Biological Flora of Central Europe

Biological Flora of Central Europe: *Euphorbia palustris* L.

Christina Wärner[a], Erik Welk[b], Walter Durka[c], Burghard Wittig[a], Martin Diekmann[a],*

[a] *Vegetation Ecology and Conservation Biology, Department of Ecology, FB 2, University of Bremen, Leobener Str., D - 28359 Bremen, Germany*
[b] *Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, D - 06108 Halle, Germany*
[c] *Department of Community Ecology, Helmholtz Centre for Environmental Research - UFZ, Theodor-Lieser-Str. 4, D - 06120 Halle, Germany*

ARTICLE INFO

ABSTRACT

Euphorbia palustris L. (Euphorbiaceae) is a tall perennial hemicryptophyte, native to Europe and small parts of adjacent Western Asia. It is considered a so-called river corridor plant that is exclusively or predominantly confined to the basins of large rivers. As most natural habitats along European rivers have been destroyed and the remaining habitats fragmented and degraded by the regulation of watercourses, land reclamation, and agricultural intensification, *E. palustris* is now endangered in most of Central Europe. To enhance its conservation, to give scientific advice for its management and to supplement the scarce information about the species available from the literature, this paper reviews its taxonomy, morphology, distribution, habitat requirements, life cycle, population biology and genetics as well as the conservation status across its distribution range.

© 2011 Elsevier GmbH. All rights reserved.

Introduction

"*Euphorbia*, which Rudbeck called *Tithymalus maximus Oelandicus*, grew abundantly here in the middle of the field close to a little brook, Fällbäcken, although we had never seen it wild in Sweden before; it grew as shrubs a few ells tall; the stem perishes each year; the leaves are alternate, lanceolate, obtuse and entire. ...We saw this plant later on during the day here and there in the meadows on the *alvar*-land." (Linné, 1745).

This citation from Linné's journey to Öland and Gotland is probably the first scientific description of the biology and ecology of *Euphorbia palustris* L., a nowadays rare and, in most parts of Central Europe, endangered species. This article deals with the taxonomy, morphology, distribution, habitat requirements, life cycle, population biology, and genetics of this species, following the outline for the Biological Flora of Central Europe (Matthies and Poschlod, 2000). To provide a comprehensive overview we used already published information as well as unpublished data. Personal observations of the species' ecology were conducted in the years 2005, 2006, and 2007 in 12 populations located along the Weser and Elbe river systems in North-western Germany. Unless otherwise stated, data given without a published literature source refer to these investigations. Most quantitative information in the sections "Morphology" and "Reproduction" is based on our own measurements in the above populations, where also data on environmental conditions were gathered (chapters "Habitat" and "Regional response to abiotic factors"). Additional information was obtained while compiling and analyzing data on the geographical distribution of the species. Information given in the section "Germination" is based on experiments conducted at the University of Bremen. Studies of the demography of *E. palustris* were carried out in three relatively large populations and form the basis for the chapters "Life cycle", "Spatial distribution of plants within populations" and "Herbivores and pathogens". Finally, genetic information provided in the section "Genetic data" is derived from own microsatellite analyses. In general, it has to be kept in mind that this monograph of *E. palustris* is based predominantly on data material and the literature from Central Europe, while the range centre of the species is located in Eastern Europe. In spite of this potential bias we hope that this paper contributes to a better understanding of the species' ecology and the causes behind its severe decline in many parts of Europe.

Taxonomy and morphology

Taxonomy

Euphorbia palustris L., Spec. Plant. I: 462 (1753) (Euphorbiaceae) – Sumpf-Wolfsmilch, marsh spurge.

* Corresponding author. Tel.: +49 421 21862920; fax: +49 421 21862929.
E-mail address: mdiekman@uni-bremen.de (M. Diekmann).

Homotypic synonyms: *Tithymalus palustris* (L.) Garsault, Fig. Pl. Méd.: 592 (1764), – *Galarhoeus palustris* (L.) Haw., Syn. Pl. Succ.: 145 (1812).

Heterotypic synonyms: *Euphorbia nuda* Velenovsky, Fl. Bulg.: 506–507 (1891) – *Euphorbia velenovsky* Bornm., Bot. Jb. 66: 117 (1933), nom. illeg. – *Euphorbia sauliana* Boreau ex Boiss., DC. Prodr. XV/2: 1266 (1866).

The genus *Euphorbia* belongs to one of the largest dicotyledonous plant families, the Euphorbiaceae, which includes 300 genera and 8000 species (Webster, 1987) occurring in all parts of the world except the arctic regions, and having its distribution centre in the tropics. Because of its tremendous morphological diversity, encompassing broad-leaved trees in the tropical rainforest, succulents in arid ecosystems, perennial herbs mainly in Europe, annual weeds, and even a floating water plant (*Phyllanthus fluitans* Benth.), the taxonomy of the family is still disputed (Webster, 1987).

Euphorbia is a large genus of over 2000 species of almost cosmopolitan terrestrial distribution, which is sub-divided into many subgenera and sections (Govaerts et al., 2000). While the genus is rich in species in subtropical, semi-arid areas, particularly in Africa, much fewer species occur in cooler regions, such as the European and West Asian temperate to boreal zones (Kuzmanov, 1964). *E. palustris* is a species of the subgenus *Esula* Pers. that consists of about 500 species and is considered a native Eurasian group (Park, 1998). Within this group, the section *Tulocarpa* (Raf.) Prokh. (sect. *Tithymalus* (Scop.) Boiss. subsect. *Galarrhaei* Boiss.) includes tall perennial herbs and small shrubs, predominantly distributed in sub-meridional and temperate Eurasia. Therein, *E. palustris* belongs to the subsection *Lutescentes* Prokh. (ser. *Lutescentes* (Prokh.) Radcliffe-Smith). Its closest relatives are *Euphorbia soongarica* Boiss., *Euphorbia lamprocarpa* Prokh., and *Euphorbia aristata* Prokh. (Baikov, pers. comm.). Govaerts (Catalogue of Life, 2007) included these species into a broader concept of *E. palustris*, although they seem to be clearly distinguished by their fruit morphology. Species like *Euphorbia semivillosa* Prokh. that was sometimes included in an *E. palustris* aggregate differ in being not entirely glabrous. While the morphological and ecological similarity of *E. lamprocarpa* and *E. aristata* to *Euphorbia soongorica* was already advocated by Lipsky (1897), there is a larger difference between *E. palustris* and *E. soongorica* with regard to their habitat preferences. The latter occurs in temporarily moist, often strongly saline, open habitats of sub-continental (mountain) steppe regions (Pavlov, 1963), whereas *E. palustris* is more strongly tied to seasonally wet riparian habitats in lowland river corridor ecosystems. The placement of *E. soongarica*, *E. lamprocarpa*, *E. aristata*, and *E. palustris* in a separate Series *Soongaricae* Baikov (Baikov, 2003a,b, 2007) seems justified (also see World Checklist, 2009). Accordingly, Meusel et al. (1978) described *E. palustris* as a lowland species within a group of mountain steppe plants of Western Asia. Molecular-genetic studies on the phylogenetic relationships of *E. palustris*, however, are lacking.

Morphology

E. palustris is a perennial herb resembling a small willow shrub in its habit. Flowering plants reach a height of 70–180 cm (120 cm on average, 95% CI 119–122). The distinct system of thick, fleshy roots shows a number of peculiarities in the course of its development. Since the main root and the hypocotyl of the seedling are building a persistent fleshy taproot, at this stage the species is classified as turnip geophyte (Rauh, 1937; Fig. 1). From the third growing season onwards the turnip starts to split into several branches. A central rootstock, however, persists, increases in size with age and lignifies. Furthermore, basal persistent segments of the new branches
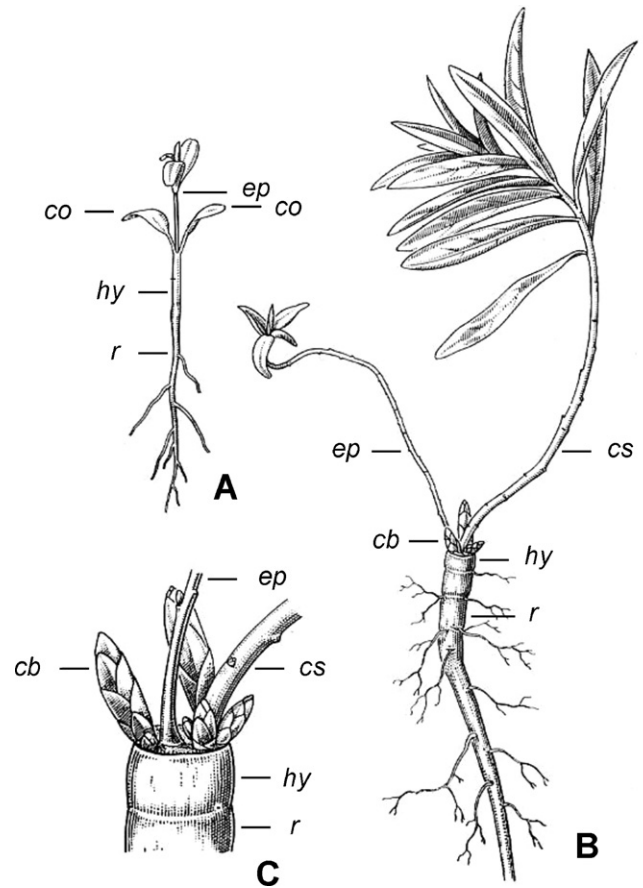

Fig. 1. *Euphorbia palustris*. (A) Seedling, (B) one year-old plant, (C) top of the beet of a one year-old plant. r—root, hy—hypocotyl, ep—epicotyl, co—cotyledon, cs—cotyledon shoot, cb—cotyledon bud.
Modified from Rauh (1937).

grow and give rise to innovation from axillary buds (Fig. 2). These branches could be identified as stem axes with adventitious rooting by means of a microscopy cross section. The belowground stem axes, which emanate laterally from the central rootstock, are thickest (diameter between 5 and 10 cm) in the upper part (Lukasiewicz, 1962). The roots grow diagonally into the soil down to a depth of 1 m (Hejny, 1960; Lukasiewicz, 1962). These characteristics indicate that the storage organ of individuals older than three years
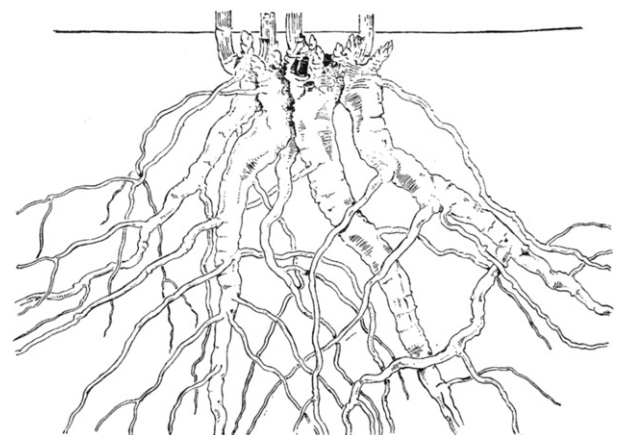

Fig. 2. Upper part of *Euphorbia palustris*' lasting organs. State in autum (Lukasiewicz, 1962).

Fig. 3. *Euphorbia palustris*. (A) Complex inflorescence (compound thyrsoid) with unripe fruits, (B) threefold branch of the inflorescence with terminal cyathia, (C) cyathium with unripe fruit, (D) cyathium with ripe fruit, (E) cross section of an ovary, (F) seed, (G) seedling, (H) sterile shoot.
Modified from Hegi (1924).

might be classified as a pleiocorm. However, the fact that *E. palustris* has been found capable of vegetative reproduction sometimes (see "Life cycle") suggests that it might be regarded as a transitional form between a pleiocorm and a rhizome.

The reddish innovation buds are arranged on the central root stock directly at the ground surface (Fig. 2). New shoots are formed mostly immediately after hibernation but sometimes also during the growing season, forming a tussock. Young flowering individuals may consist of one shoot only while large adults can build up to 120 shoots. The aboveground stems have an average diameter of 17 mm (max: 22 mm) at the basis. They are hollow, glabrous, bluishly pruinose and often with a reddish touch at the base. The upper parts of the flowering shoots are branched (Fig. 3) and, at fruiting time, sterile branches overtop the terminal inflorescences. The shoot surface does not possess any stomata (von Kirchner et al., 1932).

