referring to the tubers.



## **Morphology**

### *Habitus and life form*

*C. esculentus* is a perennial herb, producing tubers, rhizomes and stolons (Kükenthal, 1936; Castroviejo, 2007; Fig. 1A) [for the morphoanatomy of the hypogeal organs we follow Rodrigues and Estelita (2009)]. Its life-form is classified as a tuber geophyte (WCSP, 2015). In temperate climates, it usually sprouts in late spring and withers at the beginning of the winter. It may also behave as an annual (DeFilipps, 1980), but this life cycle can rarely be observed, e.g. in frequently disturbed habitats. The plant often produces a few basal buds and, especially in the cultivated form, it can show a caespitose habitus (Hu, 2005). The plant is generally 15–60 cm tall; it is glabrous and light green.

### *Hypogeal organs*

The stolons are slender (about 1 mm in diameter), soft, spongy, flexible when dried (Tucker et al., 2002), and up to 20 cm long (Kukkonen, 2001). They bear few short, narrow scales. Each stolon may terminally produce a single persistent tuber or a new shoot (Schippers et al., 1995; Rodrigues and Estelita, 2009). Numerous fibrous roots spread out from the shoots and the tubers. The stolons have also been interpreted as rhizomes (e.g., Jansen, 1971; Stoller et al., 1972; Castroviejo, 2007; Schippers et al., 1995). In a recent study, Rodrigues and Estelita (2009) recognized both rhizomes and stolons based on morphology, function and life phase. Stolons are considered to be ephemeral organs as they degenerate after the formation of the tuber. Rhizomes are intended as persistent organs with a storage function and are exclusively located in the apical region. Tubers are terminal, not more than 15 mm in diameter in the wild, but up to 25 mm in the cultivated form. They are ovoid, elliptic or subglobose. Young tubers are whitish and reddish, turning to brownish-grayish with age and transversally striate (the cover is called “tomentum” by Kükenthal, 1936; Figs. 1B, 2C). The

inner part of the tuber is white or cream-colored regardless of age. The tubers are odorless and tasteless when dry (Castroviejo, 2007), while dried tubers from the cultivated variety are sweeter and tasteful.

### *Stems and leaves*

Stems are erect, solitary or with few lateral offsprings, (6)15–60(95) cm tall (Castroviejo, 2007) (rarely more) and slightly swollen at the base (Kukkonen, 2001). The stem is trigonous and 0.6–3.4 mm in diameter, glabrous and smooth.

The stem is typically leafless in the upper half, the leaves being mostly basal and usually shorter than the stem. The ligula is lacking and the leaves are spirally arranged and sheathing. Sheaths are yellowish, grayish or reddish-brown, 50–100 mm long and have hyaline, membranous margins (Castroviejo, 2007). Leaves are linear with an acute apex, flattened or slightly keeled, antrorsely scabrid on margins and midvein, bright green, (6)15–55(80) cm long and 0.2–1 cm wide (Kükenthal, 1936; Castroviejo, 2007); the margins are often slightly revolute (Kukkonen, 2001). According to Schippers et al. (1995), the leaves can even reach a length of 70(–120 cm).

### *Inflorescence*

The inflorescence is a lax anthela, simple or compound [for a detailed description see Reutemann et al. (2012)]. Involucral bracts are 3–6 (rarely up to 11) in number, leaflike, sheathless, 5–35 cm long (rarely more) × 0.5–4 mm wide, antrorsely scabrid on the margins, patent and spirally arranged at stem apex, and at least the lowermost much longer than the inflorescence (Schippers et al., 1995; Tucker et al., 2002; Castroviejo, 2007; Fig. 2B).

Flowers are bisexual and borne in spikelets along a rachilla at the axils of distichous scales (i.e., glumes). Spikelets are in turn spirally organized in spikes, which are borne on a

conspicuous rachis, 4–17 mm long (Tucker et al., 2002; Fig. 1C). The primary spike is almost sessile, the others are pedunculated. Principal rays of the anthela are usually 3–10 in number, unequal, up to 12 cm long, trigonous. Spikelets are patent or ascending, linear to ovate, acute, compressed-quadrangular, up to 50 in number, 4.5–55 mm long and 1–3 mm wide, yellowish brown, and elongated after flowering. Rachilla is persistent, with hyaline wings, 0.3–0.5 mm wide (Tucker et al., 2002; Fig. 1E), and with internodes about 1–2 mm long. At the base of each spikelet, a glume-like bract and a glume-like prophyll occur; the latter is two-veined, slightly shorter and with a swollen base (Kukkonen, 2001). Glumes are laxely imbricate, 1.5–4.5 mm long and 1–2.4 mm wide, ovate or elliptic, concave, persistent, with obtuse, truncate or sometimes mucronulate apex (Kükenthal, 1936; Castroviejo, 2007). They are laterally yellowish to brown, and medially brownish, reddish, or greenish (Tucker et al., 2002), with 5–9 longitudinal and prominent veins (Kukkonen, 2001).

The stamens are 3 in number, basal, exert at the anthesis, and linear. Anthers are 1–2.1 mm long (Tucker et al., 2002); filaments are long about twice the anthers. The connective is prolonged in a short reddish appendix (Kükenthal, 1936). The ovary is 1–1.2 mm long and 0.3–0.6 mm wide, and pale green. The style is linear, 0.6–2.2 mm long, and bears 3 exert stigmas, each one 1.2–4.5 mm long (Schippers et al., 1995).

### *Fruits*

The fruits are 3-sided or angular achenes, with dorsal side roundish and ventral side reflex, 2-sides flat (Bojnanský and Fargašová, 2007; Fig. 1D), ellipsoid or narrowly obovoid, with apex obtuse, and smooth. They are 1.1–1.6 mm long and 0.3–0.8 mm wide (Tucker et al., 2002). The surface is granular, lustrous (Bojnanský and Fargašová, 2007), bright dark brown or reddish, grayish or blackish when ripe (Castroviejo, 2007). The achenes are sessile and about half as long as the glume (DeFilipps, 1980). For a detailed description of the

micromorphological features of the fruit, see Hefler and Longhi-Wagner (2008).

### *Anatomy*

*C. esculentus* has a C<sub>4</sub> photosynthetic pathway (Li et al., 1999), with stems and leaves which show Kranz (chlorocyperoid) anatomy (Tucker et al., 2002). A detailed description of the anatomy can be found in Wills (1987) and Hather (1988).

### *Pollen*

All Cyperaceae share an unusual type of simultaneous microsporogenesis, which leads to the formation of pseudomonads or kryptotetrads (Nagels et al., 2009). Campos-Trujillo et al. (2015) describe the pollen grain of *C. esculentus* as medium sized, micro-echinate, pantoporate, irregular, and with sunken apertures.

### *Variability*

*C. esculentus* is a very variable plant, as testified by the numerous varieties described in time (Kükenthal, 1936). New morphs have been recently noted by Tayyar et al. (2003). However, according to Schippers et al. (1995), excluding the cultivated form, only four wild varieties can be recognized by morphometrics: var. *esculentus*, var. *heermannii* (Buckley) Britton, var. *leptostachyus* Boeckeler, and var. *macrostachyus* Boeckeler.

Both var. *leptostachyus* and var. *macrostachyus* have divaricate spikelets, which form a 75–90° angle with rachis and floral scales, widest at midlength. In addition, var. *leptostachyus* is characterized by spikelets 15–20 mm long and 2 mm wide, and by floral pieces of smaller dimensions. On the contrary, var. *macrostachyus* has larger flowers, with spikelets 10–40 × 2.5–3 mm (for further details see Schippers et al. [1995]). Var. *heermannii* is more distinct, especially by its peculiar ascending-erect spikelets, which form an angle of less than 40° with

the rachis (Tucker et al., 2002). These three varieties are traditionally regarded as native to the New World: var. *leptostachyus* is reported throughout America, var. *macrostachyus* dominates the central part of the continent, and var. *heermannii* is rare and restricted to the northwestern United States. On the contrary, var. *esculentus* is widespread in the Old World (Schippers et al., 1995). This latter variety is a somewhat intermediate morph with short and often ovate spikelets (Kükenthal, 1936). Finally, var. *sativus* is the name reserved to the cultivars selected by humans, morphologically very similar to the infraspecific wild varieties of the Old World, but with larger and sweeter tubers, and longer rays of the anthela (Tucker and Simpson, 2010), but rarely flowering.

However, the diagnostic features of all the varieties of *C. esculentus* are rather weak and overlapping, and recent molecular studies have not supported their taxonomic recognition (De Castro et al., 2015; see section “Genetic diversity”). Therefore, several authors do not accept them (e.g., TROPICOS, 2015; WCSP, 2015).

### **Genetic diversity**

Different chromosome numbers are reported for *C. esculentus* ( $2n=18$ , 108, 208) ( $2n=18$  in Suzuka, 1953;  $2n=108$  in Hicks, 1929; Heiser and Whitaker, 1948;  $2n=208$  Sharma, 1970; Sanyal, 1972), underlining the important role of polyploidy in its evolution (Heiser and Whitaker, 1948; Horak and Holt, 1986). There are no definitive reports of the exact chromosome number of *C. esculentus* because of the few samples analysed and the sometimes inaccurate and contradictory information reported in the literature [e.g., in Sanyal (1972)] it is reported  $2n=18$  for Tanaka (1937), but in the latter paper *C. esculentus* is not even analysed]. According to Sanyal (1972), chromosomes have a length of 1.3–0.6 $\mu$ . To date, no chromosome counts are reported for European or African accessions according to available literature. *C. esculentus* is an obligate outcrosser (Mulligan and Junkins, 1976; Horak and

Holt, 1986) and hybrids are not known in nature (Mulligan and Junkins, 1976), although Tayyar et al. (2003) recognized possible hybridization with *Cyperus rotundus* (purple nutsedge) on the basis of isoenzyme profiles, as also indicated by Tehranchian et al. (2015).

Overall, the majority of the literature on genetic diversity is quite dated. As a consequence, statistical and/or genetic data analyses are usually not exhaustive and sampling has often been geographically restricted. A summary of the genetic diversity studies available in literature is shown in Table 1. Recently, a study has been performed on the phylogeography of *C. esculentus* that employed sequencing of nuclear and chloroplast DNA markers for its whole range (De Castro et al., 2015). The authors demonstrated a considerable genetic variation of the nuclear vs. chloroplast DNA markers (27 ribotypes vs. 6 haplotypes, respectively). Clear geographic segregation is observed within the nuclear markers (ribotypes), where a high genetic variability is observed in the New World accessions only (23 vs. 5 belonging to Old World specimens), confirming the results of some previous genetic studies (Table 1). Molecular dating and biogeographic analyses indicate that the phylogeographic origin of *C. esculentus* is Miocenic to Pliocenic (5.1 Mya; 95% HPD=2.5–10.2) and took place in subtropical or tropical African regions. From molecular phylogenetic analyses (Larridon et al., 2011b, 2013; Reid et al., 2014), it has been shown that *C. esculentus* belongs to the C<sub>4</sub> photosynthetic pathways lineage. According to Larridon et al. (2013), which implement both chloroplast (trnH-psbA and rpl32-trnL intergenic spacers) and nuclear markers [external transcribed spacer 1 (ETS1f)], *C. esculentus* from the Old World falls within a clade which contains *Cyperus* species belonging to several sections (e.g., *Bulbosi* C.B. Clarke in Hooker, *Compressi* Nees, *Papyrus* (Willd.) Thouars, *Rotundi* C.B. Clarke and *Strigosi* Kük.). This topology is not congruent with the phylogenetic position shown in Reid et al. (2014) and it may be probably caused by the different geographical accessions of *C. esculentus* (New World) and moreover, only nuclear marker were employed [internal transcribed spacers

(ITS)].

