

Biological Flora of the British Isles: *Cirsium dissectum* (L.) Hill (*Cirsium tuberosum* (L.) All. subsp. *anglicum* (Lam.) Bonnier; *Cnicus pratensis* (Huds.) Willd., non Lam.; *Cirsium anglicum* (Lam.) DC.)

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Summary

1 This account reviews information on all aspects of the biology of *Cirsium dissectum* (L.) Hill that are relevant to understanding its ecological characteristics and behaviour. The main topics are presented within the standard framework of the *Biological Flora of the British Isles*: distribution, habitat, communities, responses to biotic factors, responses to environment, structure and physiology, phenology, floral and seed characters, herbivores and disease, history and conservation.

2 *Cirsium dissectum* (meadow thistle) is a perennial, rhizomatous herb found in moist, nutrient poor grasslands and heathlands in north-west Europe. It is readily distinguishable from other *Cirsium* species in the British Isles but has been considered a subspecies of *C. tuberosum*, along with *C. filipendulum*, in some other areas of Europe.

3 It is susceptible to being out-competed by species that are able to increase biomass more rapidly. At more productive sites, greater nutrient availability increases the proportion of rosettes that flower, as well as rosette turnover. Seeds germinate readily under a range of conditions in the growth room and greenhouse but seedlings are very rarely found in the field. An examination of its population dynamics reveals that clonal propagation is the dominant form of reproduction, with the low number of seedlings primarily caused by very low establishment rates in vegetation stands.

4 *Cirsium dissectum* is relatively tolerant of drought and shade even though it is found in moist grasslands. At very low pH it suffers from ammonium and aluminium toxicity. As it has suffered habitat loss through drainage and succession, *C. dissectum* has declined in the British Isles and it is now endangered in Germany and the Netherlands.

Key-words: *Cirsium dissectum*, climatic limitation, communities, conservation, ecophysiology, geographical and altitudinal distribution, germination, herbivory, mycorrhiza, parasites and diseases, reproductive biology, soils

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*Abbreviated references are used for many standard works: see *Journal of Ecology* (1975), **63**, 335–344. Nomenclature of vascular plants follows *Flora Europaea* and, where different, Stace (1997).

Sect. *Cirsium* (Sect. *Chamaeleon* DC.). Meadow thistle. A perennial herb with short obliquely ascending stock, cylindrical roots and rhizomes up to 40 cm long. The basal-rosette leaves are 8–25 × 2–3 cm, elliptical–lanceolate, long stalked, sinuate-toothed or slightly pinnatifid. Leaves are slightly hairy above and whitish

cottony beneath with margins bearing soft prickles that are longest on the teeth or lobes. Leaves are not decurrent. The flowering stem is erect, usually simple, terete, cottony and unwinged, 6–80 cm tall. There are usually a few small bract-like leaves above the middle; these are like the basal leaves but oblong–lanceolate and semi-amplexicaul with basal auricles. Capitula are 2.5–3 × 2–2.5 cm, usually solitary. The involucre is ovoid, purplish and cottony with bracts that are lanceolate and appressed, the outer bracts being spine-tipped, the inner acuminate. Flowers are magenta-purple and hermaphrodite. Achenes 3–4 mm long, 1.3–3.6 mg, pale fawn, smooth with a long, pure-white pappus.

Fl. Eur. 4 places *C. dissectum* within the *C. tuberosum* (L.) All. group, along with *C. tuberosum* and *C. filipendulum* Lange. Within the British Isles *C. filipendulum* is not found, and *C. dissectum* is readily distinguishable from *C. tuberosum* by its less pinnatifid leaves, long rhizomes and absence of tuberous roots. All three species occur in Germany, but not in the same sites (Hegi Fl. ed. 6, 2). In France the three species can be difficult to distinguish and Fl. Eur. 4 considers that they could probably be treated as subspecies. Rouy (1905) recognized four forms of *C. anglicum* (synonym of *C. dissectum*): f. *typicum* with regular teathed leaves; f. *angustifolium* with almost linear leaves; f. *dissectum* with irregularly incised or lobed leaves, being more robust than the previous two forms; and f. *ambiguum* with very pinnatifid leaves and strong growth, often with 2–3 stems. Hegi Fl. ed. 6, 2 also describes high levels of variation in the dissection of the leaves. Sell & Murrell (2006) recognize no variants; plants from the British Isles, when grown in standard common garden conditions, typically show only slightly pinnatifid leaves but some populations have recognizably more pinnatifid leaf forms (de Vere 2007).