The sessile leaves (Figs. 1 and 3) are numerous and alternately arranged at the stem and its branches. They are of a bluish green colour, soft, glabrous and have a water repellent surface (Neinhuis and Barthlott, 1997). Leaf shape ranges from lanceolate to oblong-lanceolate and from blunt to acuminate. Stem leaves are on average 9.2 cm long and 2.0 cm wide, while branch leaves are smaller with an average length of 4.6 cm and width of 1.2 cm. Average leaf size is 616 mm^2 with a mean mass of 29.9 mg (average dry matter content of 323.8 mg/g), resulting in an average specific leaf area of 20.43 mm^2/mg (Kleyer et al., 2008). The leaves have a narrow cartilaginous light margin that is entire or very soft serrate. The anomocytic stomata are arranged at the underside of the leaf solely (von Kirchner et al., 1932) and count 210 per mm^2 on average (Sehgal and Paliwal, 1974).

The flowers of *E. palustris* are organized in complex inflorescences, in which the well-known module of the Euphorbioidae, the cyathium, typologically is a thyrsoid (Fig. 3). The cyathium is a cuplike structure of fused bracts, with four, occasionally five or six, extrafloral oval nectar glands. This so-called involucrum encloses a single terminal stalked gynoecium that is interpreted as a perianthless female flower, surrounded by five groups of three to six stamens that are interpreted as partial inflorescences of perianthless male flowers. Within a single male partial inflorescence, stamens are arranged centrifugally and open one after another from the inside outwards. The female flower has a petiolate threefold ovary with three free, basal connate styles each with a bifide stigma. Since the cyathia themselves are arranged in a thyrsoid, the entire complex is to be called a compound thyrsoid (Müller-Doblies et al., 1975) comprising 12 main rays on average that first branch three- to fivefold and subsequently threefold, each final branch carrying a terminal cyathium. The entire cyathium is coated by two yellow bracts; two bracts protrude also from the base of the second level of the thyrsoid and two to four bracts grow at the basis of each main ray. The compound thyrsoid is subdivided in the terminal main florescence, a pleiochasium with 6–13 main rays (Rössler, 1943), and accompanying lateral cymoid paraclads. The terminal inflorescence is overgrown by unbranched ananthous lateral paraclads, usually by several centimeters but sometimes also by one third of the overall height of the plant. The central cyathium within the synflorescence contains staminate flowers but mostly lacks the pistillate flower. Thus, *E. palustris* is functionally andromonoecious like many other species of the genus (Narbona et al., 2002).

Capsules are erect and three-loculate, each loculus containing one seed; correspondingly, each fruit normally carries three seeds. The capsules are round-shaped, short and rounded-warty and 5–6 mm long and wide (Hegi, 1924). The ovate to roundish seeds are of grey–brown–black colour and have a smooth and slightly shiny surface with a pale convex caruncule of 1 mm × 1.3 mm. For seed size, see "Reproduction", and for seedling morphology, see "Germination".

Distribution and habitat requirements

Distribution

E. palustris is a relatively rare species, particularly so in Central Europe. The native geographical distribution ranges from northern Spain in the Southwest to South Scandinavia in the Northwest and from northwest Kazakhstan in the Northeast to the southeast of Turkey in the Southeast (Fig. 4). Also Western Siberia and the Altai mountains are sometimes listed as distribution areas of the species (e.g., Gel'tman, 1996), but these western Asian range parts concern several closely related species, especially *E. aristata*, *E. lamprocarpa*, and *E. soongarica*, that were supposedly considered to belong to *E. palustris* by Ledebour (1833). The species is recorded from all European countries except the United Kingdom, Ireland, Belgium, Iceland, Lithuania, Portugal and Malta (Tutin et al., 1964; van Rompaey and Delvosalle, 1979; Greuter et al., 1986; Tzvelev and Gel'tman, 2006). Doubtful and inconsistent observations were reported from Corsica, the Balearic Islands, Southern Catalonia, Central Spain, Crimea, North-eastern Turkey, Middle Ural, and the Upper Tobol Valley (partly erroneous maps in Hegi, 1924; Polatschek, 1971; Hultén and Fries, 1986). The highest densities of *E. palustris* are reported from Hungary, Croatia, Serbia, the Ukraine, and in the steppe and forest–steppe regions of southeastern European Russia; thus, the Pannonian to Pontic floristic regions represent the range centre of the species, and the general distribution can be described as submeridional to north temperate
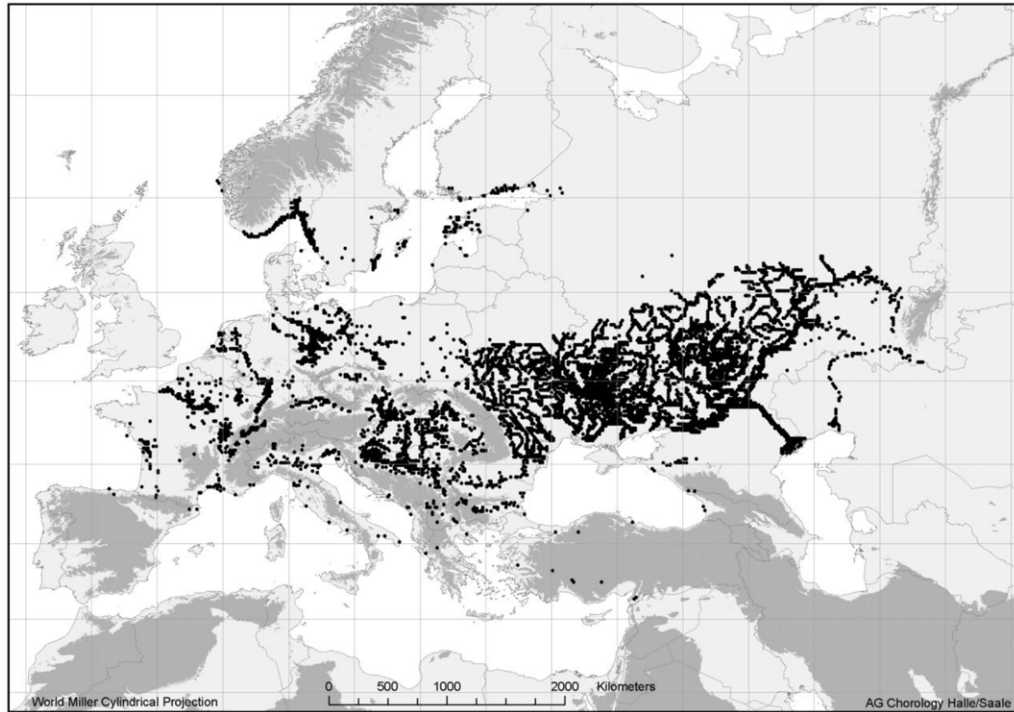
Fig. 4. Global distribution of *Euphorbia palustris*. The distribution in Ukrainia and Russia is partly derived from vegetation data by mapping the respective potential habitats and vegetation units in regions where the species is reported to be abundant, however mainly confined to floodplains of the larger rivers.

within the continentality regions (1) 3–7 (9) in Europe (Westasia) (sm-temp·c(1)3–7(9) EUR-(WAS), Meusel et al., 1978).

The species is predominantly confined to the lowland basins of large rivers and their tributaries (Fig. 4: 90% of occurrences between ca. 10 m and 300 m asl., the relic occurrences in Turkey are outliers at 800–1160 m asl.; Fig. 5). In Central Europe, several other plant species share a similar distribution pattern and are therefore called river corridor plants (Loew, 1879; Burkart, 2001). However, the mechanisms generating this pattern are diverse and not well understood (Burkart, 2001). In the Central European range parts the distribution of *E. palustris* along the rivers is usually rather irregular and erratic, and it has been hypothesized as being not predominantly caused by present-day or relatively recent changes in climatic or edaphic conditions, but most likely by extinction and recolonization events during postglacial times (Schulz, 1899), assuming that the populations spread out along the rivers in warmer periods, but became extinct at unfavourable sites in colder periods. The re-colonization of Central Europe probably originated from refugia in areas of the highest density of the species: the flood plains of the Danube were colonized from Hungary, the river Rhine from France, and the rest of the area along the melt water streamways (furrows of the glacial valleys) from Russia (Schulz, 1899). Strictly regressive processes seem to have acted in Southern Europe. Here, the isolated occurrences in coastal wetlands and on lakeshores of the Mediterranean area may be old, relic populations that represent remains of a formerly wider and more continuous distribution in moister climate periods of the Pleistocene or Pliocene. Scattered occurrences in wetlands are often supposed to originate from ornithochorous dispersal by waterfowl, although the seed characters of *E. palustris* do not make this explanation very likely. Since all the above hypotheses remain highly speculative, phylogeographic investigations using molecular markers are urgently needed for a better understanding of the distribution pattern of the species.
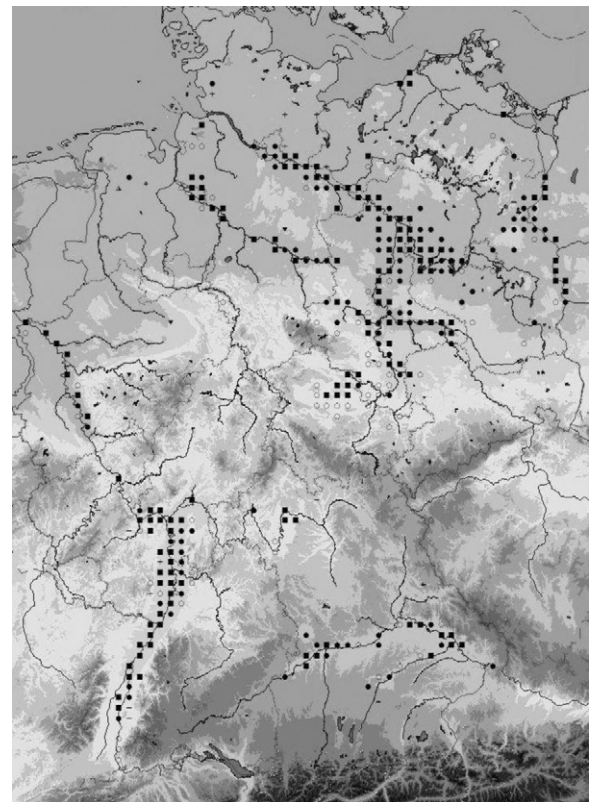
Fig. 5. Distribution of *Euphorbia palustris* in Germany, showing the species' restriction to river corridors. Symbols: open circles—reports not being confirmed after 1950; full circles—reports after 1950, but before 1981; squares—reports since 1981; triangles—synanthropic occurrences; and crosses—populations extinct. The distribution map was made available by the Bundesamt für Naturschutz, Netzwerk Phytodiversität Deutschland [NetPhyD].

E. palustris was identified in middle Pliocene (Late Brunssum-ian) browncoal sediments in Northern Germany (van der Burgh and Zetter, 1998), in late Pliocene (Akchagylian) deposits in the Kama River paleovalley in southeastern Udmurtia (Pisareva, 2006), and in Eemian (Ipswichian) interglacial deposits (Kreftenheye Formation) in the Netherlands (van der Ham et al., 2008). Present-day occurrences in open swamp forests of the Colchic region in western Georgia probably offer climatic conditions that are similar to those present in many parts of Europe during the Late Tertiary (Denk et al., 2001).

Habitat

River corridor plants such as *E. palustris* prefer flood plain habitats in the lowlands with summer-warm conditions and regular inundations in Central to Western Europe, or spring-time floods in Eastern Europe (Hejny, 1960; Burkart, 2001). The species mainly occurs along rivershores, backwaters and lakes, in swamp forests and wet grasslands (e.g., Hejny, 1960; Tutin et al., 1964; Horvat et al., 1974; Shishkin and Bobrov, 1974; Davis, 1982; Pignatti, 1982; Sebald et al., 1992; Adler et al., 1994; Tuba, 1995; Lauber and Wagner, 1996; Godreau et al., 1999; Oberdorfer, 2001; Matuszkiewicz, 2002; Muller, 2002; Hagyó, 2003; Schmeil and Fitschen, 2006; Tzvelev and Gel'tman, 2006). In Central Europe, it is nowadays mostly restricted to ditch banks, field edges and abandoned grasslands (Oberdorfer, 2001), resulting from the deterioration of natural habitats due to the regulation of watercourses, land reclamation and agricultural intensification. Today, most populations in this region are cut off from natural river dynamics and thereby from periodical inundation. In Southern Scandinavia, however, the habitat preferences of the species are different, as it nearly exclusively occupies the shores of the North Sea and Baltic Sea (Fig. 4; Nordhagen, 1939/40; Gillner, 1960; von Schantz and Hackman, 1983). Here, *E. palustris* is exposed to low to moderate concentrations of salt, which is in accordance with its indicator value for salt tolerance of 1 (Ellenberg et al., 1991; see also Frank and Klotz, 1990; Oberdorfer, 2001). The species occurs under saline conditions also in inland salt marshes in Hungary (Hagyó, 2003), at the shores of the brackish Lago di Burano in Italy (Angiolini et al., 2002), and in many of the habitats in the Lower Volga valley (Golub and Mirkin, 1986) where the mean salt content in 32 plots was about 1%.