A first step towards a better understanding of the genetic structure of *C. esculentus* using codominant markers was made by Arias et al. (2011), who developed nrSSR library from *C. rotundus* populations and tested only on New World *C. esculentus* accessions.

## **Distribution and habitat requirements**

### **Geographical distribution**

#### *Worldwide*

*C. esculentus* most likely originates from the Mediterranean and Southwest Asia. At present, it is widely distributed in tropical, subtropical, and temperate regions around the world (Holm et al., 1991; WCSP, 2015). In North America, it can be found throughout the United States except in Montana and Wyoming (USDA, 2016). In Canada, it occurs in British Columbia, Nova Scotia, New Brunswick, southern Quebec and southern Ontario (Canadensys, 2015). *C. esculentus* is widespread in Central America and the Caribbean (Villaseñor and Espinosa-Garcia, 2004; Acevedo-Rodríguez and Strong, 2012). In South America, *C. esculentus* is mainly distributed in the lowlands (pampas) of Argentina, Brazil, Uruguay and Paraguay (Eyherabide et al., 2001; Zuloaga et al., 2008). It occurs only sporadically, mostly in coastal areas of eastern Australia in the states of New South Wales, Victoria and Queensland (Commonwealth of Australia, 2015) and locally in New Zealand (Healy and Edgar, 1980). *C. esculentus* grows throughout Africa (African Plants Database, 2015) and is widespread in South and West Tropical Africa as well as Southern Africa at elevations < 2000 m (e.g., Germishuizen and Meyer, 2003; Phiri, 2005). *C. esculentus* can be found from East Asia (e.g., China, Jiang et al., 2011; Japan, Shimizu, 2003), India (Punjab to the Nilgiri hills, Singh et al., 1996) to Western Asia and the Near East (e.g., Turkey, Arslan et al., 2015; Georgia, Kikodze et al., 2009).

## Europe

Currently, *C. esculentus* is most widespread in Western and Southern Europe as well as in parts of Central Europe (Fig. 3). The species is almost absent from the British Isles, Northern and Eastern Europe except for a few and casual occurrences (e.g., Gederaas et al., 2012; Tyler et al., 2015; Fig. 3). In Central Europe, *C. esculentus* is confined to the lowlands and to hilly regions with favourable mild climates. In Germany, infested areas are in Lower Saxony (Oldenburg region) and Baden-Württemberg (Rhine valley), and in Austria, Styria, Carinthia and locally Lower and Upper Austria are infested. In Switzerland, both the Swiss Mittelland and southern Ticino are invaded by *C. esculentus* (Follak et al., 2015; Info Flora, 2016). In Hungary, *C. esculentus* occurs in the Somogy county (south of Lake Balaton), where it has already infested more than 10,000 ha of crop fields. Smaller centres of infestation can be found throughout the country according to Novak et al. (2009). Scattered occurrences of *C. esculentus* have been reported from Poland and Slovenia (Dajdok et al., 2007; Anderle and Leban, 2011), while there are no reports from Slovakia and the Czech Republic (Medvecká et al., 2012; Pyšek et al., 2012).

In Western Europe, in the Netherlands, *C. esculentus* can be found throughout the country with large infestations in the provinces of Gelderland and North Brabant (Q-Bank, 2015). In Belgium, it occurs in large parts of Flanders, especially in the Campine region and between Bruges and Ghent, while it is nearly absent from Wallonia in the southern part of the country (Verloove, 2006a). In France, there are invasion hotspots in the departments Pyrénées-Atlantiques and Landes and in the Sologne region according to Bernard (1996) and Dodet (2006). In Northern Italy, *C. esculentus* can be locally found in several provinces such as Brescia and Bergamo (Zanotti, 1988) and Piacenza (e.g., along the river Po; Bracchi and Romani, 2010). It is common along the Tyrrhenian coast and in lowlands regions in Southern



Italy (Pignatti, 1982; Conti et al., 2005). Likewise, *C. esculentus* is mostly confined to coastal and lowland regions of the Iberian Peninsula (Anthos, 2015; Flora-On, 2015).

In southeastern Europe, *C. esculentus* has a scattered distribution. It is present in Croatia (Nikolić, 2015), while in Romania, *C. esculentus* has been mentioned from a few localities, but its presence has not been confirmed in the last five decades (Anastasiu and Negrean, 2009). Similarly, it is claimed to occur in Albania (Vangjeli, 2015) but there seem to be no records since the 1920s (Z. Barina, pers. comm.). *C. esculentus* occurs locally in Greece (Vladimirov et al., 2007). However, it does not occur in Cyprus (Hand et al., 2011) and Bulgaria (Assyov et al., 2012).

### **Habitat**

*C. esculentus* is a species of humid tropical to temperate climates around the world (Holm et al., 1991). Similarly, in Europe, the species grows optimally in climates that are characterized by the absence of strong frost, i.e. sub-mediterranean and western European temperate climates (ter Borg et al., 1998). In Mediterranean southern Europe, drought during summer severely constrains *C. esculentus* growth and limits its occurrence to wet sites. Low extreme temperatures in winter have been identified as an important limiting factor for *C. esculentus*, as its tubers are susceptible to harsh frost (Groenendael and Habekotté, 1988). *C. esculentus* colonizes a wide range of soil types, but grows best on mesic to wet soils. It is a light demanding species, and it thrives best on nutrient-rich sites (Holm et al., 1991; see section “Response to abiotic factors”). In Europe, *C. esculentus* occurs predominately in open and disturbed habitats while it is most frequent in crop fields (Novak et al., 2009; Follak et al., 2015; Fig. 4). In Switzerland, *C. esculentus* is common in areas where agronomic crops and vegetable production are mingled (Bohren et al., 2014). In less invaded regions, *C. esculentus* is largely restricted to ruderal habitats such as, roadsides, construction and landfill

sites as well as nursery gardens (ter Borg et al., 1998; Follak et al., 2015). Moreover, it occurs regularly in semi-natural habitats like pioneer riverine vegetation in France (e.g., Loire, Allier) (Felzines and Loiseau, 2005) and Italy (e.g., Po, Tiber) (Lastrucci et al., 2012), and wetland communities (Dajdok et al., 2007).

### **Plant communities**

Since *C. esculentus* grows optimally in disturbed, open habitats, many of the most commonly associated species recorded in phytosociological relevés within its central and western European range are diagnostic species of thermophilic segetal vegetation of the phytosociological class Stellarietea, i.e. summer annuals such as *Chenopodium album*, *Digitaria sanguinalis*, *Echinochloa crus-galli*, *Setaria faberi* and *S. pumila* (Fragner, 2010). Populations of *C. esculentus* in disturbed wetland habitats such as documented by Dajdok et al. (2007) for southwestern Poland are accompanied by annual pioneer species of the classes Isoeto-Nanojuncetea (e.g., *Cyperus fuscus*, *Plantago intermedia*) and Bidentetea (e.g., *Persicaria hydropiper*), by species of reedbeds of the class Phragmitetea (e.g., *Eleocharis palustris*, *Galium palustre*), and by species of mesic grasslands of the Molinio-Arrhenatheretea (e.g., *Agrostis stolonifera*). Along the Loire, *C. esculentus* occurs regularly, but in low abundance, in communities dominated by annual species of eutrophic, wet riverine habitats of the Bidentetea (e.g., *Bidens frondosa*, *Leersia oryzoides*, *Persicaria lapathifolia*, *Xanthium saccharatum* s.l.) (Felzines and Loiseau, 2005). Such occurrences have been described as a distinct plant community (Cyperetum esculenti) (Wisskirchen, 1995).

### **Response to abiotic factors**

#### *Temperature*

Sprouting of tubers and growth of *C. esculentus* are temperature dependent. In experiments

under controlled conditions, Holt and Orcutt (1996) reported that the lower temperature threshold (LTT) for tuber sprouting was 5.8°C while the upper temperature threshold was 42.7°C using tubers from locations in California. The LTT value is lower than the LTT of 12°C reported by Stoller and Wax (1973) in a laboratory experiment. Similarly, Wilen et al. (1996b) estimated a base temperature for tuber sprouting of 12°C in a field experiment (arid southwestern United States) using the same genotype from California as Holt and Orcutt (1996). Li et al. (2000) studied how temperature affects sprouting rate of Japanese *C. esculentus* populations. The percentage of sprouting increased with increasing temperature within the range of 12 to 38°C, while no sprouting occurred at 10°C and a few tubers sprouted at 42°C. Differences in base temperatures can be attributed to the experimental design and factors like e.g. tuber age and storage conditions as well as genetic variation between geographical populations (Holt, 1994).

Tuber mortality was 100% for *C. esculentus* when using diurnal oscillations in soil temperature with >50°C maxima and a minimum of 26°C (Chase et al., 1999). *C. esculentus* grows rapidly under high temperature conditions. Sprouting rate of tubers (half-final sprouting, i.e. the time required for half the final sprouting to be achieved) and sprout size (shoot height and shoot dry weight) increased with increasing temperature up to 35°C according to Li et al. (2000).

### *Frost*

*C. esculentus* is sensitive to freezing and tubers are the only vegetative part of the *C. esculentus* plant that overwinters. It can survive in temperate climates, as tubers can withstand cold temperatures but they are susceptible to harsh frost as shown by several studies. In a laboratory experiment, exposures to -6.5°C for 4 h killed 50% of *C. esculentus* tubers (Stoller, 1973). Tubers placed on the soil surface over winter and exposed to temperatures

lower than  $-15^{\circ}\text{C}$  still had germination rates up to 32% (Bell et al., 1962). Nearly 100% of tubers collected in 2013 on the soil surface after frost period of 10 days ( $-10^{\circ}\text{C}$ ) germinated in the glasshouse (C. Bohren, unpubl. data). In a comprehensive study, Groenendael and Habekotté (1988) reported that tubers from locations in the Netherlands were able to withstand low temperatures for a longer period of time. For example, at  $-2^{\circ}\text{C}$  for 32 days almost 43% of large tubers (0.174 g mean weight) emerged while at  $-4^{\circ}\text{C}$  for 8 days 62% of the tubers survived. Frost hardiness depended on tuber size and was lower for small tubers (0.048 g mean weight). These studies reflect that there is variability between ecotypes in tuber cold hardiness.

Survival of tubers is greatest in deeper soil layers. Tubers buried at a depth of 2.5 and 5 cm in Illinois were more susceptible to winterkill than tubers which were buried deeper, most likely due to the lower soil temperature at these more shallow levels during cold periods (Stoller and Wax, 1973).

### *Shade*

*C. esculentus* is dependent on direct sunlight for optimum growth and tuber production. It requires high levels of irradiation and is sensitive to shading (Groenendael and Habekotté, 1988). Santos et al. (1997) demonstrated that increasing artificial shading (20–80% of incident sunlight) resulted in reduced height of *C. esculentus*, shoot and tuber dry weight matter and number of tubers compared to the control (0% shading) in a greenhouse experiment. However, it tolerated moderate shade as the parameters decreased only slightly until light intensity was reduced by more than 20% shade (i.e., 80% full sunlight) and a few tubers were produced even under heavy shade (80%). Lotz et al. (1991) showed that the number of tubers per plant was greatly reduced at an intermediate (43% of the unscreened control) and low irradiance (18%) level by almost 49% and 96%, respectively. The effects of

shade were similar in field studies in California (Keeley and Thullen 1978) and in the southern part of the Netherlands (Groenendael and Habekotté 1988).