E. palustris mostly grows on calcareous, humous or peaty mud and clayey soils with stagnant moisture but most often alternately wet and drier conditions (soil moisture indicator value: ~8, Ellenberg et al., 1991; Sebald et al., 1992; Oberdorfer, 2001). It is highly tolerant of varying nutrient regimes, corresponding to the indicator value for soil nitrogen of '*x*' reflecting an indifferent response to this factor (Frank and Klotz, 1990; Table 1). Although the species is described as an indicator for alkaline soils (Frank and Klotz, 1990; Ellenberg et al., 1991 [indicator value for soil reaction: 8]; Sebald et al., 1992; Oberdorfer, 2001), in North-western Germany it mainly occurs on slightly acidic sites (pH 4, 1–5, 2; Table 1). *E. palustris* is classified as a light-demanding species (Frank and Klotz, 1990; Ellenberg et al., 1991 [light indicator value: 8]; Oberdorfer, 2001), but can grow also under more shady conditions, for example in swamp forests or in closed reed beds. The regional classification of *E. palustris* as a somewhat thermophilous species (Frank and Klotz, 1990; Ellenberg et al., 1991 [temperature indicator value: 6]) corresponds to its natural distribution pattern along the large flood plains providing warmer summer conditions than the surrounding regions.

Communities

In Central Europe, *E. palustris* is by most authors considered as a characteristic species of the Veronico longifoliae–Euphorbietum palustris as part of the alliance Filipendulion within the order Molinietalia and the class Molinio-Arrhenatheretea (Oberdorfer, 2001). This association is confined to river corridors and characterized mainly by tall herbs such as the eponymous *Euphorbia* and *Pseudolysimachion* (*Veronica*) *longifolium*. Other authors (e.g., Berg et al., 2004) proposed to assign the association to the alliance Senecionion fluviatilis within the order Convolvuletalia, while Dierschke (1996) stressed its floristic affinity to the class Phragmitetea. As *E. palustris* occurs also in other communities such as *Phragmites* reeds, the fringe of willow shrubs and abandoned meadows (Sebald et al., 1992; Oberdorfer, 2001), the syntaxonomical affiliation of the species remains unclear.

To describe the community ecology of the species more precisely, we compiled all phytosociological relevés with *E. palustris* from Central and northern Europe that were available to us. The data set is summarized in Table 2 showing a list of the most frequent species associated with *E. palustris* and their relative frequencies in four different geographic regions. One result emerging from this table is that, in general, the most frequent companions of the species belong to the class Phragmitetea (*Phragmites australis*, *Lysimachia vulgaris*, *Iris pseudacorus*, *Phalaris arundinacea*, *Carex acutiformis*, etc.), followed by taxa typical for the units Filipendulion and Calystegietalia (*Lythrum salicaria*, *Calystegia sepium*, *Stachys palustris*, *Thalictrum flavum*, *Filipendula ulmaria*). Typical Molinio-Arrhenatheretea grassland species, including *Vicia cracca*, *Sanguisorba officinalis*, *Alopecurus pratensis* and *Caltha palustris*, are clearly less frequent. This observation supports the opinion that the species in Central Europe mainly occurs in community types that are part of the class Phragmitetea (according to Berg et al., 2004, including the syntaxa Filipendulion and Senecionion) rather than Molinio-Arrhenatheretea. However, Table 2 also shows that there is a strong geographic differentiation, which is also supported by a TWINSPAN classification (results not shown). Whereas most German and the Dutch relevés (columns 1 and 2) correspond to the above description, the composition of *E. palustris* communities at the species' northern range margin and in the south-eastern part of Central Europe is different. Here, several elements of reeds and tall-herb communities are less prominent, and some Phragmitetea species with high frequencies especially in the Netherlands (e.g., *Calamagrostis canescens*, *Lysimachia thyrsiflora* and *Typha latifolia*) are almost completely lacking. In eastern Central Europe (including data from Eastern Austria, Czech Republic and Hungary), *E. palustris* is often associated with wet meadow species assigned to the alliances Cnidion or Molinion, such as *Cnidium dubium*, *Allium angulosum* and *Gratiola officinalis*, and *Serratula tinctoria* and *Iris spuria*, respectively. In Scandinavia and in the Baltic area in Germany, as already pointed out, *E. palustris* is largely confined to coastal sites. This is also reflected in Table 2 in which relevés from S Norway, SW Sweden and NE Germany are summarized in column 3: most of the differential species possess a weak, but distinct salt tolerance (Ellenberg et al., 1991) and are characteristic elements of marine drift lines (alliance Agropyro-Rumicion) and other tidal habitats, for example *Elymus repens*, *Angelica archangelica* subsp. *archangelica*, *Potentilla anserina*, *Festuca rubra*, *Atriplex* sp., *Bolboschoenus maritimus*, *Sonchus arvensis* subsp. *uliginosus* and *S. palustris* (Nordhagen, 1940; Dahl and Hadac, 1941; Gillner, 1960; Rehbein and Berg, 1999). The coastal distribution is especially striking in Bohuslän in SW Sweden, where *E. palustris* assembles with *Beta vulgaris* subsp. *maritima*, *Crambe maritima*, *Ligusticum scoticum*, *Glaucium flavum* and *Mertensia maritima* on boulder and shingle shores (Rydin et al., 1999). However, on

Table 1

Soil conditions in 12 *Euphorbia palustris* populations in North-western Germany. In 2005, 2006 and 2007, mixed soil samples were collected from all populations during a rainless period in August (for methods of soil analyses see Winter et al., 2008). Population means, minima and maxima are given for each of the years studied.

Soil factor	2005			2006			2007		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Moisture in summer [%]	32.6	12.8	55.5	23.3	1.9	49.0	33.0	11.7	67.5
pH	4.6	4.0	5.4	4.7	4.1	5.4	4.7	4.2	5.4
Total carbon [%]	6.5	1.2	21.8	7.4	2.7	27.8	8.8	1.6	33.5
Total nitrogen [%]	0.6	0.1	1.5	0.6	0.1	1.9	0.7	0.1	2.3
C/N ratio	11.3	9.8	14.5	12.5	10.9	14.5	12.1	10.7	14.4
Phosphorus content [mg/100 g]	5.2	1.4	14.4	2.3	0.5	5.5	5.2	0.9	10.2
Potassium content [mg/100 g]	19.8	6.6	38.3	21.5	6.9	49.1	20.6	9.0	36.2
Magnesium content [mg/100 g]	29.2	5.3	50.6	25.8	3.8	42.5	31.1	6.8	53.7
Calcium content [mg/100 g]	357.1	36.2	629.0	190.7	25.8	356.4	274.3	57.2	511.3

the Swedish island of Öland under more subcontinental climatic conditions, the species grows in wet meadows and along mires on calcareous soils characterized by a strongly fluctuating water table. These sites have a high ecological and floristic affinity to the SE European communities.

The literature from other parts of Europe is in agreement with the community affiliation of *E. palustris* as depicted in the synoptic table. In Western France, the species accompanies communities of the Phragmition australis, Magno-Caricion elatae, Molinietalia caeruleae, Molinio-Holoschoenion and Convolvulion sepium (Lombard and Arnal, 2001). It is also reported from managed alluvial grasslands corresponding to the Senecioni-Brometum, but nowadays shows a higher abundance in abandoned moist grasslands with *F. ulmaria*, *Althaea officinalis* and *T. flavum* (Muller, 2002).

On the Balcan peninsula, *E. palustris* exhibits a broader habitat spectrum. The species occurs in sedge swamps (e.g., Caricetum elatae, Caricetum gracilis, Caricetum ripariae, Carici-Menyanthetum), reeds (Phragmitetum), willow shrubs and open alluvial forests and their mantle communities (Salicetum albo-triandrae, Populetum nigro-albae, Leucojo-Fraxinetum, Euphorbio palustris-Crataegetum nigrae, Filipendulion ulmariae, Filipendulo-Petasition) as well as grasslands (Bromo-Cynosuretum cristati, Agrostio-Beckmannion, Deschampsietum cespitosae, Ventenato-Trifolietum pallidi, Molinietum arundinaceae) (Horvat et al., 1974; Dragulescu, 1995; Dragulescu and Macalik, 1997; Hagyó, 2003; Čarni et al., 2004; Dimopoulos et al., 2005). For Eastern Europe, information is available for the Desna floodplain (Ukraine, Shelyag-Sosonko et al., 1987) where *E. palustris* is confined to the Phalaridetum arundinaceae that covers the periodically flooded narrow hollows. In the Lower Volga valley (Golub and Mirkin, 1986; Golub and Saveljeva, 1991; Golub and Kuzmina, 1997), the species occurs in Phragmitetea communities (reed and sedge associations: Phragmitetum australis, Sagittario-Sparganietum, Calystegio-Phragmitetum, Beckmannio-Rorippetum austriacae, Cirsio incani-Caricetum distichae), in Molinio-Arrhenatheretea communities (wet meadows: Rumici-Eleocharitetum palustris, Rumici-Tragopogonetum orientale, Stachyo-Achilleetum septentrionalis), in Glycyrrhizetea glabrae communities (steep meadow slopes: Cichorio-Lactucetum serriolae, Lepidio-Cynodontetum), in halophytic Bolboschoenetea communities (Bolboschoeno-Inuletum britannicae, Bolboschoeno-Glycyrrhizetum echinatae), and also in floodplain oak-elm forests (Poo angustifoliae-Quercetum roboris).

Response to abiotic factors

Within its distribution range, *E. palustris* occurs predominantly in suboceanic to subcontinental regions (Fig. 4), but under particular habitat conditions also in the climatic continentality zones 1–2 and 8–9. In coastal regions of North-western Europe a special littoral range sector exists as it is typical for several continental species from Middle and Central Asia. Apart from a more continuous soil water supply and lower competition, another precondition for its occurrence in this area is salt tolerance, which is even more pronounced in the closely related Asian species. In the range parts of the continentality zones 8–9 the habitat of *E. palustris* shows a soil moisture regime that stands in strong contrast to the macroclimate of the surrounding landscape. Table 3 lists statistics for selected climatic variables that appear to be important for the response of the species to abiotic factors at the distribution range scale.

The lowest winter temperatures occur at the easternmost range limit in the southern Ural mountain region (Bashkortostan) with long and cold winters with mean monthly minimum temperatures of the coldest month (*TMIN*) down to −20 °C. Dry and hot summers (mean temperature of the driest quarter above 20 °C and precipitation below 150 mm) occur in S European lowlands below 45° northern latitude, where *E. palustris* is restricted to isolated wetland habitats. Along with the wide continentality amplitude, the species occurs under strongly varying precipitation regimes. The lowest values (160–340 mm/a) are measured at the lower Volga and Ural valleys in the steppe zone of the south-eastern range sector, where the species is independent of the regional precipitation due to its restriction to areas inundated by spring floods fed from snowmelt in northern regions. Because of the spatial difference between the often mountainous catchment areas and the lowland river habitats, the within-range winter precipitation values (*MP_CQ*) are highly variable (ranging from 34 to 583 mm). Maximum precipitation values of 1000–2000 mm per year are present only at higher elevation sites (*MAP*, perhaps somewhat inexactly geo-referenced) exposed to moist western air masses (northern Spain, Jura Mountains, northern Italy, western Balkan Peninsula, and the Colchic region). While the general distribution pattern appears to be rather independent of precipitation (*CV* = 0.25), it shows relatively high summer warmth requirements (*CV* = 0.09). Minimum values of the warmest 90 days (mean temperature of the warmest quarter *MT_WQ*) below 15 °C are confined to isolated occurrences at higher elevations (but see above) and the coastal populations in Norway. However, 90% of the geographical distribution range is situated at locations with mean temperatures of the warmest quarter between 16.5 and 22.5 °C (*MT_WQ*, Table 3). The same applies for the mean temperatures of the warmest month (*MT_WM*, Table 3). Accordingly, a sufficiently long growing season and summers with temperature means higher than 15 °C appears to be a pre-requisite for the successful establishment of populations.

In Central Europe, *E. palustris* is frequently recorded from surrogate habitats in which abiotic conditions are likely to be less favourable than those in its natural habitats. The species is, due to its longevity, able to exist for decades also under deteriorated

Table 2

Constancy table of the most frequent plant species in 472 sample plots with *Euphorbia palustris* in Central and Northern Europe compiled from literature data. The four columns show the relative frequencies (in %) of the species in different sub-regions. Species are clustered into groups, which are ordered according to their presence in, first, the geographic sub-regions, and, second, in different phytosociological syntaxa. C—character species and D—differential species.

Region	Germany [except Baltic sea area]	Netherlands	Eastern Central Europe	N Europe and Baltic sea area in Germany
No. of sample plots	146	196	93	37
Euphorbia palustris	100	100	100	100
Western Central Europe				
Calamagrostis canescens D Phragmitetea	14	57	0	5
Lysimachia thyrsiflora C Phragmitetea	0	40	5	0
Typha latifolia C Phragmitetea	0	41	1	0
Cirsium palustre C Molinietalia	3	34	6	0
Thelypteris palustris	0	35	8	0
Carex paniculata C Phragmitetea	0	33	0	0
Angelica sylvestris subsp. *sylvestris* Molinietalia	0	28	0	3
Potentilla palustris D Phragmitetea	0	28	0	0
Ventenata dubia	0	27	2	0
Juncus subnodulosus	1	24	1	0
Persicaria amphibia	18	10	6	0
Dryopteris cristata	0	21	0	0
Viola palustris	0	19	0	0
Eastern Central Europe				
Lysimachia nummularia	3	8	32	0
Serratula tinctoria D Molinion	2	0	29	11
Iris spuria C Molinion	0	0	29	0
Potentilla reptans D Cnidion	12	4	20	0
Cnidium dubium C Cnidion	1	0	18	0
Galium verum D Molinion	2	0	17	5
Molinia arundinacea D Molinion	0	0	16	0
Allium angulosum C Cnidion	3	0	14	0
Leucojum aestivum	1	1	12	0
Alisma plantago-aquatica D Phragmitetea	0	3	12	0
Gratiola officinalis C Cnidion	0	0	10	0
Viola elatior C Cnidion	0	0	10	0
Trifolium medium	0	0	10	0
N Europe and NE Germany				
Elymus repens	12	3	3	51
Angelica archangelica subsp. *archangelica*	0	0	0	46
Potentilla anserina	1	2	10	43
Festuca rubra	1	3	5	38
Sonchus palustris C Convolvuletalia	0	11	0	32
Sonchus arvensis	1	0	1	29
Rumex crispus	3	3	6	24
Galeopsis tetrahit	1	7	0	24
Galeopsis bifida	1	7	0	22
Atriplex littoralis	0	0	0	19
Agrostis gigantea	4	1	4	16
Oenanthe lachenalii	0	0	0	16
Aster tripolium	0	0	0	16
Bolboschoenus maritimus	1	0	0	14
Artemisia vulgaris	0	1	0	14
Atriplex prostrata	3	0	0	11
Tripleurospermum perforatum	0	0	0	11
Molinietalia				
Caltha palustris C Calthion	3	27	15	0
Lathyrus palustris	8	12	10	5
Silene flos-cuculi	1	9	11	8
Epilobium palustre	2	16	1	3
Myosotis scorpioides	2	8	12	0
Molinia caerulea	1	9	5	5
Juncus effusus	1	6	2	11
Succisa pratensis D Molinion	2	5	11	0
Inula salicina C Molinion	5	1	10	0
Molinio-Arrhenatheretea				
Vicia cracca	26	8	24	46
Sanguisorba officinalis	15	5	24	0
Alopecurus pratensis	17	6	20	0
Poa pratensis agg.	5	1	15	19
Cardamine pratensis	1	25	11	0
Lathyrus pratensis	9	1	17	8
Ranunculus acris	0	3	18	5
Galium album	5	2	4	14
Achillea millefolium	1	2	9	11
Holcus lanatus	1	14	2	5

Table 2 (*Continued*)

Region	Germany [except Baltic sea area]	Netherlands	Eastern Central Europe	N Europe and Baltic sea area in Germany
No. of sample plots	146	196	93	37
Rumex acetosa	2	11	8	0
Festuca pratensis	0	1	10	8
Prunella vulgaris	0	5	13	0
Convolvuletalia and Filipendulion				
Lythrum salicaria	41	68	54	5
Calystegia sepium	41	72	26	48
Stachys palustris	27	33	33	8
Thalictrum flavum	23	25	22	5
Filipendula ulmaria	25	32	8	5
Eupatorium cannabinum	1	31	8	24
Valeriana officinalis	12	1	15	8
Pseudolysimachion longifolium	17	1	12	0
Phragmitetea				
Phragmites australis	53	85	34	73
Lysimachia vulgaris	60	47	49	14
Iris pseudacorus	44	65	30	24
Phalaris arundinacea	67	28	28	16
Galium palustre	23	46	51	19
Carex acutiformis	20	38	18	16
Carex riparia	16	12	28	22
Carex acuta	28	14	22	0
Peucedanum palustre	0	49	1	16
Carex elata	8	42	13	0
Lycopus europaeus	2	26	22	3
Poa palustris	10	8	24	0
Carex disticha	16	8	9	3
Glyceria maxima	13	9	12	0
Sium latifolium	2	8	12	11
Scutellaria galericulata	5	16	3	3
Rumex hydrolapathum	2	4	15	8
Rorippa amphibia	4	4	10	0
Oenanthe aquatica	1	2	10	0
Others				
Symphytum officinale	49	31	41	3
Urtica dioica	36	22	28	27
Rubus caesius	37	7	30	5
Mentha aquatica	4	28	14	35
Cirsium arvense	26	7	15	24
Galium aparine	16	13	10	22
Poa trivialis	12	28	9	11
Solanum dulcamara	11	18	15	11
Glechoma hederacea	23	6	10	3
Ranunculus repens	7	5	34	8
Deschampsia cespitosa	8	4	28	3

environmental conditions where the recruitment of populations is impossible in most cases.

In a study of twelve populations of *E. palustris* in North-western Germany over three years, the differences in seed production across sites between years were strongly affected by soil quality via weather conditions (Wärner et al., unpubl.; Table 1), particularly in terms of excessive or relatively low precipitation and its influence on soil moisture. Seed production was highest (on average 57 seeds per flowering shoot) when weather conditions conformed to the long-term mean. As the species prefers a fluctuating water table

with periodically wet and dry conditions (Ellenberg et al., 1991), constantly high soil moisture over spring and summer reduces growth and seed production (on average 6 seeds per flowering shoot). The negative relationship between the latter and nitrogen availability is possibly caused by the low activity of soil organisms under wet conditions making the nutrients unavailable to the plants. The number of shoots per plant increased with decreasing C/N ratio. The recruitment in the populations (proportion of seedlings), however, declined with decreasing C/N ratio and content of organic matter (carbon content). Furthermore, the number

Table 3
Climate statistics for selected variables throughout the distribution range of *Euphorbia palustris*. Climate data are extracted from WORLDCLIM (Hijmans et al., 2005). *TMIN* = monthly mean of minimum temperatures of coldest month, *MT_WM* = mean temperature of warmest month, *MT_WQ* = mean temperature of warmest quarter, *AP* = annual precipitation, *MP_CQ* = mean precipitation of coldest quarter. Variable minimum, 5th percentile, 95th percentile, maximum, mean, range, standard deviation, and coefficient of variation are given.

Climate variable	Min	P 5th	P 95th	Max	Range	Mean	SD	CV
TMIN [°C]	−20.80	−16.10	−1.20	6.80	27.60	−8.67	4.59	−0.53
MT_WM [°C]	13.25	17.25	23.65	27.32	14.35	20.31	1.91	0.09
MT_WQ [°C]	12.40	16.47	22.56	27.32	14.92	19.41	1.82	0.09
MAP [mm]	160	391	829	1982	1822	577.68	144.86	0.25
MP_CQ [mm]	34	86	190	583	549	123.04	37.84	0.31

of seedlings was positively affected by winter floodings, providing free space for seed germination and seedling establishment.

While soil pH and phosphate contents had no effects on plant performance (Wärner et al., unpubl.), both parameters had a significant impact on the growth and survival of individuals in a re-introduction experiment. Under extreme shade in reed populations, seed production is reduced and plants grow to above-average height to reach to the light. Recruitment was basically not observed under these conditions.

Life cycle and biology

Life cycle

E. palustris is generally a long-lived hemicryptophyte, but in the first two years of life it behaves like a turnip geophyte (see "Morphology"). Geophytic behaviour is occasionally also observed in older plants, as stem axes separated from the rootstock have the ability to overwinter in the soil and to resprout in the following growing season. The rootstock of a plant that had been dug out and divided into several pieces continued to grow after re-planting. The species can reach a very high age, but, to our knowledge, the literature provides no exact data on its life span. Observations within the plant inventory programme of Lower Saxony in Germany indicate that it may live for several decades. A life span of 5–50 years given by Kleyer et al. (2008) is probably an underestimation.

Successful reproduction of *E. palustris* is almost exclusively dependent on seeds. Contrary to what was reported by von Kirchner et al. (1932) and Hegi (1924) it only rarely propagates vegetatively by forming short horizontal stem axes that emerge from the soil: In 12 natural populations that were observed over a period of three years, this way of clonal growth was observed only in 1% of all surveyed individuals. This finding is corroborated by microsatellite genotyping of all individuals in another population in which we found only two neighbouring individuals out of 100 with an identical genotype, indicating a low fraction of clonal growth within sites. During its generative life cycle stage the species normally flowers and forms seeds each year. Abiotic factors like unfavourable weather conditions, however, may inhibit flowering and seed set (Wärner et al., unpubl.).

Detailed investigations of the demography of *E. palustris* were conducted in relatively large populations at three sites in Northwestern Germany. Two of the populations can be considered as static because of a lack of recruitment, whereas one population with seedling establishment was classified as dynamic. Four different life cycle stages are distinguished: seed, seedling, juvenile, and adult (small, medium, large). At the juvenile stage, we also found dormant individuals (2.5%) whose above-ground organs were not visible for a whole growing season. While annual seedling mortality is high (86%), the mortality of juveniles and adults falls below 5% (Fig. 6). Individuals grow in height until they have reached the adult stage and a medium size, then there is only an increase in the number of flowering shoots (Fig. 7). Senescent plants decrease in height, the number of shoots, and flowering shoots. Also in younger established plants the number of shoots may decline in unfavourable years, even though plant size generally increases up to a certain age (Table 4).