Li et al. (2001a) showed under controlled conditions using different light environments that light quantity and quality (i.e., photosynthetically active radiation, red/far red ratio) had an influence on growth and reproduction and morphological traits of *C. esculentus*. For example, the number of tubers was considerably reduced in shaded plants, but was influenced only by light quantity, but not by light quality. However, both reduced light quantity and quality decreased the proportion of flowering ramets and the fraction of biomass allocated to flowers and fruits.

#### *Soil moisture*

In Central Europe, *C. esculentus* is highly adaptable as it occurs under periodically wet conditions, e.g. along ditches, the margins of rivers, streams and lakes (e.g., Schmitt and Sahli, 1992), while in cultivated fields it often grows under well-drained or drier conditions (Oesau, 1995). However, it grows and propagates best under high soil moisture conditions. Wilen et al. (1996a) demonstrated in the southwestern United States (pots, buried in field sites) that total shoot production decreased and emergence was delayed when tubers were grown in soil-moisture limited soil rather than under wet conditions. Accordingly, Li et al. (2001b) showed that *C. esculentus* shoot number and dry weight as well as tuber number and dry weight were higher in treatments irrigated to saturation compared with those maintained at field capacity (FC) in pot trials. Growth and reproductive potential of individual *C. esculentus* plants were examined under three soil moisture regimes (soil water potentials of –20, –50, and –80 kPa; representing soil moisture conditions similar to dry bulb onion, sugar beet, and wheat production systems) by Ransom et al. (2009) in Oregon in a field experiment. When plots were irrigated at a soil water potential of –20 kPa, one individual plant produced

up to 3,000 shoots and 20,000 tubers depending on the year, which was much greater than the two other irrigation treatments.

### *Soils*

In North America, *C. esculentus* occurs in a wide range of soil types: sand, sandy-loam, sandy-gravel, loam, clay-loam and clay (Mulligan and Junkins, 1976). Likewise *C. esculentus* colonizes many soil types in Central Europe (e.g., Schroeder and Wolken, 1989; Dancza et al., 2004.). The type of substrate influences tuber production. Tumbleson and Kommedahl (1961) reported that a single tuber planted in peat and silt loam produced 1,017 and 1,202 tubers, respectively, compared to 251 tubers in a sandy soil 16 weeks after planting in a pot experiment. At the same time, tubers produced substantially more shoots in peat (129) and silt loam (146) than in sand (31). Bell et al. (1962) found that tuber sprouting was greatly reduced when soil was compacted. After four months sprouting was 96, 93, 67, and 47%, respectively, for the soils with bulk densities of 0.97, 1.17, 1.36, and 1.68 g/cm<sup>3</sup>.

Growth is better on nutrient-rich soil. Garg et al. (1967) showed a positive response to increased availability of nutrients in controlled environmental chambers: nitrogen promoted vegetative growth of *C. esculentus* rather than reproductive growth, leading to increased shoot production in contrast to tuber formation. Similarly, Ransom et al. (2009) demonstrated in a field study that the higher rate of nitrogen application increased (300 kg N/ha vs. 100 kg N/ha) shoot number (1,003 vs. 732 shoots/plot), but there was no effect on shoot biomass, tuber number and total tuber weight per plot, respectively. In contrast, Li et al. (2004) reported that increasing nitrogen increased both shoot and tuber production in a glasshouse experiment. *C. esculentus* is considered to be non-mycorrhizal according Muthukumar et al. (2004).

### *Indicator values*

No Ellenberg indicator values for *C. esculentus* are available for Great Britain and Central Europe (Ellenberg et al., 1992; Hill et al., 1999; BOKU, 2015). However, Denk and Berg (2014) established a temperature indicator value of 8 (grows best under high temperatures conditions) for *C. esculentus* according to the approach of Ellenberg et al. (1992). In Switzerland, values are given of 3 for soil pH (grows best under moderately acid to neutral conditions), 4w<sup>+</sup> for moisture (indicating a preference for periodically wet soils), 6 for nitrogen level (for intermediate soil fertility), 4 for light and 5 for temperature (grows best under high light and temperature conditions) and 2 for continentality (suboceanic climate with mild winters) (Landolt, 2010).

### *Atmospheric carbon dioxide*

The response of *C. esculentus* to projected increases in atmospheric carbon dioxide (CO<sub>2</sub>) was tested by Rogers et al. (2008). Plants were exposed to ambient (375 µmol/mol) or elevated CO<sub>2</sub> (ambient + 200 µmol/mol) for 71 d in open top chambers. Total dry weight (above- and belowground) increased at elevated CO<sub>2</sub> by 10.7%, while the response was larger for belowground structures (+ 15.1%). Photosynthetic rate did not differ significantly among CO<sub>2</sub> treatments while trends for decreased transpiration and stomatal conductance and increased water use efficiency were noted for *C. esculentus* when grown under CO<sub>2</sub> enrichment. Similar to Rogers et al. (2008), Marble et al. (2015) found that *C. esculentus* shoot, root, and tuber dry weight and tuber counts were significantly greater in treatments under CO<sub>2</sub> enrichment of an additional 200 µmol/mol vs. ambient CO<sub>2</sub> concentrations.

### *Air pollution*

*C. esculentus* exhibits a substantial sensitivity to ambient O<sub>3</sub> according to Grantz and Shrestha (2006) and Grantz et al. (2010). In the latter study, the authors showed that aboveground biomass (stem plus leaves) did not respond to increasing O<sub>3</sub> exposure (60 nL/L and 115 nL/L O<sub>3</sub>; 12 h daylight mean O<sub>3</sub> concentration) while belowground biomass declined by 34% at 115 nL/L O<sub>3</sub>. Moreover, with increasing O<sub>3</sub> exposure, chlorophyll content, specific leaf weight, and carbon assimilation were reduced, while intercellular CO<sub>2</sub> concentration increased, reducing water use efficacy (Grantz and Shrestha, 2006; Grantz et al., 2010).

### **Abundance**

In regions heavily invaded in Central Europe, *C. esculentus* frequently builds up dense and large populations, which often extend continuously over many hectares (Novak et al., 2009; Fragner, 2010; Follak et al., 2015), by vegetative propagation via stolons and tubers in agricultural landscapes. In such populations, *C. esculentus* often is the most abundant plant species with high cover values, and few species are able to co-occur with *C. esculentus*. For instance, in 11 phytosociological relevés from crop fields in Austria (southern Styria), *C. esculentus* has cover values >50% in all cases and total accompanying species number per relevé was only one to five species (Fragner, 2010). Populations in other habitats than crop fields (e.g., riverine pioneer vegetation) are smaller in extent and often less dense (Felzines and Loiseau, 2005), although populations of *C. esculentus* with high cover values (>50%) were described along the banks or in the external parts of some islets of the river Tiber by Lastrucci et al. (2012).

### **Life cycle and biology**

#### **Phenology**

The seasonal development of *C. esculentus* has been described in different European



countries, namely in the Netherlands (ter Borg et al., 1998), Austria (Kassl 1992), France (Jauzein 1996) and Spain (Costa 1985). The following scheme can be briefly outlined: in April (northwest Spain) and early May (Austria), tubers start to sprout when soil temperatures have reached approximately 10°C. Axillary buds of the tubers generate shallowly buried stolons, which grow upward and end in swollen tips. These tips give rise to a compact set of leaves. After a few weeks, stolons sprout from the base of the swollen stem stem (also called the basal bulb) and radiate horizontally belowground. Initially these lateral stolons give rise to new aerial shoots which in their turn produce further aerial shoots (Fig. 2A). Stolons also grow downward and form a tuber at their extremity. The result is a dense network of stolons with numerous tubers (Fig. 1A; cf. Rodrigues and Estelita, 2009). When a photoperiod of 12 to 14 hours is reached, inflorescences appear. Thus, under Central European conditions flowering starts end of June and seeds ripen in the middle of September. In late summer, stolons form final tubers. In autumn, shoots die off and later (November) frost kills most of the plant except the tubers. The newly produced tubers remain dormant over winter in soil until spring. Dormancy is broken again by increasing soil temperatures in spring.

## **Reproduction**

Seed set of *C. esculentus* is very variable throughout its range and at many sites seeds are not even produced. Moreover, the amount of seed set can vary from year to year, ranging from very high to extremely low (Mulligan and Junkins, 1976). In North America, several studies have shown that on average nearly 10% of the infestations produce seed. However, if seeds are produced they can be quite numerous. Justice and Whitehead (1946) found that 25 inflorescences of *C. esculentus* from a population in Maine yielded 50,260 seeds with an average germination of 75.6%, the equivalent of 1,521 potential seedlings per inflorescence. According to Lapham (1985) in Zimbabwe up to 100 million seeds can be produced annually

per hectare. Even at an assumed low germination rate of 1–2% which corresponds to 1–2 million seedlings per year and hectare. In Central Europe, *C. esculentus* may also produce abundant seeds (Gieske et al., 1992; Schmitt, 1995; Hoffmann et al., 2006). Schmitt (1995) showed a germination rate of seeds from different Swiss populations ranging from 5 to 35% in a laboratory test. In a recent experiment, a germination rate of 70% has been reported (Keller et al., 2015). However, at many sites no seedlings were found in Europe and elsewhere (Mulligan and Junkins, 1976; Schmitt, 1995). Even in experimental settings seedlings appear to be very tender and grow very slowly (Rotteveel, 1993; Keller et al., 2015).

Larssen (1960) and Bell et al. (1962) reported that seeds of *C. esculentus* become viable as soon as 2–3 weeks after the onset of flowering. As a rule, cool and rainy weather seems to favour vegetative reproduction, while warm, dry weather conditions enhance sexual reproduction. It has been suggested that seeds would be a more important factor in the spread of *C. esculentus* if they could overwinter under dry and warm conditions (Bellue, 1946). There is general agreement, however, that seeds are not considered important for the propagation of *C. esculentus* (Holm et al., 1991).

Vegetative reproduction undoubtedly prevails in *C. esculentus* and large infestations usually are in fact large clones which have been created by vegetative reproduction of one founder individual (see section “Morphology”). It was shown in a pot trial (30 L volume/pot, n =15) without shade, irrigation and soil disturbance, that one tuber produced on average 746 tubers in one season in Switzerland (Bohren et al., 2015a). In Minnesota, one tuber has even given rise to 1,900 shoots and 6,900 new tubers (Tumbleson and Kommedahl, 1961; Bell et al., 1962) and to 1,700–3,000 shoots and 19,000–20,000 tubers within four months in irrigated fields in Oregon (Ransom et al., 2009). In temperate latitudes, tuber formation is triggered by shortening day length in late summer and accelerates while aboveground growth

rates decline (Jordan-Molero and Stoller, 1978).