Spatial distribution of plants within populations

Although vegetative reproduction via horizontal stem axes is possible, lateral growth is limited and individuals are therefore usually easily distinguished. Owing to its shrub-like habit, one adult individual may occupy an area of up to 2 m². This large plant size
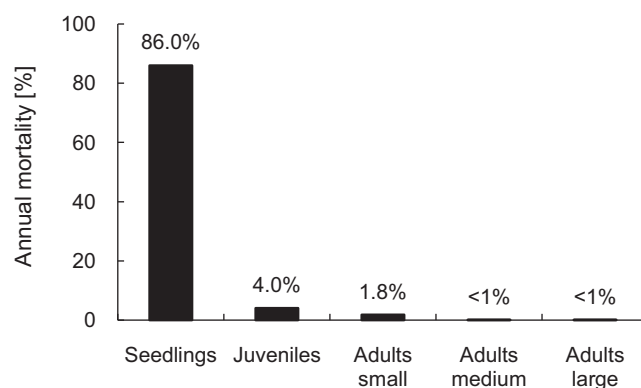

Fig. 6. Annual mortality of seedlings, juveniles and adult (small, medium, large) plants of *Euphorbia palustris*. Demographic data were gathered between 2005 and 2007 in one dynamic and two static natural populations ($n > 100$ in each population) in North-western Germany.
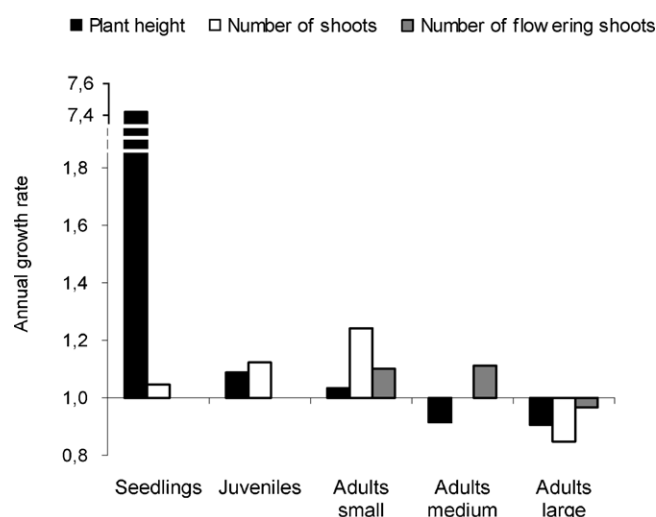

Fig. 7. Annual growth rates ($\lambda = A(t)/(A(t_0)^{1/N})$) of plant height, number of shoots and number of flowering shoots of seedlings, juveniles and adult (small, medium, large) plants of *Euphorbia palustris*. Demographic data were gathered between 2005 and 2007 in three natural populations in North-western Germany ($n > 100$ in each population).

causes a low average population density of 0.46 individuals/m². Static and aged populations (see "Life cycle") are even less dense with only 0.17 individuals/m², whereas dynamic populations may reach an average density of 1.31 individuals/m².

Table 4
Mean changes in total plant height, number of shoots and number of flowering shoots (only adult plants) of one dynamic (with recruitment) and two static (without recruitment) populations of *Euphorbia palustris* in North-western Germany. Demographic data were gathered in 2005, 2006 and 2007 ($n > 100$ in each population).

Plant traits	Dynamic population	Static population I	Static population II
Mean % change in total height			
2005–06	47.4	−7.4	−19.6
2006–07	36.6	10.9	10.9
Mean change in no. of shoots			
2005–06	1.73	1.69	−7.58
2006–07	0.40	−2.32	1.66
Mean change in no. of flowering shoots			
2005–06	−0.71	2.45	5.91
2006–07	−0.47	−2.20	−7.18

Phenology

In North-western Germany, shoot elongation of the deciduous *E. palustris* starts in March, and in early April the first leaves are unfolded. Shoots grow from reddish above-ground buds that have been initiated in the previous year. The main period of vegetative growth lasts from mid-April to mid-June. Inflorescences appear in late April, reach peak flowering in mid-May and finish flowering in mid-June. At the time of fruit ripening (from the end of May till the end of July), sterile branches already overtop the inflorescences because shoot elongation of the main stems ends only after seed maturity has started during the first half of July. The phenology of the reproductive phase in the more subcontinental Czech Republic is almost identical to that in North-western Germany, only seed maturity already starts at the end of June (Hejny, 1960). All bracts turn green with seed maturity. When all seeds are shed at the beginning of August, the above-ground parts start to degenerate. In autumn, the leaves are shed from the crimson-coloured shoots that determine the colour of the whole population. The dead shoots remain on the plant as grey stems and wither for the most part over the course of the following growing season.

Reproduction

In general, *E. palustris* reaches sexual maturity at the beginning of the third or fourth growing season. Occasionally, flowering occurs already in one year-old individuals. The species is monoecious, the reduced female and male flowering organs form a pseudoflower (cyathium) and show pronounced protogyny at the level of the cyathium. However, within one inflorescence, male and female flowers are present at the same time, potentially allowing for geitonogamy. However, pollination experiments demonstrated that caged and manually self-pollinated flowers do not generate any seeds ($n = 8$ and $n = 9$ inflorescences) indicating pronounced self-incompatibility. The species, thus, has an obligate outcrossing breeding system. *E. palustris* is exclusively pollinated by insects, mostly by flies (Muscidae, Conopidae; Knuth, 1898). Typical pollinators also include syrphids, as well as beetles (Scarabidae, Dermestidae, Chrysomelidae, Cerambyicidae, Curculionidae, Elateridae), wasps (Braconidae, Tenthredinidae, Chrysididae), ants (Formicidae) and medium-tongued bees (Apidae). Vroege et al. (1987) report a possible case of arachnophily (spider pollination). Insects are attracted by the ostentatious yellow nectar-glands and bracts forming a showy inflorescence. The nectar contains fructose, glucose and sucrose (Papp, 2004a). A characteristic weak musty odour may preferentially attract flies. The species' self-incompatibility system and its dependence on insect pollination were identified as the most important reasons for the reduced reproductive success of small populations in Northwestern Germany (Wärner et al., unpubl.).

A female flower has three ovules; each fruit thus usually contains three seeds. More rarely, two or four seeds are formed in a flower. Plants analyzed in 7 populations near Halle (Saale) had on average 14.9 flowering shoots (95% CI: 11.3–18.5, $n = 47$), each bearing 146 cyathia (CI: 11.3–18.5) producing 104 (CI: 78–131) seeds per inflorescence. Only 38 (CI: 23–52) seeds per inflorescence (36.5%) were blackish and proved to be viable, while 63.5% were pale brown or brown and non-viable due to herbivory or an aborted embryo. The seed:ovule ratio was 0.244.

The number of fruits (mean 160, 95% CI: 130–192, $n = 591$) and seeds (mean 479, CI: 390–576, $n = 591$; Table 5) per plant varied significantly between three years in populations of North-western Germany, whereas the mass of well-developed viable seeds (mean 9.5 mg, CI: 9.2–9.8, $n = 4.480$) calculated from data over two growing seasons varied only slightly. Mean seed mass values given in
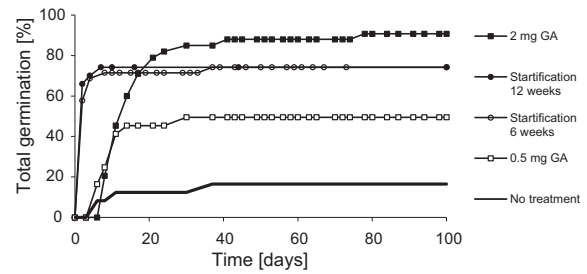

Fig. 8. Total germination of a mixture of 100 seeds collected in 8 *Euphorbia palustris* populations in North-western Germany. The germination curves show the chronological sequence over 100 days for different pre-treatment of the seeds: no treatment, treatment with 2 mg/ml Gibberellin acid, treatment with 0.5 mg/ml Gibberellin acid, cold-wet stratification for 6 weeks and cold-wet stratification for 12 weeks. Seeds were placed on a double layer of wet filter paper in Petri dishes and kept in a growth chamber at a temperature and light regime of 14 h/day at 25 °C and 10 h/night at 20 °C.

other studies, however, differed considerably from our own data. On average, seeds are 3.3 mm long, 2.7 mm wide and 2.6 mm high (Table 5).

The primary dispersal of seeds is autochorous as it results from the bursting of the desiccated capsules and subsequent hurling. Seeds can be transported up to a few meters by this mechanism. As seeds fall relatively fast to the ground at a terminal velocity of 4.08 m/s (SD ± 0.04, $n = 50$), wind dispersal is unlikely (Poschlod et al., 2003). Owing to their oleiferous elaiosom (caruncula), seeds may also be dispersed by foraging ants. As *E. palustris* often occurs along rivers, long-distance dispersal by water is possible. Seeds contain aerenchyma and float on water. Buoyancy experiments showed that 50% of the germinable seeds still floated after 7 days, 30% even longer than 50 days. Moreover, zoochorous dispersal of seeds attached to the plumage of birds was mentioned as another potential agent for long-distance dispersal (Hegi, 1924; von Kirchner et al., 1932), but this seems unlikely due to the high mass and large size of the seeds. Up to now, detailed studies of the dispersal mechanisms and distances are lacking.

Germination

Under experimental field conditions (Hölzel and Otte, 2004a) and in the laboratory, the seeds of *E. palustris* showed the ability to germinate directly after shedding: Seeds sown in an experiment germinated to more than 80% in July and August of the same growing season, while only a small proportion germinated in the springs of the following two growing seasons. In contrast, in natural populations in North-western Germany, germination was observed only in spring.

When seeds are dry-stored at room temperature for several weeks, most of them fall in a secondary, induced physiological dormancy (Hölzel and Otte, 2004a). Experiments in a growth chamber showed that only 18% of the seeds germinated after storage and most seeds were dormant (Fig. 8), but stratification increased the germination percentage considerably. Nearly all seeds (95%) germinated if they were treated with a high concentration (2 mg/ml) of Gibberelline acid (GA). Wet stratification at 4 °C for six or 12 weeks resulted in a germination percentage of 74%. The start and velocity of germination, however, were enhanced under cold-wet stratification (4 °C), as most seeds already germinated on the second day of the experiment (Fig. 8). After a treatment with 2 mg/ml GA, a similar germination percentage was not reached before day ten. Highest germination rates were achieved under moist conditions at a light and temperature regime of 14 h/day at 20–25 °C and 10 h/night at 15–20 °C.

Table 5

Number, mass and size of seeds. Wärner et al. (unpubl.): the number and mass of seeds were measured in populations of the Weser and Elbe systems in North-western Germany in 2005, 2006 and (2007) (number $n \geq 180$ plants; mass $n \geq 2000$ seeds). Klotz et al., 2002: Data on seed size were obtained from the database BiolFlor. Hölzel and Otte, 2004a: Seed mass was calculated for populations of the northern Upper Rhine River ($n \geq 1000$). Bojnanský and Fargasová (2007): Data on seed size were collected in the Carpathian Mountains. (−) No data available.

Seed trait	Year	Number			Mass [mg]			Size (length × width × thickness) [mm]		
		Mean [95% CI]	Min	Max	Mean [95% CI]	Min	Max	Mean	Min	Max
Wärner	2005	856 [643–1098]	0	16,380	9.4 [8.9–9.9]	5.6	13.4	–	–	–
et al.	2006	309 [251–377]	0	2940	9.6 [9.3–10.0]	7.6	11.4	–	–	–
(unpubl.)	2007	201 [119–299]	0	4347	–	–	–	–	–	–
Klotz et al. (2002)	–	–	–	–	8.2	–	–	3.3 × 2.7 × 2.6	2.8 × 2.4 × 2.2	3.7 × 3.2 × 3.2
Hölzel and Otte (2004a)	–	–	–	–	10.5	–	–	–	–	–
Bojnanský and Fargasová (2007)	–	–	–	–	–	–	–	–	3.2 × 2.6	3.7 × 3.0

The radicula emerged, at the earliest, two days after the start of the germination experiment. During the following seven days, the radicula kept on elongating until the two cotyledons were unfolded. The species forms a long epicotyl and a thick hypocotyl (Fig. 1) and belongs to the epigeal germination type (Rauh, 1937). In a common garden experiment seedlings in their first year formed up to 14 leaves and reached a height of up to 10 cm.

In the field, seeds of *E. palustris* are only present in the upper layer (0–5 cm) of the soil with a maximum of 70 seeds/m^2 (Hölzel and Otte, 2004b). The authors calculated a seed accumulation index, which expresses the tendency of a species to accumulate seeds in the soil on a scale from 0 (transient) to 100 (persistent). According to this index, the seed bank of *E. palustris* with a value of 16 was classified as largely transient.

In 12 natural populations in North-western Germany, seedling establishment was positively affected by vegetation gaps and relatively high contents of topsoil organic matter (Spearman correlation: $r_s = -0.707$, $P < 0.01$ [cover of vegetation]; $r_s = 0.615$, $P < 0.05$ [C-content]), both most likely originating from periodical inundations. As most populations of *E. palustris* in this region are cut off from flooding events, seedling establishment is hampered, causing the populations to be over-aged and static.

Response to competition and management

According to the Grime model of primary ecological strategies (Grime, 1988), *E. palustris* is classified as intermediate between a competitor and a stress-tolerator (Frank and Klotz, 1990; Klotz et al., 2002). This strategy is characteristic for perennial competitive plants in extreme habitats, for example swamps. Although communities with *Euphorbia* have a close affinity to the class Phragmitetea (see above), the species is suppressed if reed and willows grow too high or dense. Annual autumn mowing of reed resulted in an increase in seed production from 159 seeds per plant to 280 in the following growing season and to 380 two seasons later, even though, in untreated populations of the region, seed production decreased during this time due to unfavourable weather conditions. If the species has accomplished reproduction, mowing is not deleterious for its viability in spite of its general sensitivity to mowing. Furthermore, the species is sensitive to trampling but very tolerant of grazing (Klotz et al., 2002). Muller (2002) suggested, in order to preserve the species, to abandon land use, to cut only the colonizing shrubs from time to time, or to conduct only a low-intensity agricultural management. Crucial factors for the long-term survival of a population are, however, regular inundation in combination with periodical drought; only these conditions, which are typical for the natural sites of the species, enable seedling establishment and avoid competitive replacement by other species. As most populations at present suffer from a lack of winter flooding, habitats should be re-attached to the natural river dynamics.

Small population size has strong negative effects on the reproductive success of *E. palustris*, possibly due to reduced pollinator services in small populations (Winter et al., 2008; Wärner et al., unpubl.). Thus, a further important management measure for increasing population growth would be the enlargement of suitable habitats, possibly supported by augmentation of additional plant material. Another labour-intensive measure to preserve *E. palustris* would be the reintroduction of the species to restored sites where the species has gone extinct. A reintroduction experiment showed that the plants used for such conservation actions should be at least one year old to enhance survival and long-term establishment.

Herbivores and pathogens

In North-western Germany, damage by deer browsing was observed from June onwards. Leaves and infructescences were browsed while the stems were spared. Between 20 and 71% of the plants in the affected populations were partially damaged, but this appeared to have no effect on the performance of individuals in the following year, although the species tolerates only moderate grazing intensity according to Briemle (2002). As most populations were static, it was also not possible to detect a negative impact on the recruitment of populations through the reduction of seeds.

It appears that *E. palustris* is only weakly affected by phytophagous insects, most likely due to the deterrent effect of latex production. In our field studies in Germany insect feeding on the leaves was not observed. Together with the habitually similar species *Euphorbia virgata* and *Euphorbia lucida*, *E. palustris* is the sole food plant for *Chamaesphecia palustris* and *Chamaesphecia hungarica* (Lepidoptera, Sesioidea) which feed on roots and stems (FUNET, 2009). *Aphthona violacea* (Coleoptera, Chrysomelidae) has been reported to be oligophagous on *E. palustris* and *E. lucida* (cited in Nowierski et al., 2002), and *Oberea euphorbiae* (Coleoptera, Cerambycidae) to be monophagous on *E. palustris*. Remaudière and Leclant (2000) report on an aphid species *Acyrthosiphon (Aphis) euphorbiae* to feed on *E. palustris* in Turkey. Bud galls on the species are formed by *Dasyneura schulzei* (Diptera, Cecidomyiidae; Gagne, 1990). Larvae of an unknown insect feeding on the embryo within the seeds were found in 29% of all seeds in populations near Halle, Germany.

Phytopathogenic fungi known to attack *E. palustris* include the rusts *Melampsora euphorbiae* Castagne, *M. euphorbiae-dulcis* Otth, *Uromyces verrucosae-craccae* Mayor and powdery mildew *Podosphaera (Sphaerotheca) euphorbiae* (Erysiphales; Braun, 1995). Another species-specific fungus is *Plagiostoma euphorbiae* (Diaporthales; Sogonov et al., 2008).

Papp (2004b) found an antimicrobial effect of plant extracts from *E. palustris* against the bacteria *Bacillus subtilis*, *Staphylococcus aureus*, *Escherichia coli* and *Candida albicans*.

Mycorrhiza

No information available.

Physiological data

No information available.

Biochemical data

All parts of *E. palustris* contain latex, a characteristic of the genus *Euphorbia*. It partly consists of different terpene esters (e.g., 20-desoxyingenol) that are, depending on the species, slightly or highly caustic and skin-irritant, and have tumor-enhancing qualities. Data on the effects of the latex of *E. palustris* is scarce, but it seems that the above-mentioned properties are only weakly pronounced in this species. Most likely, the latex protects the plants against phytophagous insects and snails. Although the species is described as poisonous to grazing animals (List and Hörhammer, 1973), intensive herbivory by deer and the absence of cutaneous reactions indicate that the latex of this species has only weak effects on mammals and humans. When sap gets into the eye, however, burning or stinging pain with blurred vision has been reported (Eke et al., 2000) and wearing eye protection is recommended when working with *Euphorbia* species.

Bondarenko et al. (1969) found different phenol compounds in the latex of the above-ground parts of *E. palustris* and identified them as quercetin, kaempferol, myricetin, steppogenin, (+)-robidanol, (+)-robidanolgallate, gallic acid, hyperoside, isomericitrin, stepposide, 3-rhamnogycosides of qercetin and 3-rhamnoglycoside of kaempferol. In addition, the tanning agents catechine and phorbine were extracted from the plant (Nordal and Ogner, 1964). The root stocks contained 21–23% tanning agents (cited in Hegnauer, 1966). The combination of flavonol glycosides, stepposide and robidanol gallate is known to release muscle cramps, to enhance the excretion and the function of the bile and to increase capillary strength. In general, flavonoids, for example as quercetin, kaempferol and myricetin, feature antioxidant activities and function as a protection from herbivores, bacteria, fungi and viruses.

Genetic data

E. palustris is diploid ($2n = 2x = 20$). Genetic variability was analyzed at 7 microsatellite loci (Durka, 2009) in 23 local populations in two German regions (Wärner et al., unpubl.; Durka, unpubl. results). Measures of genetic diversity (mean values for number of alleles $A = 5.2$, expected heterozygosity $H_e = 0.67$, inbreeding coefficient $F_{is} = -0.03$) showed high levels of within-population diversity and values typical for outcrossing species. While allelic diversity (A) was positively correlated with population size, indicating genetic drift, expected heterozygosity (H_e) was not. Local populations were strongly differentiated genetically in the two German regions studied with $F_{ST} = 0.228$ and 0.139 and standardised $F_{ST} = 0.667$ and 0.506, respectively. Genetic distance among populations was only weakly correlated to geographic distance in one region. Overall, these analyses show that genetic drift is strong, leading to a loss of diversity within small populations, and that current amounts of gene flow among sites cannot counteract genetic drift. Consequently, gene exchange by pollen or seed should be facilitated by site management enabling functional connections by flooding.

Hybrids

Hybrids of *E. palustris* have not been reported so far.

Conservation status of the species

Although *E. palustris* is a relatively rare species throughout its entire distribution area and occupies sites that are heavily affected, at least in densely populated Central Europe, by human influence, it is neither included in the IUCN red list of threatened species (IUCN, 2009) nor in the compilation of Central European plants requiring special attention from nature conservation authorities (Schnittler and Günther, 1999). However, the species is mentioned in four national Red lists: according to IUCN-criteria, it is categorized as vulnerable in Germany (Ludwig and Schnittler, 1996; for its decline see Fig. 5), the Netherlands (Weeda et al., 1990), Switzerland (Moser et al., 2002) and Austria (Nikfeld, 1999), not only due to its rarity, but also to the ongoing loss and deterioration of its habitats along the flood plains. The species is characterized as generally rare and significantly declining in France (Lombard and Arnal, 2001) where it is protected by law in several provinces. Furthermore, *E. palustris* is protected at the national level in Germany (Bundesamt für Naturschutz, 2005). Here, the following processes are recognized as being responsible for its decline: (i) cultivation, (ii) peat and soil mining, (iii) destruction of particular small-scale habitats (e.g., fringes, ditches and hedgerows), (iv) melioration, drainage and afforestation of wet meadows, and (v) grassland transformation into crop fields (Korneck et al., 1998). In North-western Germany where the species is critically endangered, the most important reasons for its decline are, apart from habitat fragmentation, the regulation of watercourses and lowering of the ground water table. In addition, periodical inundation is essential for the recruitment of the populations. As a consequence of the cut-off from flooding dynamics, most populations in this region are over-aged and static and occur in surrogate habitats like ditch banks, field edges and abandoned grasslands. The consequence is that the species will, in spite of its longevity, continue to decline steadily. Only selective management measures might stop or reverse this development.

Loss of populations is reported also from southern range parts. A decline appears to take place in Catalonia due to habitat alteration and destruction (Sáez and Soriano, 2000). All occurrences in Southern Italy refer to historical findings that could not be confirmed in recent times (Marchiori et al., 2000). The localities Zambana and Rovereto in Northern Italy (Trentino) are reported by Prosser and Sarzo (2002) to have gone extinct. Several of the populations shown for Friuli Venezia Giulia (Poldini, 2002) and for Venetia-Oriental (Zanetti, 1997) are also indicated as having disappeared. Most of the isolated lake-wetland occurrences in Turkey are highly endangered by human impact, and several of the lakes dried out. One of the isolated outposts in the extreme southeast was destroyed by the construction of an airport.

Owing to its large colourful inflorescence and high stature, *E. palustris* is also used as an ornamental plant (Bosi et al., 2009). It has proved to be particularly successful when planted into native grasslands to enhance visual appeal of urban parks (Hitchmough, 2009). Today the species is commercially traded worldwide for gardening of terrestrial sites, ponds and wetlands. Furthermore, *E. palustris* is also used as a medicinal plant. The root is applied against fever and the latex against warts (List and Hörhammer, 1973). Whether and how these direct human activities have affected or will influence populations in natural habitats or enable invasive spread outside its natural range is unknown.

Appendix A.

List of references including phytosociological relevés with E. palustris from Central and northern Europe.

Ahlmer, W., 1989. Vegetationskundliche Untersuchungen in den Donau-Auen bei Osterhofen als Grundlage für den Naturschutz. Hoppea. Denkschr. Regensb. Bot. Ges. 47, 403–503.

Balatova-Tulackova, E., Hübl, E., 1974. Über die Phragmitetea- und Molinietalia-Gesellschaften in den Thaya-March- und Donau-Auen Österreichs. Phytocoenologia 1, 263–305.

Bellin, F., Gehlken, B., Moes, G., Hülbusch, K.-H., Klauck, E.-J., Kulla, J., Kurz, P., Lorberg, F., Lührs, H., Sauerwein, B., Schröder, H.-H., Troll, H., 2003. Von der Klassenfahrt zum Klassenbuch. Lythro-Filipenduletea-Gesellschaften an Hamme, Wümme und Oste. Notizbuch 63 der Kasseler Schule, Bremen.

Böger, K., 1991. Grünlandvegetation im Hessischen Ried. Pflanzensoziologische Verhältnisse und Naturschutzkonzeption. Botanik und Naturschutz in Hessen. Beiheft 3, 1–285.

Böhnert, W., Reichhoff, L., 1981. Die Vegetation des Naturschutzgebietes "Krägen-Riß" im Mittelgebiet bei Wörlitz. Arch. Naturschutz u. Landschaftsforsch. Berlin 21, 67–91.

Dierschke, H., 1986. Botanische Exkursionen ins Hannoversche Wendland. Bericht über eine Exkursion der Jahrestagung der Floristisch-soziologischen Arbeitsgemeinschaft in Lüneburg am 25.06.1983. Tuexenia 6, 431–444.

Dister, E., 1980. Geobotanische Untersuchungen in der hessischen Rheinaue als Grundlage für die Naturschutzarbeit. PhD Thesis, University of Göttingen.

Gillner, V., 1960. Vegetations- und Standortuntersuchungen in den Strandwiesen der schwedischen Westküste. Acta Phytogeogr. Suec. 43, 1–198.

Görs, S., Müller, T., 1976. Flora der Farn- und Blütenpflanzen des Taubergießengebietes. Die Natur- und Landschaftsschutzgebiete Baden-Württembergs 7, 207–283.

Hagyó, A., 2003. The vegetation of the marsh meadow of Zákányszék. Tiscia 34, 3–13.

Hofmeister, H., 1970. Pflanzengesellschaften der Weserniederung oberhalb Bremens. Diss. Botan. 10, 1–116.

Horvat, I., Glavac, V., Ellenberg, H., 1974. Vegetation Südosteuropas. Gustav Fischer, Stuttgart.

Korneck, D., 1963. Die Pfeifengraswiesen in der nördlichen Oberrheinebene und im Schweinfurter Trockengebiet. Beitr. Naturk. Forsch. SW-Deutschl XXII, 19–44.

Korsch, H., 1994. Die Kalkflachmoore Thueringens. Flora, Vegetation und Dynamik. Haussknechtia, Beiheft 4, 1–123.