### **Response to competition**

The production of ramets and tubers is density-dependent and is likely to be reduced when growing in mixtures with other species. Interspecific competition was studied between *C. esculentus* and different crops (e.g., Keeley and Thullen, 1978; Lotz et al., 1991). Competitive crops like hemp (*Cannabis sativa*) reduced tuber and shoot production of *C. esculentus* by 99 to 100%, but tuber production with winter barley (*Hordeum vulgare*) or winter rye (*Secale cereale*) was reduced only by 40% in field experiments in the Netherlands (Lotz et al., 1991). Collins et al. (2007) evaluated the competitiveness of three cover crops, namely cowpea (*Vigna unguiculata*), sunn hemp (*Crotalaria juncea*), and velvetbean (*Mucuna pruriens*), when grown in combination with *C. esculentus* in greenhouse replacement-series experiments. The authors reported that there was no significant difference in the number of tubers produced per plant and tuber dry weight per plant as *C. esculentus* proportion changed.

Morales-Payan et al. (2003) determined the extent of full, above- and belowground interference of *C. esculentus* with tomato (*Lycopersicon esculentum*) in a greenhouse study. Tuber number decreased 50% when *C. esculentus* competed with tomato either above- or belowground. *C. esculentus* under full interference produced only 20% fewer tubers. The reduction of tuber weight was 50% when *C. esculentus* plants interfered with tomato either fully or aboveground (decrease of 25 % under subterranean interference).

### **Spatial distribution of plants within populations**

In crop fields, *C. esculentus* is not uniformly distributed. The species occurs in clustered patches and size and shape of these patches varies within the field. Spatial distribution is affected by two factors: growth from the mother plant and cultivation practices. *C. esculentus*

populations expand radially by vegetative reproduction and within close proximity to the initial mother plant (Schippers et al., 1993; Webster et al., 2008) and thus, clearly defined patches are produced. Field equipment and cultivation practices distribute tubers vertically and horizontally, especially in the direction of tillage (Schippers et al., 1993).

### **Herbivores and pathogens**

Many organisms have been documented as causing disease or feeding on *C. esculentus* with a focus on the United States (Phatak et al., 1987).

#### *Insecta*

*C. esculentus* is attacked by many phytophagous insects (Table 2). The insect fauna reported to feed on *C. esculentus* is dominated by hemiptera and coleoptera followed by lepidoptera and diptera. However, data on the number of insects associated with *C. esculentus* in Europe is limited. For example, in Spain, two moths of the family Tortricidae, *Bactra lancealana* and *B. furfurana*, have been found on *C. esculentus* (Albajes and Garcia-Baudin, 1980). The larvae tunnel in the stems and their galleries extend downwards to the base. Furthermore, *C. esculentus* acts as a host for known agricultural pests like aphids (*Sitobion avenae* and *Rhopalosiphum* spp.) or flies of the Chloropidae family, which are commonly found throughout Europe (e.g., Leather et al., 1989).

#### *Fungi*

The list of fungi genera associated with *C. esculentus* includes *Ascochyta*, *Cercospora*, *Cintractia*, *Claviceps*, *Dactylaria*, *Fusarium*, *Puccinia* and *Sclerotinia* (Table 2). For example, Blaney and Van Dyke (1987) isolated several fungi from *C. esculentus* in North Carolina while the only ones consistently associated with disease symptoms were *Puccinia*

*canaliculata* and *Cercospora caricis*. The survey showed that *C. esculentus* was relatively free of fungal diseases early in the growing season while the disease symptom associated with these two fungi were observed in mid-to-late summer. Most fungi pathogens associated with *C. esculentus* have been found outside of Europe. A tuber rot of cultivated *C. esculentus* caused by *Rosellinia necatrix* was described in 1998 in the Valencia province in Spain and rapidly became an important disease (García-Jiménez et al., 1998). Several control practices have been adopted to control the disease (e.g., hot-water treatment of tubers, soil solarization) (García-Jiménez et al., 2004). A new fungal disease in this area is the leaf apical necrosis. It is caused by an ascomycete fungus, which was recently identified as *Alfaria cyperi-esculenti* (Crous et al., 2014).

#### *Nematoda*

*C. esculentus* was classified as a host for 11 species of nematodes (Nemabase, 2015) (Table 2). These include root-knot nematodes (*Meloidogyne* spp.), the cyst nematode *Heterodera cyperi*, the sting nematode *Belonolaimus longicaudatus* and others like *Hemicycliophora hesperis*, *Helicotylenchus dihystra*, *Rotylenchulus reniformis* and *Tylenchorhynchus acutus* (McSorley and Parrado, 1983; Bekal and Becker, 2000; Trojan et al., 2006; Lawrence et al., 2008). Nearly all of them have been studied in the United States except for *H. cyperi*, which has been detected on *C. esculentus* in Spain (Romero and Lopez-Llorca, 1996). It was classified as a poor host for *Pratylenchus penetrans* and *Longidorus americanum* (Fraedrich and Cram, 2003; Bélair et al., 2007), respectively and as a non-host (immune) for *Heterodera zea* (Ringer et al., 1987) and *Cactodera galinsogae* (Tovar-Soto et al., 2008). However, there are contradictory data on host status (i.e., susceptibility) assignment in the literature (Table 2), which can be attributed to a genetic variation between *C. esculentus* plants tested and different experimental conditions.

### *Viruses and bacteria*

A limited number of viruses infecting *C. esculentus* has been reported worldwide (Table 2). In Hungary, the Brome streak mosaic virus (BrSMV), family Potyviridae, genus Tritimovirus has been described by Takács et al. (2008). *C. esculentus* is an artificial host of *Xylella fastidiosa*, the bacterium that causes Pierce's disease of grape (Table 2). In greenhouse tests, plants were inoculated with the STL strain of *X. fastidiosa*, a grape strain from California. *Xylella fastidiosa* was recovered in *C. esculentus* in more than 40% of inoculation attempts. It supported bacterial populations in excess of 6.0 CFU/g of plant tissue (Wistrom and Purcell, 2005).

### **Physiological data**

*C. esculentus* with its C<sub>4</sub> photosynthetic pathway (Li et al., 1999) allows a higher net photosynthesis under conditions of higher temperatures, moisture stress, and high irradiance (Ehleringer et al., 1997). Photoperiod is one of the main factors that influence growth, tuber production, and flowering (Jansen, 1971). Long photoperiods (>14 h) promote vegetative growth (shoot development, root proliferation) in *C. esculentus*. The rate of differentiation of indeterminate stolon tips to new shoots is highest at 16 h, while short photoperiods (8 to 12 h) stimulate tuber formation. Jansen (1971) reported that a photoperiod of 12 to 14 h was required to induce flowering. Santos et al. (1997) showed in a greenhouse study that the average light compensation point under full sunlight for *C. esculentus* was 84.2  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , which indicated that it was more tolerant to low light intensities than its congener *C. rotundus* (see section "Response to abiotic factors").

### **Allelopathy**

Numerous literature reports indicate that the interference of *C. esculentus* with neighbouring plants includes biochemical interactions (allelopathy) or other phytotoxic effects of secondary metabolites released by the plant (allelochemicals). Evidence that *C. esculentus* may be allelopathic is primarily provided by studying extracts of tubers, roots or foliage inhibiting various crop and weed species including *C. esculentus* itself (e.g., Sánchez Tamés et al., 1973; Buzsáki et al., 2008). *C. esculentus* produces active metabolites in quantities that harm other plants and reports of harmful effects of plant soil residues and root exudates (e.g., Drost and Doll, 1980; Reinhardt and Bezuidenhout, 2001) indicate that these metabolites may actually function as allelochemicals in plant interactions. Moreover, *C. esculentus* metabolites were shown to impair legume-rhizobia symbiosis and ectomycorrhizal growth (Mallik and Tesfai, 1988; Reinhardt and Bezuidenhout, 2001).

Inhibition by *C. esculentus* extracts showed a dose-dependent promotion or inhibition of germination and growth of test species (Sánchez Tamés et al., 1973; Buzsáki et al., 2008) and varied with extracted growth stage and plant organ of *C. esculentus*. For instance, foliage extracts of immature plants proved more toxic than extracts of mature plants or tubers (Reinhardt and Bezuidenhout, 2001). Also, root extracts proved more inhibitory than foliage extracts (Buzsáki et al., 2008). Furthermore, tuber allelopathy seems to vary between biotypes (Drost et al., 1980). Autotoxicity via tuber allelopathy has been further speculated to regulate tuber dormancy since tuber extracts proved to inhibit tuber sprouting and the number of sprouts per tuber and washing of tubers increased their sprouting capacity (Tumbleson and Kommedahl, 1962; Drost and Doll, 1980). The inhibitors involved may thus be located in or on the tuber epidermis (Tumbleson and Kommedahl, 1962).

Studies unravelling the active metabolites involved in *C. esculentus* allelopathy in general are rare and restricted to the identification and quantification of phenolic acids in allelopathic plant extracts. Several phenolic compounds were identified with *p*-coumaric acid and ferulic

acid as the major phenols in foliage and tubers (Jangaard et al., 1971; Sánchez Tamés et al., 1973). The quantities of phenols found in extracts were, however, too low to deduce a major role for allelopathy of *C. esculentus* (Jangaard et al., 1971). Hence, *C. esculentus* biosynthesizes phytotoxic metabolites that are self-inhibitory and inhibitory to other plants via allelopathy, however, the main allelochemical(s) involved remain to be identified.

## Uses and cultivation

### Uses

The domesticated form *C. esculentus* var. *sativus* (chufa) is cultivated for its tubers in tropical and subtropical areas worldwide. In Africa, it is frequently grown in Ivory Coast, Ghana, Mali, Niger, Nigeria, Senegal and Togo (Omode et al., 1995). There, tubers are mainly consumed fresh, as a vegetable, and dried, as a sweet snack (Bado et al., 2015). In America it is cultivated in Chile, Brazil and the United States, where it is largely used as animal feed (Sánchez-Zapata et al., 2012). In Asia, it is predominantly grown in India (Sánchez-Zapata et al., 2012) and China (Pascual-Seva et al., 2015).

In Europe, *C. esculentus* is only cultivated in the L'Horta Nord de València region (Spain; Fig. 3) where nearly 400 ha are dedicated annually to this crop, producing close to 7,000 kg tubers (MAGRAMA, 2015; Fig. 2D). Although tubers are consumed to some extent fresh, most of them are used to prepare a beverage called “horchata de chufa”, which is a popular drink, based on the milky aqueous extract of chufa tubers. In the last decade, the industrial horchata manufacturing has greatly increased and currently uses up to 80% of the total tuber harvest. The Regional Administration of the Valencian Community has developed specific legislation regarding chufa qualitative parameters (CAPA, 2010). Chufa oil is of high nutritional quality, with similar characteristics as of olive oil, and it can be employed for similar uses (Coskuner et al., 2002). It has been recently introduced in the cuisine and



nowadays, different products made of chufa or horchata are available on the Spanish market, such as chocolates, beer, liquor, gin, and even cosmetic products (e.g., mousses, oils and creams).

### **Cultivation**

In Spain, chufa is cultivated in rotation with other vegetables such as potato, onion, carrot, cabbage, watermelon and artichoke. Autochthonous tubers are ovoid, ranging from spherical to elongated shapes. In 2012, two cultivars were registered by the Spanish Ministry of Agriculture: ‘Bonrepos’ (spherical) and ‘Alboraia’ (elongated) (Pascual-Seva et al., 2013b). The planting is normally undertaken in the first half of April, after the preceding crop is harvested. Tubers are planted in ridges, which are spaced 0.60 m, and tubers are deposited at 7–8 cm depth, and spaced 8–10 cm within lines.