Koska, I., 1994. Klasse: Phragmito-Magno-Caricetea Klika in Klika & Novák 1941 - Röhrichte, Großseggenriede und Feuchtstaudenfluren nährstoffreicher Standorte. In: Berg, C., Dengler, J., Abdank, A., Isermann, M. (Eds.), Die Pflanzengesellschaften Mecklenburg-Vorpommerns. Weissdorn, Jena, pp. 196–224.

Lájer, K., Botta-Dukát, Z., Csiky, J., Horváth, F., Szmorad, F., Bagi, I., Dobolyi, K., Hahn, I., Kovács, J. A., Rédei, T., 2008. Hungarian phytosociological database (COENODATREF): sampling methodology, nomenclature and its actual stage. Annali di Botanica Nuova Serie 7, 197–201.

Liepelt, S., Suck, R., 1989. Die Stromtalwiesen und ihre charakteristischen Arten in Rheinland-Pfalz – ein Schutz- und Pflegekonzept. Beitr. Landespfl. Rh.-Pf. 12, 77–176.

Philippi, G., 1978. Die Vegetation des Altrheingebietes bei Rußheim. Nat.- u. Landschaftsschutzgeb. Bad.-Württ. 10, 103–267.

Passarge, H., 1964. Pflanzengesellschaften des nordostdeutschen Flachlandes I. Gustav Fischer, Jena.

Pott, R., 1995. Die Pflanzengesellschaften Deutschlands, 2nd ed. Ulmer, Stuttgart.

Rehbein, R., Berg, C., 1999. Bemerkenswerte Pflanzen und Pflanzengesellschaften aus dem Rostocker Raum III: Euphorbia palustris L. Bot. Rundbr. Meckl.-Vorp. 33, 47–54.

Niemann, E., Heinrich, W., Hilbig, W., 1973. Mädesüß-Uferfluren und verwandte Staudengesellschaften im hercynischen Raum. Wiss. Ztschr. Friedrich-Schiller-Univ. Jena, Math.-Nat. R. 22, 591–635.

Nordhagen, R., 1940. Studien über die maritime Vegetation Norwegens I. Die Pflanzengesellschaften der Tangwälle. Bergens Mus. Arb. 1939–40. Naturv. Rekke 2, 5–123.

Sebald, O., Philippi, G., Seybold, S., 1992. Die Farn- und Blütenpflanzen Baden-Württembergs. Band 4: Spezieller Teil. Spermatophyta, Unterklasse Rosidae. Haloragaceae bis Apiaceae. Ulmer, Stuttgart.

Thomas, P., 1990. Grünlandgesellschaften und Grünlandbrachen in der nordbadischen Rheinaue. Diss. Botan. 162, 1–257.

Walther, K., 1955. Veronica longifolia-Scutellaria hastifolia-Ass. Mitt. Flor.-Soziol. Arb.-Gem. N.F. 5, 103.

Wollert, H., Sluschny, H., Schlüter, U., 1999. Zum Vorkommen einiger kontinental verbreiteter Pflanzengesellschaften im mecklenburgischen Tal der Elbe sowie in den Niederungen ihrer Nebenflüsse Sude und Löcknitz. Bot. Rundbr. Meckl.-Vorp. 33, 23–40.

Zeh, H., 1990. Beiträge zur Kenntnis hessischer Pflanzengesellschaften. Ergebnisse der pflanzensoziologischen Sonntagsexkursionen der Hessischen Botanischen Arbeitsgemeinschaft. Verlandungs- und Bachgesellschaften (Phragmitetea). Botanik u. Naturschutz in Hessen, Beiheft 2, 60–68.

We also used relevés from the Dutch database provided by Stephan M. Hennekens, from the Czech database provided by Lubomir Tichy and from the Austrian database provided by Wolfgang Willner.

References

Adler, W., Oswald, K., Fischer, R., 1994. Exkursionsflora von Österreich. Ulmer, Stuttgart.

Angiolini, C., Riccucci, C., De Dominicis, V., 2002. La flora vascolare della Riserva Naturale Lago di Burano (Grosseto, Toscana meridionale). Webbia 57, 115–152.

Baikov, K.S., 2003a. On systematics of Euphorbia soongarica and allied species in flora of Northern Asia. Bull. Mosc. Soc. Nat. (Biological Series) 108, 41–47.

Baikov, K.S., 2003b. Phylogenetic relations of spurges (Euphorbia, Euphorbiaceae) from Northern Asia. Posterabstract F_01. In: Abstr of the Symposium "Phytogeography of Northeast Asia: Tasks for the 21st century", July 21–25, 2003, Vladivostok, Russia.

Baikov, K.S., 2007. Synopsis of the genus Euphorbia (Euphorbiaceae) in Northern Asia. Bot. Zh. 92, 135–159.

Berg, C., Dengler, J., Abdank, A., Isermann, M. (Eds.), 2004. Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Textband, Weissdorn, Jena.

Bojnanský, V., Fargasová, A., 2007. Atlas of Seeds and Fruits of Central and East-European flora: The Carpathian Mountains Region. Springer, Berlin.

Bondarenko, O.M., Chagovets, R.K., Litvinenko, V.I., Obolentseva, G.V., Sila, V.I., Kigel, T.B., 1969. Euphorbia palustris and Euphorbia stepposa flavonoids and their pharmacological properties. Farm. Zh. Kiev. 26, 46–48.

Bosi, G., Mercuri, A.M., Guarnieri, C., Mazzanti, M.B., 2009. Luxury food and ornamental plants at the 15th century a.d. Renaissance court of the Este family (Ferrara, northern Italy). Veg. Hist. Archaeobot. 18, 389–402.

Braun, U., 1995. The Powdery Mildews (Erysiphales) of Europe. Gustav Fischer, Jena.

Briemle, G., 2002. Nutzungswertzahlen für Gefäßpflanzen des Grünlandes. In: Klotz, S., Kühn, I., Durka, W. (Eds.), BIOLFLOR - Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schriftenr. Vegetationsk., vol. 38, pp. 203–225.

Bundesamt für Naturschutz, 2005. Verordnung zum Schutz wild lebender Tier- und Pflanzenarten (Bundesartenschutzverordnung - BArtSchV). Bonn.

Burkart, M., 2001. River corridor plants (Stromtalpflanzen) in Central European lowland: a review of a poorly understood plant distribution pattern. Glob. Ecol. Biogeogr. 10, 449–468.

Čarni, A., Franjić, J., Škvorc, Ž., 2004. Crataegus nigra Waldst. et Kit. dominated community in the flooded Danube River Area in Croatia. Hacquetia 3, 81–90.

Catalogue of Life, 2007. Annual checklist, World checklist of selected plant families. URL: http://data.gbif.org/datasets/resource/1566 [29.09.2009].

Dahl, E., Hadac, E., 1941. Strandgesellschaften der Insel Ostøy im Oslofjord. Nytt. Mag. Naturvidens. 82, 251–312.

Davis, P.H., 1982. Flora of Turkey and the East Aegean Islands. University Press, Edinburgh.

Denk, T., Frotzler, N., Davitashvili, N., 2001. Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia (Transcaucasia). Biol. J. Linn. Soc. 72, 287–332.

Dierschke, H., 1996. Syntaxonomische Stellung von Hochstauden-Gesellschaften, insbesondere aus der Klasse Molinio-Arrhenatheretea (Filipendulion). Ber. Reinhold-Tüxen-Ges. 8, 145–157.

Dimopoulos, P., Sykora, K.V., Gilissen, C., Wiecherink, D., Georgiadis, T., 2005. Vegetation ecology of Kalodiki Fen (NW Greece). Biol. Bratislava 60, 69–82.

Dragulescu, C., 1995. The flora and vegetation of the Mures (Maros) valley. In: Hamar, J., Sárkány-Kiss, A. (Eds.), The Maros/Mures River Valley. A Study of the Geography, Hydrobiology and Ecology of the River and its Environment. Szolnok - Szeged - Târgu Mureş.

Dragulescu, C., Macalik, K., 1997. The aquatic and paludal flora and vegetation from the Cris/Körös valleys. In: Sárkány-Kiss, A., Hamar, J. (Eds.), The Kris/Körös Rivers Valleys. A Study of the Geography, Hydrobiology and Ecology of the River System and its Environment. Szolnok - Szeged - Târgu Mureş.

Durka, W., 2009. Isolation and characterisation of microsatellite loci for Euphorbia palustris (Euphorbiaceae). Genome 52, 1037–1039.

Eke, T., Al-Husainy, S., Raynor, M.K., 2000. Spectrum of ocular inflammation caused by Euphorbia plant sap. Arch. Ophthalmol. 118, 13–16.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Scr. Geobot., 18.

Frank, D., Klotz, S., 1990. Biologisch-ökologische Daten zur Flora der DDR. Wissenschaftliche Beiträge der Martin Luther-Universität Halle-Wittenberg, p. 19.

FUNET, 2009. URL: http://www.funet.fi/pub/sci/bio/life/index.html [29.09.2009].

Gagne, R.J., 1990. Gall midge complex (Diptera, Cecidomyiidae) in bud galls of palaearctic Euphorbia (Euphorbiaceae). Ann. Entomol. Soc. Am. 83, 335–345.

Gel'tman, D.V., 1996. Euphorbiaceae. Flora Europae Orientalis, vol. 9, pp. 256–287.

Gillner, W., 1960. Vegetations- und Standortsuntersuchungen in den Strandwiesen der schwedischen Westküste. Acta Phytogeogr. Suec. 43, 1–198.

Godreau, V., Bornette, G., Frochot, B., Ambros, C., Castella, E., Oertli, B., Chambaud, F., Oberti, D., Craney, E., 1999. Biodiversity in the floodplain of Saône: a global approach. Biodivers. Conserv. 8, 839–864.

Golub, V.B., Kuzmina, E.G., 1997. The communities of Querco-Fagetea Br.Bl of the Lower Volga Valley. Peddes Repertorium 108, 205–218.

Golub, V.B., Mirkin, B.M., 1986. Grasslands of the lower Volga valley. Folia Geobot. Phytotaxon. 21, 337–395.

Golub, V.B., Saveljeva, L.F., 1991. Vegetation of lower Volga limans (basins without outflow). Folia Geobot. Phytotaxon. 26, 403–430.

Govaerts, R., Frodin, D.G., Radcliffe-Smith, A., 2000. World Checklist and Bibliography of Euphorbiaceae (and Pandaceae), vol. 1–4. The Board of Trustees of the Royal Botanic Gardens, Kew.

Greuter, W., Burdet, H.M., Long, G., 1986. Med-checklist: A Critical Inventory of Vascular Plants of the Circum-Mediterranean Countries. Dicotyledones (Convolvulaceae - Labiataceae). Conservatoire et Jardin botaniques de la Ville de Genève, Genève.

Grime, J.P., 1988. The C-S-R model of primary plant strategies: origins, implications, and tests. In: Gottlieb, L.D., Jain, S.K. (Eds.), Plant Evolutionary Biology. Chapman & Hall, London, pp. 371–393.

Hagyó, A., 2003. The vegetation of the marsh meadow of Zákányszék. Tiscia 34, 3–13.

Hegnauer, R., 1966. Chemotaxonomie der Pflanzen. Birkhäuser, Basel.

Hegi, G., 1924. Illustrierte Flora von Mittel-Europa. Dicotyledones V 1. Lehmanns, München.

Hejny, S., 1960. Ökologische Charakteristika der Wasser- und Sumpfpflanzen in den slowakischen Tiefebenen. Verlag der Slowakischen Akademie der Wissenschaft, Bratislava.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hitchmough, J., 2009. Diversification of grassland in urban greenspace with planted, nursery-grown forbs. J. Landscape Architect. 2009, 16–27.

Hölzel, N., Otte, A., 2004a. Ecological significance of seed germination characteristics in flood meadow species. Flora 199, 12–24.

Hölzel, N., Otte, A., 2004b. Assessing soil seed bank persistence in flood meadows: the search for reliable traits. J. Veg. Sci. 15, 93–100.

Horvat, I., Glavac, V., Ellenberg, H., 1974. Vegetation Südosteuropas. Gustav Fischer, Stuttgart.

Hultén, E., Fries, M., 1986. Atlas of North European Vascular Plants. North of the Tropic of Cancer, vol. II. Koeltz, Königsstein.

IUCN, 2009. Red List of Threatened Species. Version 2009.1. URL: http://www.iucnredlist.org [25.05.2009].

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J.M., Klimes, L., Klimesová, J., Kocvarová, M., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Willmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA Traitbase: a database of life-history traits of Northwest European flora. J. Ecol. 96, 1266–1274.