Chufa is demanding in water and is traditionally irrigated by furrow irrigation. The first irrigation event is applied when the plants are 15–20 cm high (25–30 days after planting). Usually, they are irrigated fortnightly until June, and then from June to September the fields are irrigated every 10 days. The seasonal number of irrigation events ranges between 10 and 15, depending on the weather conditions (Pascual-Seva et al., 2013a). Drip irrigation could be an alternative to traditional irrigation, as recent studies have shown (Pascual-Seva et al., 2015). In furrow irrigated plots, greater yields ( $2.18 \text{ kg/m}^2$ ) were produced by plants irrigated when the soil moisture dropped to 60% of FC, than when they were irrigated at 45% FC ( $1.94 \text{ kg/m}^2$ ) (Pascual-Seva et al., 2013a). In drip irrigated plots, plants irrigated at 90% FC produced  $2.58 \text{ kg/m}^2$ , while only  $1.64 \text{ kg/m}^2$  were obtained when irrigating at 70% FC (Pascual-Seva et al., 2015).

*C. esculentus* is a nutrient demanding crop, extracting 583:109:355 kg NPK/ha (Pascual-Seva et al., 2009). Basal dressing consists of an application of sheep manure (20,000 kg/ha)

and mineral fertilization (500 to 1000 kg/ha of NPK 15:15:15 fertilizer). Top dressing, usually applied in June-July, involves an application of  $\text{NO}_3\text{K}$  (120 to 300 kg/ha), applied in the irrigation water.

Harvesting takes place between mid-November and mid-December. Commonly, a locally handmade harvester incorporates the tubers and soil by a straight horizontal blade followed by a rotary tiller and a bucket elevator carries the tubers and soil to a sieving drum, where the soil is sieved out. The tubers, plant residues and small stones are moved by a conveyor belt to a tipping trailer. Usually, producers sell the tubers just after washing, although the sale may also be made after drying, in which approximately 45% weight is lost. In order to obtain a high-quality product, the drying process is done slowly for more than three months. Tubers are stored in 10 cm layers in drying warehouses with adequate ventilation where they are periodically stirred (CRDO, 2016).

## **History of introduction**

### **Introduction and spread**

In Central Europe, *C. esculentus* was first recorded in 1900 and 1902 in Germany (Hamburg and Neustadt a. d. Weinstraße, Rhineland-Palatinate; Hegi, 1980), and further records were made much later in the districts of Ortenau/BadenWürttemberg in 1976 (Gengenbach; Oesau, 1995) and of Vechta/Lower Saxony in 1987 (Damme; Schroeder and Wolken, 1989). *C. esculentus* was first collected in Switzerland in 1967 (Pfäffikon/Zurich; Becherer, 1968). Further introductions have been reported only in the early 1990s (Schmitt and Sahli, 1992). Subsequently, the species has spread rapidly (Schmitt, 1995). In Austria, *C. esculentus* was first recorded in 1987 in Carinthia and in 1998 in Styria and it expanded quickly to adjacent areas and large populations emerged particularly in crop fields (Follak et al., 2015). In Hungary, first observations of *C. esculentus* were made in 1993 in Hévíz near

Lake Balaton (Zala County) and a few years later in 1998 in northwestern Hungary in Pápasalamon (Veszprém county) (Dancza et al., 2004; Hoffmann et al., 2006). The most recent first national records were in 1999 for Slovenia (Soča Valley; Dakskobler & Čušin, 2002) and in 2003 for Poland (Węglińiec/Lower Silesia; Dajdok et al., 2007).

In Western Europe, this species was first recorded in 1947 in the Sologne region (Loire-et-Cher) in central France (Dodet, 2006). However, *C. esculentus* started to spread further from the mid-1970s onwards, which was most likely due to increasing agricultural usage of that area. Later, in the 1980s, *C. esculentus* was observed in southwestern France (Dodet, 2006). In Belgium, *C. esculentus* was first mentioned in 1981 (Verloove, 2006b). In the Netherlands, it was first found in the early 1970s; by 1986 almost 600 infested fields were known, then infestations declined noticeably due to the implementation of legal measures (ter Borg et al., 1998; Rotteveel, 2001). In northern Italy, *C. esculentus* has been increasingly reported from the late 1970s onwards (e.g., Zanotti, 1988). The data suggests that the spread of *C. esculentus* became most evident in Europe after the 1980s as the number of records increased considerably and invasion foci with a clustered distribution pattern emerged (Follak et al., 2015). The future expansion of *C. esculentus* in Europe may accelerate with climate change (Simpson et al., 2011).

## **Pathways**

Natural dispersal mechanisms play a minor role in the spread of *C. esculentus*. The importance of seeds for propagation is negligible (Stoller and Sweet, 1987; Dodet, 2006). Hence, spread occurs primarily vegetatively (see section “Reproduction”). Using a three dimensional spatial model developed by Schippers et al. (1993), local population growth was predicted to be limited to less than 1 m/yr. Lapham (1985) showed in a field study in Zimbabwe that expansion of clones of *C. esculentus* was greater (1.3 m/yr), however the

study was conducted in the absence of interfering vegetation and under warmer climatic conditions.

Zoochory has been discussed by ter Borg et al. (1998) as a dispersal agent. For example, mice (*Microtus* spp.) may collect and displace tubers. The transport of tubers during floods is well known to be important for Cyperaceae (Bryson and Carter, 2008), so this process might have assisted the colonization of riverbanks (e.g., Elbe, Loire, Rhine) and lakesides (Lago Maggiore) in Europe (Follak et al., 2015).

The spread of *C. esculentus* is mainly driven by a range of human activities with differing relative importance and spatial range (Table 3). Agricultural machinery and the handling of crop waste are strongly implicated in the transport of tubers of *C. esculentus* within and between fields (ter Borg et al., 1998; Dodet et al., 2008a; Bohren and Wirth, 2015). Schippers et al. (1993) simulated the dispersal of *C. esculentus* on the field level. Results showed that farming operations were the main cause of dispersal within and between fields. Soil mixing (ploughing, hoeing) was more effective for tuber dispersal than soil adhering to machinery (less soil and tubers are involved); however, the distance of transportation can be high. Potato and sugar beet harvesters are of more concern, because they transport potentially large amounts of soil (and tubers). Likewise, the transportation of soil, gravel, riverbed sand, construction material and landfill waste is involved in the spread of *C. esculentus* as well. For example, the first record in Austria has been linked to contaminated soil attached to machinery from Italy used for the construction of a gas pipeline (Neururer, 1990). Roadsides are occasionally invaded by *C. esculentus*, indicating its function for accidental transport of tubers of *C. esculentus* during construction and maintenance work (Bryson and Carter, 2008).

It was suggested that (small) tubers of *C. esculentus* could be a contaminant of uncertified crop seeds (maize) (Dancza et al., 2004; Hoffmann et al., 2006), however no evident explanations were available and thus, this pathway remains uncertain and unproven (ter Borg

et al., 1998). Tubers can be dispersed by nursery activities (e.g., in soil or media in containers for living plants) and animal feed. In France and in the Netherlands, it has most likely been introduced as a contaminant of gladiolus and lily bulbs imported from the United States (ter Borg et al., 1998; Dodet, 2006). In Germany, Schroeder and Wolken (1989) presumed that *C. esculentus* has been introduced with imported animal feed (tapioca) for poultry and then dispersed with manure. In this respect, Gieske et al. (1992) reported that seeds of *C. esculentus* fed to poultry and dispersed by manure were able to germinate. Likewise in Belgium, *C. esculentus* was initially introduced with contaminated manure from the Netherlands (Verloove, 2002).

## **Impact and management**

### **Impact**

#### *Agriculture*

*C. esculentus* occurs as a weed on arable land, in orchards, and greenhouses (Keeley, 1987). In the United States, it has become a serious weed problem in the last 60 years and it was once described as a “menace in the corn belt” (Stoller, 1981). In Central Europe, *C. esculentus* has emerged locally as a weed in crop fields in Austria (Follak et al., 2015), Germany (Schroeder and Wolken, 1989; Follak et al., 2015), Hungary (Novak et al., 2009) and Switzerland (Bohren and Wirth, 2013). In Western Europe, *C. esculentus* is increasingly found in crop fields in central and southwestern France (Dodet, 2006), in the Netherlands (ter Borg et al., 1998) and in northwestern Spain (Costa, 1985; Fraga et al., 1992). Most of the infested fields in Europe involve vegetables and row crops like maize and soybean (Fraga et al., 1992; Dodet et al., 2008a; Novak et al., 2009; Fig. 2E). ). Worldwide it has been ranked as the 16<sup>th</sup> worst weed (Holm et al., 1991).

Early and rapid establishment and high growth rates are important factors for its

competitive success (Holt and Orcutt, 1991). Yield loss can be substantial, but depends largely on the crop type (i.e., interference with competitive crops), management practices (e.g., date of planting, crop density – row vs. drill spacing), and density of *C. esculentus*. Losses are especially high in low-growing crops in part because of the large amount of photosynthetically active radiation available for *C. esculentus* (Keeley and Thullen, 1978; Holt and Orcutt, 1991) and when it emerges together with the crop (Dodet et al., 2008b; Nelson and Smoot, 2010). Individuals that sprout late do not develop as rapidly as earlier emerging individuals and therefore are less competitive with the crop. For example, the latter study demonstrated that *C. esculentus* (1 tuber/15 cm of soybean row, 8.6/m<sup>2</sup>) did not reduce soybean yield if it emerged later than four weeks after planting. Additionally, frequent irrigation and high nitrogen fertilization levels stimulate competitiveness of *C. esculentus* (Ransom et al., 2009). Of note, *C. esculentus* thrives and consequently occurs in high densities when weed control practices, in particular herbicide use, reduce competitive pressure from other weeds (Keeley, 1987; Fig. 2E).

In Europe, quantitative data on the impact of *C. esculentus* on crop yield is limited. Interference data are merely accessible from North American studies, but these results can only be transferred with caution to the European situation because of different climatic conditions and cropping practices. Keeley (1987) reviewed interference studies of *C. esculentus* with agronomic and horticultural crops. In the United States, yield losses have been reported for vegetables, maize, and soybean (e.g., Stoller et al., 1979; Holt and Orcutt, 1991). For example, Stoller et al. (1979) showed a maize yield reduction of 8% for every 100 shoots/m<sup>2</sup>. Without control, maize yield declined 17% with 300 *C. esculentus* tubers/m<sup>2</sup> and 41% with 1,200 tubers/m<sup>2</sup>.

#### *Nature conservation*

*C. esculentus* has not been described as a weed in natural areas and no evident negative impacts on invaded plant communities have been identified so far. The synthesis of habitat affiliation of *C. esculentus* in Central Europe (Follak et al., 2015; Fig. 4) revealed that it rarely invades areas of high nature conservation value, although occasionally suitable soil disturbance regimes in riparian, lake side or wetland areas facilitates its establishment and spread.

## **Management**

Integrated control strategies are necessary and must include the prevention of dispersal and the combination of cultural, mechanical and chemical control options. In the Netherlands and Switzerland, such strategies were proposed by Productschap Akkerbouw (2014) and Bohren and Wirth (2015), respectively. The latter authors suggest a combined strategy with repeated soil cultivation, soil incorporated herbicides and competition by crops or cover crops. The aim of all measures is the reduction of the number of tubers. However, their number can significantly increase again when control efforts decrease (Bohren and Wirth, 2015). Although efficient biocontrol methods have not been developed so far, they may be prospectively a valuable addition to current management strategies provided further research efforts.

### *Cultural and mechanical control*

Crop management practices (e.g., crop choice, row spacing, and planting date) can improve the competitive advantage of crops over *C. esculentus*. Most crops are effective competitors for light with *C. esculentus* in particular maize and hemp (e.g., Lotz et al., 1991; Keller et al., 2014; see section “Response to competition”). Narrow row spacing is more advantageous than wide spacing, because an early and a rapid canopy closure suppress *C.*

*esculentus* (Nelson and Smoot, 2010). In southwestern France, Dodet et al. (2008b) showed that the number of shoots and tubers were significantly reduced as emergence was delayed in the growing season (crop planting dates in May, June and July). Frequent tillage (e.g., with rotary tillers) can reduce the density and propagation of *C. esculentus*: tillage clips tubers from shoots and roots, bringing them close to the surface where they are subjected to drought or freezing. In this respect, Thomas (1969) showed in the laboratory that low temperatures (4 °C) and the duration of dry conditions (using different desiccation treatments) resulted in a lower percentage of tuber survival compared to higher temperatures (22 °C) and more humid conditions. Although tubers can regrow after each tillage event, subsequent growth occurs on the expense of the remaining carbohydrate reserves reserves (or viable buds) in in the tubers, resulting in decreased proliferation of *C. esculentus* (Bangarwa et al., 2012). In Georgia, fallow tillage (powertiller, 7.6 cm deep) at monthly intervals (5 times) throughout the summer effectively decreased *C. esculentus* density in sweet maize cultivated in the following year (Johnson III et al., 2007). Mechanical control (hoe, harrow) is often used in field crops, but is effective only in row middles (Keller et al., 2014).

Soil solarisation (plots were covered with clear-colourless poly-ethylene) has been shown to control *C. esculentus* (Johnson III et al., 2007), but high efficacy depends on soil temperatures raising a lethal level (>50°C) and a sufficient duration of exposure to high soil temperatures (Webster, 2003). In Europe, solarisation is presumably most applicable in the Mediterranean Area. Poly-ethylene sheeting or biodegradable mulch materials are commonly used in vegetable production for the control of *Cyperus* spp. (Webster, 2005a,b; Cirujeda et al., 2012).

### *Chemical control*

Herbicides from different chemical groups (e.g. growth regulators, cell division and



photosynthesis inhibitors, acetolactate synthase [ALS] inhibitors) have been extensively tested for the control of *C. esculentus* in crop fields in particular in the United States (e.g., Pereira et al., 1987; Ackley et al., 1996). *C. esculentus* can be controlled with pre- (PRE) and post- (POST) emergence herbicides but most of them provided only poor (temporary) or inconsistent control. Reasons included low rates of absorption and translocation to sites of action, tuber depth and dormancy, and environmental factors that directly affect herbicide efficacy (Pereira et al., 1987). Moreover, *C. esculentus* varieties can differ in their response as demonstrated for some of older herbicides (atrazine, metribuzin, 2,4-D) (Costa and Appleby, 1976).

In Europe, two of the more common herbicides used include halosulfuron (chemical group: sulfonyleurea) and glyphosate (glycine). Data from various studies showed that the application of halosulfuron can control *C. esculentus* by 85 to 97% (e.g., Nelson and Renner, 2002; Armel et al., 2008; Keller et al., 2014). The efficacy of glyphosate is based upon its ability to translocate into the tubers of *C. esculentus*. The  $I_{50}$  (herbicide rate that provides 50% response) for foliar growth suppression was 0.73 kg active ingredient [a.i]/ha of glyphosate, whereas total tuber biomass required less glyphosate (0.41 kg a.i/ha) (Webster et al., 2008). The highest tested glyphosate rate (2.57 kg ai/ha) reduced tuber biomass by 83% compared to the non-treated control. Control efficacy also depends on the plant age of *C. esculentus*. Applications of glyphosate were more effective in suppressing resprouting of parent tubers from 2-week than 4-week-old plants (Keeley et al., 1985).

Other herbicides used have a lower efficacy and are selective only in a few major field crops. For example, metolachlor (chloroacetamide) applied PRE (2.2. kg ai/ha) in soybean controlled *C. esculentus* only by 21% (visual rating) but the number of total tubers/m<sup>2</sup> was reduced by 37% compared to the control (Akin and Shaw, 2001). In field and greenhouse studies, mesotrione (triketone) applied POST in maize at rates of 105 to 210 g ai/ha controlled

*C. esculentus* by 43 to 70% (visual rating) (Armel et al., 2008). Productschap Akkerbouw (2014) provides a list of herbicides, which are recommended for the control of *C. esculentus* in the main crops in the Netherlands. However, high efficacy warrants an intensive and costly control program including multiple treatments (Akin and Shaw, 2001; Armel et al., 2008; Keller et al., 2014). In Europe, herbicide-resistant populations of *C. esculentus* have not been detected so far, but a *C. esculentus* biotype resistant to halosulfuron (target-site mutation – amino acid substitution from Trp574 to Leu) has been documented in Arkansas (Tehranchian et al., 2014).

### *Biological control*

Many natural enemies of *C. esculentus* have been documented (Table 2) and some of them have been studied and were proposed as potential biocontrol agents (Phatak et al., 1987; Morales-Payan et al., 2005). However, in most cases results of evaluations were insufficient (i.e., lack of ongoing research), *C. esculentus* was not sufficiently controlled, and/or difficulties in large-scale production of inoculum prevented profitable utilization (Morales-Payan et al., 2005).

In Europe, fungal pathogens have not been considered and exploited as biological agents, except for the rust fungus *Puccinia canaliculata* (Scheepens and Hoogerbrugge, 1991). Phatak et al. (1983, 1987) showed that *C. esculentus* was successfully controlled by *P. canaliculata* (i.e., inhibition of flowering and new tuber formation) under experimental and field conditions. However, its utilization (Dr. BioSedge) failed as *C. esculentus* biotypes exhibited a different level of susceptibility to *P. canaliculata* due to its genetic variability and ostensibly due to problems with the commercial mass production of the rust spores. In the Netherlands, this pathogen was subsequently rejected due to a lack of host specificity and the biotypes tested were differentially susceptible (Scheepens and Hoogerbrugge, 1991).

*Dactylaria higginsii* was reported to cause a foliar disease in *C. esculentus* (Kadir and Charudattan, 2000). However, *C. esculentus* was less susceptible to *D. higginsii* than *C. rotundus*, thus research efforts were concentrated on the control of *C. rotundus*.

Several insects are known to attack *C. esculentus*. Although most of them feed also on crop plants, a very few insects are adequately host-plant specific, but none have proved effective as classical biocontrol agents (e.g., Habib, 1976; Frick et al., 1979). In particular, moths of the genus *Bactra* (Lepidoptera, Tortricidae) offered some promise as biocontrol agents for the control of *C. esculentus*. In Spain, the indigenous *B. lancealana* and *B. furfurana* were thought to be of potential value for control of *C. esculentus* (Albajes and Garcia-Baudin, 1980), however high rates of parasitism and their role as a pest for cultivated *C. esculentus* prevented further research efforts. Likewise, in the United States, the indigenous *B. verutana*, the javelin moth, caused extensive damage to shoots of *C. esculentus* under field and glasshouse conditions, but the moth was not able to produce sustainable control (Keeley et al., 1970; Frick et al., 1979). Moreover, the leaf miner *Taphrocerus schaefferi* (Coleoptera, Buprestidae) was considered for control of *C. esculentus* in the United States, but damage caused by larvae was negligible as their cannibalism kept numbers at low levels (Story and Robinson, 1979).

Small scale growers use animals such as geese and ducks (*Anas* spp, *Anser* spp.) to control *C. esculentus* (Phatak et al., 1987). Geese were also effective for early season weed control in cotton fields where *Cyperus* spp. and other grass weeds have been the main problem, but geese require high levels of management (e. g., supplementary feeding, shading) for effective utilization (Miller et al., 1962).

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**Figure 1.** *Cyperus esculentus* (original drawing by Rosaria Manco): (A) habit of the flowering plant; (B) mature tuber; (C) spikelet; (D1) achene: dorsal view; (D2) achene: ventral view; (E) details of flower and rachilla.

**Figure 2.** Appearance of *Cyperus esculentus*: (A) juvenile plants; (B) flowering plant; (C) tuber development during the growth period (D) cultivated field of chufa; (E) infestation in oil-pumpkin (Photos A, B, E by S. Follak, C by C. Parodi and D by N. Pascual-Seva).

**Figure 3.** Geographical distribution of *Cyperus esculentus* in Europe. Black circles represent the locations of populations growing in the wild. Distribution data of *C. esculentus* were assembled from the Global Biodiversity Information Facility (GBIF.org, 2015), Follak et al. (2015) and other literature sources. The main area of cultivation of *C. esculentus* (var. *sativus*) is grey-shaded (Province of Valencia/Spain).

**Figure 4.** Invasion curves for *Cyperus esculentus* in different habitats in Central Europe (including Austria, Germany, Hungary, Poland, Slovenia, and Switzerland; time period 1965–2015,  $n = 258$ ). Habitats: arable land (collected within and at the margin of a crop field), ruderal habitats (collected along transport networks and at waste deposits), riverine vegetation (collected at the bank of drainage ditches, streams, rivers, ponds or lakes) and grassland (Follak et al., 2015; modified).

**Table 1.** Genetic diversity literature for *Cyperus esculentus*.

Reference*	Locality	Molecular marker	Genetic diversity pattern in <i>Cyperus esculentus</i> **	Note
<b>Old World</b>				
Abad et al., 1998	Spain, Togo	RAPDs	Genetic indexes are not reported. Nei-Li similarity coefficient was used to prepare an UPGMA phenogram. Cultivated (var. <i>sativus</i> , <i>Chufa</i> ) and weedy clones clustered in two groups. A high level of genetic variability was showed among the specimens, particularly among the cultivated ones.	<i>Chufa</i> cultivars were analysed: Spain (Ametlla Bonrepos and Llangueta Alboraria, registered in 2012 as Bonrepos and Alboraria, respectively; Pascual-Seva et al., 2013b) and Togo (Gegant Africana). One clonal specimen from each of five weedy populations with different geographic origins [Africa (Ivory coast and Ghana), southern America (Argentina) and Europe (Spain)] was also included in the analyses.
Pascual España et al., 2000	Spain, Togo	Total proteins and RAPDs	Genetic indexes are not reported. Total protein electrophoresis was unable to distinguish among the different <i>Chufa</i> cultivars. A genetic similar matrix using RAPD data showed different distances among the cultivars in study.	<i>Chufa</i> cultivars analysed by Abad et al. (1998).
Dodet et al., 2008a	France	AFLPs	Polymorphic loci (P) = 50%; total gene diversity ( $H_T$ ) = 0.14; gene diversity intra-population ( $H_S$ ) = 0.006; coefficient of differentiation ( $F_{ST}$ ) = 0.95; Mantel test, $\rho_s$ = 0.31 ( $p < 0.001$ ) (geographic vs. genetic distance).	Wild population analysed.
<b>New World</b>				
Horak and Holt, 1986	California (United States)	Isoenzymes	Genetic indexes are not reported. Five populations were isoenzymatically uniform and	Wild population analysed.

			apparently composed of a single genotype. The remaining five populations were genotypically variable.	
Horak et al., 1987	California (United States)	Isoenzymes	Total gene diversity ( $H_T$ ) = 0.237; gene diversity intra-population ( $H_S$ ) = 0.109; gene diversity inter-population ( $D_{ST}$ ) = 0.129; coefficient of differentiation ( $G_{ST}$ ) = 0.341.	Populations analysed by Horak and Holt (1986). A comparison with <i>C. rotundus</i> is carried out.
Holt, 1994	California (United States)	Isoenzymes	Genetic indexes are not reported. Morphological and phenological characters were compared with previous isoenzymatic data. Results indicate that isozymes do not reflect the high level of morphological and phenological character plasticity of <i>C. esculentus</i> .	Populations analysed by Horak and Holt (1986).
Okoli et al., 1997	California, Florida, South Carolina, Kansas, Oregon, Mississippi (United States)	RAPDs	Genetic indexes are not reported. The gel electrophoresis profile revealed a far greater level of variation in nine Californian samples than was previously shown by isozyme analysis (Horak and Holt, 1986; Horak et al., 1987).	Nine Californian population used by Horak and Holt (1986). A comparison with <i>C. rotundus</i> is carried out.
Tayyar et al., 2003	California (United States)	Isoenzymes and RAPDs	Isoenzyme data: polymorphic loci (P) = 66.7%; observe heterozygosity ( $H_O$ ) = 0.67; diversity index ( $H_E$ ) = 0.36. UPGMA phenograms were generated from the isozyme genetic distance estimates and the RAPD similarity indices. Conspicuous variability is present in the RAPD phenogram even if no genetic indexes are reported.	Wild population analysed. A comparison with <i>C. rotundus</i> is carried out.