Klotz, S., Kühn, I., Durka, W., 2002. BIOLFLOR - Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schriftenr. Vegetationsk. 38.

Knuth, P.E.O.W., 1898. Handbuch der Blütenbiologie, unter Zugrundelegung von Hermann Müllers Werk. W. Engelmann, Leipzig.

Korneck, D., Schnittler, M., Klingenstein, F., Ludwig, G., Takla, M., Bohn, U., May, R., 1998. Warum verarmt unsere Flora? Auswertung der Roten Liste der Farn- und Blütenpflanzen Deutschlands. Schriftenr. Vegetationsk. 29, 299–444.

Kuzmanov, B., 1964. On the origin of Euphorbia subgen. Esula in Europe (Euphorbiaceae). Blumea 12, 369–379.

Lauber, K., Wagner, G., 1996. Flora Helvetica. Paul Haupt, Bern, Stuttgart, Wien.

Ledebour, C.F.A., 1833. Flora Altaica IV. G. Reimer, Berlin.

Linné, C.von, 1745. Öländska och gotländska resa År 1741. [Linnaeus's Öland and Gotland Journey 1741]. Translated by Åsberg, M. and Stearn, W.T. 1973. Biol. J. Linn. Soc. 5, 1–107.

Lipsky, W., 1897. Euphorbia Soongarica Boiss. auf der Balkanhalbinsel. Österr. Bot. Zeitschr. 47, 1–2.

List, P.H., Hörhammer, L., 1973. Hagers Handbuch der Pharmazeutischen Praxis IV. Springer, Berlin, Heidelberg, New York.

Loew, E., 1879. Über die Perioden und Wege ehemaliger Pflanzenwanderungen im norddeutschen Tieflande. Linnaea 42, 511–660.

Lombard, A., Arnal, G., 2001. Euphorbia palustris L. in Muséum national d'Histoire naturelle. Conservatoire botanique national du Bassin parisien, URL: http://www.mnhn.fr/cbnbp [01.06.2009].

Ludwig, G., Schnittler, M., 1996. Rote Liste gefährdeter Pflanzen Deutschlands. Schriftenr. Vegetationsk. 28.

Lukasiewicz, A., 1962. Morfologiczno-rozwojowe typy bylin. Poznanskie Towarzystwo Przyjaciol Nauk, 27.

Marchiori, S., Medagli, P., Mele, C., Scandura, S., Albano, A., 2000. Piante ed habitat rari, a rischio e vulnerabili della Puglia. Cah. Opt. Méd. 53, 155–170.

Matthies, D., Poschlod, P., 2000. The biological flora of Central Europe—aims and concept. Flora 195, 116–122.

Matuszkiewicz, M., 2002. Przewodnik do oznaczania zbiorowisk roslinnych Polski. Wydawnictwo Naukowe PWN, Warszawa.

Meusel, H., Jäger, E., Rauschert, S., Weinert, E., 1978. Vergleichende Chorologie der Zentraleuropäischen Flora. Bd. 2. Text und Karten. Gustav Fischer, Jena.

Moser, D., Gygax, A., Bäumler, B., Wyler, N., Palese, R., 2002. Rote Liste der gefährdeten Farn- und Blütenpflanzen der Schweiz. BUWAL, Bern.

Muller, S., 2002. Diversity of management practices required to ensure conservation of rare and locally threatened plant species in grasslands: a case study at a regional scale (Lorraine, France). Biodivers. Conserv. 11, 1173–1184.

Müller-Doblies, U., Albert, G., Müller-Doblies, D., 1975. Der Blütenstand von Euphorbia fulgens Karw. ex Klotzsch und seine variablen Grössen. Bot. Jb. Syst. 96, 290–323.

Narbona, E., Ortiz, P.L., Arista, M., 2002. Functional andromonoecy in Euphorbia (Euphorbiaceae). Ann. Bot. 89, 571–577.

Neinhuis, C., Barthlott, W., 1997. Characterization and distribution of water-repellent, self-cleaning plant surfaces. Ann. Bot. 79, 667–677.

Nikfeld, H., 1999. Rote Listen gefährdeter Pflanzen Österreichs. Grüne Reihe des Bundesministeriums für Umwelt. Jugend und Familie, 10.

Nordal, A., Ogner, G., 1964. The detection of phorbic acid in Euphorbia palustris L. Acta Chem. Skan. 18 (832), 1979.

Nordhagen, R., 1940. Studien über die maritime Vegetation Norwegens I. Die Pflanzengesellschaften der Tangwälle. Bergens Mus. Arb. 1939–40. Naturv. Rekke 2, 5–123.

Nowierski, R.M., Zeng, Z., Schroeder, D., Gassmann, A., Fitzgerald, B.C., Cristofaro, M., 2002. Habitat associations of Euphorbia and Aphthona species from Europe: development of predictive models for natural enemy release with ordination analysis. Biol. Control 23, 1–17.

Oberdorfer, E., 2001. Pflanzensoziologische Exkursionsflora für Deutschland und angrenzende Gebiete. Eugen Ulmer, Stuttgart.

Papp, N., 2004a. Nectar and nectary studies on seven Euphorbia species. Acta Bot. Hung. 46, 225–234.

Papp, N., 2004b. Antimicrobial activity of extracts of five Hungarian Euphorbia species and some plant metabolits. Acta Bot. Hung. 46, 363–371.

Park, K., 1998. Monograph of Euphorbia sect. Tithymalopsis (Euphorbiaceae). Edinb. J. Bot. 55, 161–208.

Pavlov, N.V. (Ed.), 1963. Illustrirovanny opredelitel rastenij Kasachstana, vol. 6 – Izd. AN Kaz. SSR, Almaty.

Pignatti, S., 1982. Flora d'Italia. Edagricole, Bologna.

Pisareva, V.V., 2006. The Akchagylian flora and vegetation of the Udmurtian Kama river Region. Paleont. J. 40, 648–655.

Polatschek, A., 1971. Die Verwandtschaftsgruppe um Euphorbia villosa W. et K. ex Willd. Ann. Naturhist. Mus. Wien 75, 183–202.

Poldini, L., 2002. Nuovo atlante corologico delle piante vascolari nel Friuli Venezia Giulia. Regione Autonoma Friuli Venezia Giulia, Udine.

Poschlod, P., Kleyer, M., Jackel, A.-K., Dannemann, A., Tackenberg, O., 2003. BIOPOP—a database of plant traits and internet application for nature conservation. Folia Geobot. 38, 263–271.

Prosser, F., Sarzo, A., 2002. Flora e vegetazione dei fossi nel settore Trentino del fondovalle dell'Adige (Trentino, Italia settentrionale). Ann. Mus. Civ. Rovereto 18, 89–144.

Rauh, W., 1937. Die Bildung von Hypokotyl- und Wurzelsprossen und ihre Bedeutung für die Wuchsformen der Pflanzen. Nova Act. Leopold. 4, 395–553.

Rehbein, R., Berg, C., 1999. Bemerkenswerte Pflanzen und Pflanzengesellschaften aus dem Rostocker Raum III: Euphorbia palustris L. Bot. Rundbr. Mecklenburg-Vorpommern 33, 47–54.

Remaudière, G., Leclant, F., 2000. Les espéces d'Acyrthosiphon vivant en Europe sur Euphorbia spp. (Hemiptera, Aphididae). Revue Française d'Entomologie (Nouvelle Série) 22, 233–238.

Rössler, L., 1943. Vergleichende Morphologie der Samen europäischer Euphorbia-Arten. Beih. Bot. CentralBl. Abt. B 62, 97–174.

Rydin, H., Snoeijs, P., Diekmann, M. (Eds.), 1999. Swedish Plant Geography. Acta Phytogeogr. Suec., 84, pp. 1–238.

Sáez, L., Soriano, I., 2000. Catàleg de plantes vasculars endèmiques, rares o amenaçades de Catalunya. II. Tàxons no endèmics en situació de risc. Bull. Inst. Cat. Hist. Nat. 68, 35–50.

Schmeil, O., Fitschen, J., 2006. Flora von Deutschland. Quelle & Meyer, Wiesbaden.

Schnittler, M., Günther, K.-F., 1999. Central European vascular plants requiring priority conservation measures—an analysis from national Red Lists and distribution maps. Biodivers. Conserv. 8, 891–925.

Schulz, A., 1899. Entwicklungsgeschichte der phanerogamen Pflanzendecke Mitteleuropas nördlich der Alpen. Forschungen zur deutschen Landes- und Volkskunde 11, 231–447.

Sebald, O., Philippi, G., Seybold, S., 1992. Die Farn- und Blütenpflanzen Baden-Württembergs. Band 4: Spezieller Teil. Spermatophyta, Unterklasse Rosidae. Haloragaceae bis Apiaceae. Ulmer, Stuttgart.

Sehgal, L., Paliwal, G.S., 1974. Studies on the leaf anatomy of Euphorbia. VII. General conclusions and systematic considerations. Phytomorphology 24, 141–151.

Shelyag-Sosonko, Y.R., Sipaylova, L.M., Solomakha, V.A., Mirkin, B.M., 1987. Meadow Vegetation of the Desna Flood Plain (Uraine. USSR). Folia Geobotanica 22, 113–169.

Shishkin, B.K., Bobrov, E.G., 1974. Flora of the U.S.S.R. Geraniales, Sapindales, Rhamnales. Keter Press, Jerusalem.

Sogonov, M.V., Castlebury, L.A., Rossman, A.Y., Mejía1, L.C., White, J.F., 2008. Leaf-inhabiting genera of the Gnomoniaceae, Diaporthales. Stud. Mycol. 62, 1–79.

Tuba, Z., 1995. Overview of the flora and vegetation of the Hungarian Bodrogköz. Tiscia 29, 11–17.

Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M., Webb, D.A., 1964. Flora Europaea. II Rosaceae to Umbelliferae. Cambridge University Press, Cambridge, New York, New Rochelle, Melbourne, Sydney.

Tzvelev, N.N., Gel'tman, D.V., 2006. Flora of Russia—The European Part and Bordering Regions. Volume IX. Magnoliophyta (=Angiospermae), Magnoliopsida (=Dicotyledones). Taylor and Francis, Leiden.

van der Burgh, J., Zetter, R., 1998. Plant mega- and microfossil assemblages from Brunssumian of 'Hambach' near Düren. B. R. D. Rev. Palaeobot. Palynol. 101, 209–256.

van der Ham, R.W.J.M., Kuijper, W.J., Kortselius, M.J., van der Burgh, J., Stone, G.N., Brewer, J.G., 2008. Plant remains from the Kreftenheye formation (Eemian) at Raalte, The Netherlands. Veg. Hist. Archaeobot. 17, 127–144.

van Rompaey, E., Delvosalle, L., 1979. Atlas de la flore Belge et Luxembourgeoise – Ptéridophytes et Spermatophytes. Jardin Botanique National de Belgique, Meise.

von Kirchner, O., Loew, E., Schröter, C., 1932. Lebensgeschichte der Blütenpflanzen Mitteleuropas. Band 3. Geraniaceae. Oxalidaceae. Euphorbiaceae. Callitrichaceae. Eugen Ulmer, Stuttgart.

von Schantz, M., Hackman, W., 1983. En förekomst av *Euphorbia palustris* i Bormav. Memo. Soc. Fauna Flora Fenn. 59, 139–140.

Vroege, P.W., Meeuse, A.D.J., Vinkenoog, S., 1987. A probable case of arachnophily involving *Euphorbia*. J. Plant Sci. Res. 3, 7–10.

Webster, G.L., 1987. The saga of the spurges: a review of classification and relationships in the Euphorbiales. Bot. J. Linn. Soc. 94, 3–46.

Weeda, E.J., van der Meijden, R., Bakker, P.A., 1990. FLORON Red Data List 1990. Red data list of the extinct, endangered and vulnerable plants in the Netherlands in the period 1980–1990. Gorteria 16, 2–26.

Winter, C., Lehmann, S., Diekmann, M., 2008. Determinants of reproductive success: a comparative study of five endangered river corridor plants in fragmented habitats. Biol. Conserv. 141, 1095–1104.

World checklist of selected plant families, 2009. The Board of Trustees of the Royal Botanic Gardens, Kew. URL: http://www.kew.org/wcsp/ [30.09.2009].

Zanetti, M., 1997. Atlante della flora notevole della pianura veneta orientale. Ediciclo, Portogruaro.