\* References are in chronological order according to the locality (Old World and New World, respectively); \*\* genetic values are expressed as means.

**Table 2** Herbivores and pathogens associated with *Cyperus esculentus* (Phatak et al., 1987; modified).

<b>Taxon</b>	<b>Country</b>	<b>Source*</b>
INSECTA		
COLEPOTERA		
<i>Athesapeuta cyperi</i> (Marshall)	Pakistan	26
<i>Barinus squamolineatus</i> (Casey)	United States	16
<i>B. curticollis</i> (Casey)	United States	16, 26
<i>Barilepis grisea</i> (Casey)	United States	16, 26
<i>Chaetocnema denticulata</i> (Illiger)	United States	16
<i>Diabrotica undecimpunctata howardi</i> (Barber)	United States	16
<i>Lissorhoptrus brevirostris</i> (Suffrian)	Caribbean, Cuba	16
<i>Meligethes</i> sp.	United States	16
<i>Orthoperus</i> sp.	United States	16
<i>Phalacrus politus</i> (Melsheimer)	United States	16
<i>Pleurophorus</i> sp.	United States	16
<i>Sibariops confusa</i> (Casey)	United States	26
<i>Sphenophorus callosus</i> (Schoenherr)	United States	29
<i>S. cariosus</i> (Olivier)	United States	16
<i>S. parvulus</i> (Gyllenhal)	United States	16
<i>S. zaeae</i> (Walsh)	United States	16
<i>Stilbus apicalis</i> (Melsheimer)	United States	16
<i>S. pallidus</i> (Casey)	United States	16
<i>Taphrocerus schaefferi</i> (Nicolay & Weiss)	United States	16
<i>Telephanus velox</i> (Haldeman)	United States	16
<i>Toramus</i> sp.	United States	16
<i>Trigonorhinus sticticus</i> (Boheman)	United States	16
DIPTERA		
<i>Anthomyza</i> sp.		16
<i>Chaetopsis fulvifrons</i> Macquart	United States	16
<i>Elachiptera nigriceps</i> (Loew)	United States	16
<i>Elliponeura debilis</i> (Loew)	United States	16



<i>Mumetopia occipitalis</i> (Melander)	United States, Mexico	16
<i>Oscinella</i> sp.	United States	16
<i>Stenomicro angustata</i> (Coquillett)	United States	16
<i>Stenoscinis atriceps</i> (Loew)	United States	16
<i>Thaumatomyia glabra</i> (Meigen)	United States	16
HEMIPTERA		
<i>Carolinaia cyperi</i> (Ainslie)	United States	16
<i>Chorizococcus rostellum</i> (Lobdell)	United States	16
<i>Corimelaena pulicaria</i> (Germar.)	United States	16
<i>Haplaxius crudus</i> (Van Duzee)	United States	16
<i>Isodelphax basivitta</i> (Van Duzee)	United States	16
<i>Liburniella ornata</i> (Stål)	United States	16
<i>Microtechnites bractatus</i> (Say)	United States	16
<i>Megaloceroea recticornis</i> (Geoffroy)	United States	16
<i>Rhopalosiphum maidis</i> (Fitch)	United States	16
<i>R. padi</i> (Linnaeus)	United States	16
<i>R. rufiabdominale</i> (Sasaki)	United States	16
<i>Sanctanus sanctus</i> (Say)	United States	16
<i>Schizaphis minuta</i> (van der Goot)	United States, Malawi	16
<i>S. rotundiventris</i> (Signoret)	São Tomé und Príncipe	16
<i>Sitobion avenae</i> (Fabricius)	United States	16
<i>S. hillerislamberti</i> (van Harten)	Angola	16
<i>Spissistilus festinus</i> (Say)	United States	28
LEPIDOPTERA		
<i>Bactra minima</i> (Meyrick)	China	16
<i>B. lancealana</i> (Hubner)	Spain	31
<i>B. furfuruna</i> (Haworth)	Spain	31
<i>B. venosana</i> (Zeller)	United States	16, 25
<i>B. verutana</i> (Zeller)	United States	16
<i>Elasmopalpus lignosellus</i>	United States, Brazil	27
<i>Diploschizia impigritella</i> (Clemens)	United States	16
<i>Spodoptera frugiperda</i> (Smith)	United States	16

ORTHOPTERA		
<i>Locusta migratoria capito</i> (Saussure)	Madagascar	16
HYMENOPTERA		
<i>Pachynematus corniger</i> (Norton)	United States	16
THYSANOPTERA		
<i>Frankliniella occidentalis</i> (Pergande)	United States	30
<i>Thrips tabaci</i> (Lindemann)	United States	30
FUNGI		
<i>Alfaria cyperi-esculenti</i> Crous, N.J. Montaño-Mata & García-Jim.	Spain	32
<i>Ascochyta</i> sp.	India	22
<i>Cintractia limitata</i> (Clinton)	United States-	16
<i>Claviceps cyperi</i> (Loveless)	South Africa	18
<i>Cercospora caricis</i> (Dearn. & House)	United States	19
<i>Dactylaria higginsii</i> (Lutrell) M. B. Ellis	United States	17
<i>Fusarium oxysporum</i> f. sp. <i>vasinfectum</i> (G.F. Atk.) W.C. Snyder & H.N. Hansen	United States	16, 21
<i>Phyllachora cyperi</i> (Rehm)	United States	16
<i>Puccinia canaliculata</i> (Schw.) Lagerh.	United States	16
<i>Rosellinia necatrix</i> (Berl. ex Prill.)	Spain	23
<i>Sclerotinia minor</i> (Jagger)	United States	20
<i>Ustilago scitaminea</i> (Syd.)	Africa	16
<i>Verticillium dahliae</i> (Kleb.)	United States	16
NEMATODA		
<i>Belonolaimus longicaudatus</i> (Rau) [S**]	United States	24
<i>Helicotylenchus dihystra</i> (Sher.) [S]	United States	1
<i>Hemicycliophora hesperis</i> (de Man) [S]	United States	2
<i>Heterodera cyperi</i> (Golden, Rau & Cobb) [S]	Spain	3
<i>Meloidogyne arenaria</i> (Chitwood) [R, S]	United States	4, 5
<i>M. graminicola</i> (Golden & Birchfield) [S]	United States	6

<i>M. hapla</i> (Chitwood) [S]	United States	7
<i>M. incognita</i> (Chitwood) [R, MS, S]	United States	4, 5, 7
<i>M. javanica</i> (Chitwood) [R, S]	United States, Zimbabwe	4, 7, 8
<i>Rotylenchulus reniformis</i> (Linford & Oliveira) [I, R, S]	United States	1, 9
<i>Tylenchorhynchus acutus</i> (Allen) [MS]	United States	1
VIRUSES		
Brome streak mosaic virus (BrSMV)	Hungary	12
Impatiens necrotic spot virus (INSV)	United States	10
Rice yellow mottle virus (RYMV)	Nigeria	13
Turnip mosaic virus (TuMV)	Zimbabwe	11
BACTERIA		
<i>Xylella fastidiosa</i> (Wells et al.)	United States	14, 15

\* (1) McSorley & Parrado (1983); (2) Siddiqui et al. (1973); (3) Romero & Lopez-Llorca (1996); (4) Kokalis-Burelle & Roskopf (2012); (5) Rich et al. (2008); (6) Minton et al. (1987); (7) Trojan et al. (2006); (8) Martin (1958); (9) Lawrence et al. (2008); (10) Martínez-Ochoa et al. (2004); (11) Chivasa et al. (2002); (12) Takács et al. (2008); (13) Salaudeen et al. (2008); (14) Freitag (1951); (15) Wistrom & Purcell (2005); (16) Phatak et al. (1987); (17) Kadir & Charudattan (1996); (18) van der Linde & Wehner (2007); (19) Blaney & Van Dyke (1987); (20) Hollowell & Shew (2001); (21) Smith & Snyder (1975); (22) Upadhyayet al. (1991); (23) García-Jiménez et al. (1998); (24) Bekal & Becker (2000); (25) Poinar (1964); (26) Habib (1976); (27) Kahn et al. (1991); (28) Moore & Mueller (1976); (29) Wright et al. (1982); (30) Doederlein & Sites (1993); (31) Albajes & Garcia-Baudin (1980); (32) Crous et al. (2014)

\*\* S = susceptible – high level of nematode reproduction; MS = moderately susceptible – reproduction somewhat reduced; R = Resistant – reproduction severely suppressed; I = immune – no evidence of nematode feeding or reproduction.

**Table 3.** Dispersal pathways for *Cyperus esculentus* in Europe. Shown are their spatial range (short distance <1 km; medium distance 1–10 km; long distance >10 km) and their relative importance.

<b>Pathway</b>	<b>Spatial range</b>	<b>Relative importance</b>	<b>References</b>
<i>Natural dispersal</i>			
Vegetative spread	Short distance	Low	Lapham, 1985; Schippers et al., 1993
Hydrochory	Short/medium/long distance	Low	Bryson and Carter, 2008
Zoochory	Short distance	Low	Ter Borg et al., 1998
<i>Human-mediated dispersal</i>			
Agricultural Machinery	Short/medium distance	High	Schippers et al., 1993; Dodet et al., 2008a; Bohren and Wirth, 2015
Contaminated soil	Short/medium/long distance	High	Bryson and Carter, 2008
Contaminated plant material	Medium/long distance	Medium	Ter Borg et al., 1998; Dodet, 2006
Animal feed	Medium/long distance	Low	Schroeder and Wolken, 1989; Gieske et al., 1992

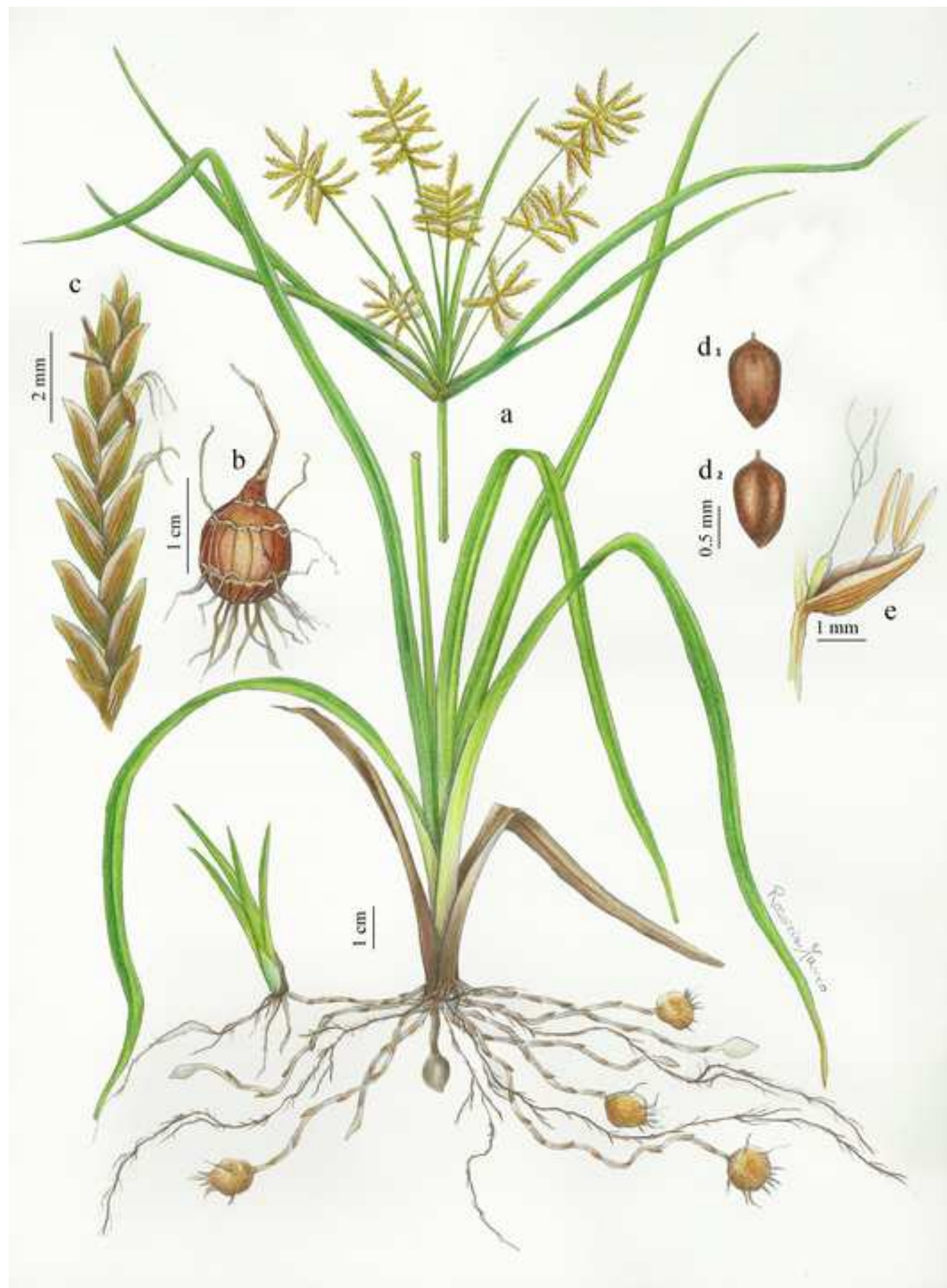


Figure 3

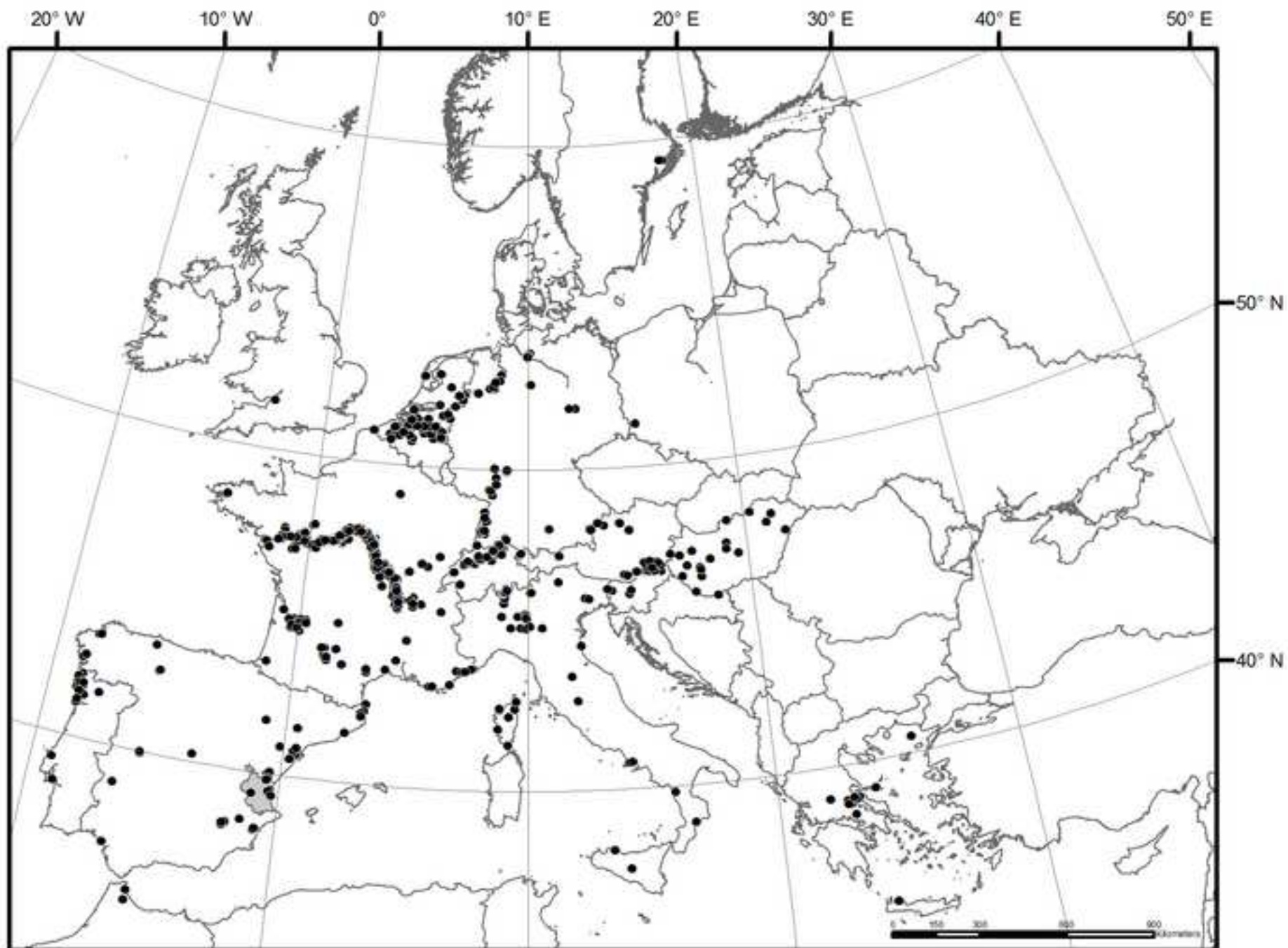


Figure 4

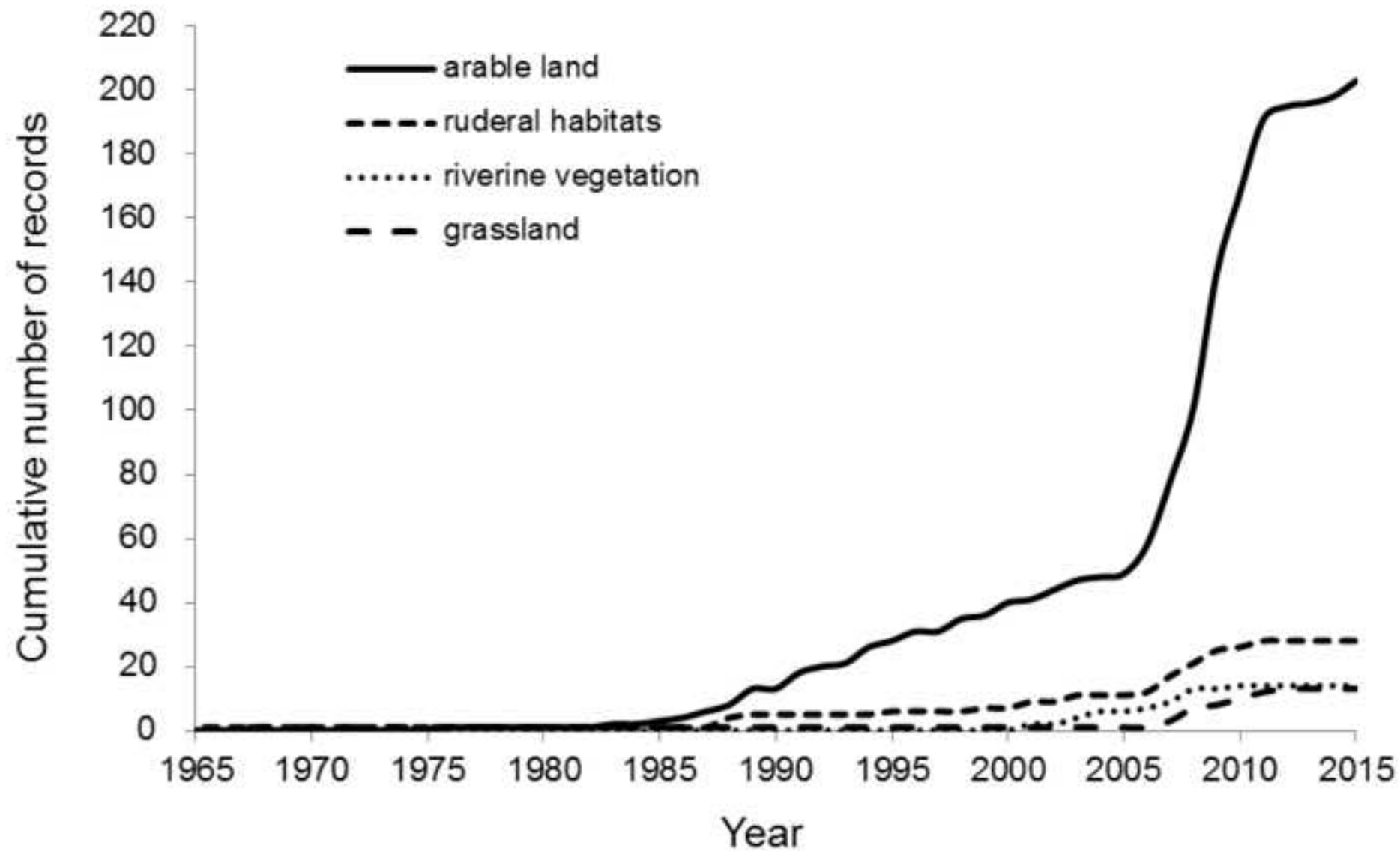


Figure 2a





Figure 2b



Figure 2c



Figure 2d



Figure 2e