Cirsium dissectum is largely confined to oligotrophic, weakly to strongly calcareous, wet grasslands and heathlands, fens and dune slacks, often on peaty soils. It tends to grow on sites subject to flushes of base-rich water (Preston *et al.* 2002).

I. Geographical and altitudinal distribution

Cirsium dissectum is an Oceanic West European (Dist. Br. Fl.) or Oceanic Temperate (Preston & Hill 1997) plant, concentrated in the British Isles in south-west England, south Wales and western Ireland (Fig. 1). It is found frequently in Devon, Dorset and Hampshire (particularly the New Forest) and in South Wales. It becomes patchy further north and east, has declined greatly since 1930 (Preston *et al.* 2002) and is still in decline since 1970 (Fig. 1). It is apparently extinct in 8 vice-counties in eastern England (Stace *et al.* 2003) and has been lost from many localities elsewhere, although counties such as Oxfordshire and Berkshire still have a number of sites. The fens of Norfolk and to a lesser extent Suffolk still represent a stronghold for the species. It becomes sporadic as it extends northwards but it has a

number of sites in Yorkshire, north to Roxby, 54°32' N. In Scotland it is found only on Islay and south-east Jura and the adjacent mainland of Kintyre, where it may have colonized naturally from Northern Ireland or possibly been introduced. *Cirsium dissectum* is frequent throughout western Ireland, but it is rare and declining in the north-east (Hackney 1992). Its European distribution is western (Fig. 2): it is found in the Netherlands (Rossenaar & Groen 2003) and has a limited distribution in Belgium (Van Rompaey & Delvosalle 1972) and north-west Germany (Haeupler & Schonfelder 1989). It extends southwards through France, being relatively common (at least formerly) throughout the west, north and centre of the country (Bonnier 1851–1922). In Germany 57% of populations have become extinct since 1930 (Buck-Sorlin 1993) and strong declines have also occurred in the Netherlands (Rossenaar & Groen 2003) and in eastern sites in northern France (Institut floristique Franco-Belge 1995).

Fl. Eur. 4 and Hegi Fl. ed. 6, 4 list *C. dissectum* from Spain but such records are regarded as almost certainly errors by de Bolòs & Vigo (1995). Fl. Eur. 4 describes its occurrence in Italy as doubtful and reports of its presence have not been confirmed (Fiori 1969; Pignatti 1982). It is naturalized in Hungary and Norway (Fl. Eur. 4) (Fig. 2).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Cirsium dissectum has an Atlantic distribution, with Ellenberg (1988) classifying it as having a continentality value of 1, which indicates an extremely oceanic species. In Britain, however, it is also found in the warmer south-east, indicating that it has an Oceanic rather than Hyperoceanic distribution (Preston & Hill 1999), distinguishing it from such Atlantic species as *Dryopteris aemula*, *Pinguicula lusitanica* and *Ulex gallii*. Buck-Sorlin (1993) states that the distribution in north-west Germany is determined by three climatic factors: a mean temperature in January greater than 0 °C, an annual fluctuation of mean temperature less than 16 °C and annual precipitation between 600 mm and 800 mm.

Cirsium dissectum is found in sites that are permanently damp and can be found in sites with standing water during the winter months. This corresponds with an Ellenberg water value (recalibrated for British plants) of 8, intermediate between a damp and a wet site indicator (Hill *et al.* 1999).

A lowland species, it has been recorded up to 500 m in County Sligo (Preston *et al.* 2002).

(B) SUBSTRATUM

In the British Isles *C. dissectum* is a characteristic species of rhos pastures. These are wet grasslands occurring on acidic to neutral soils that comprise a

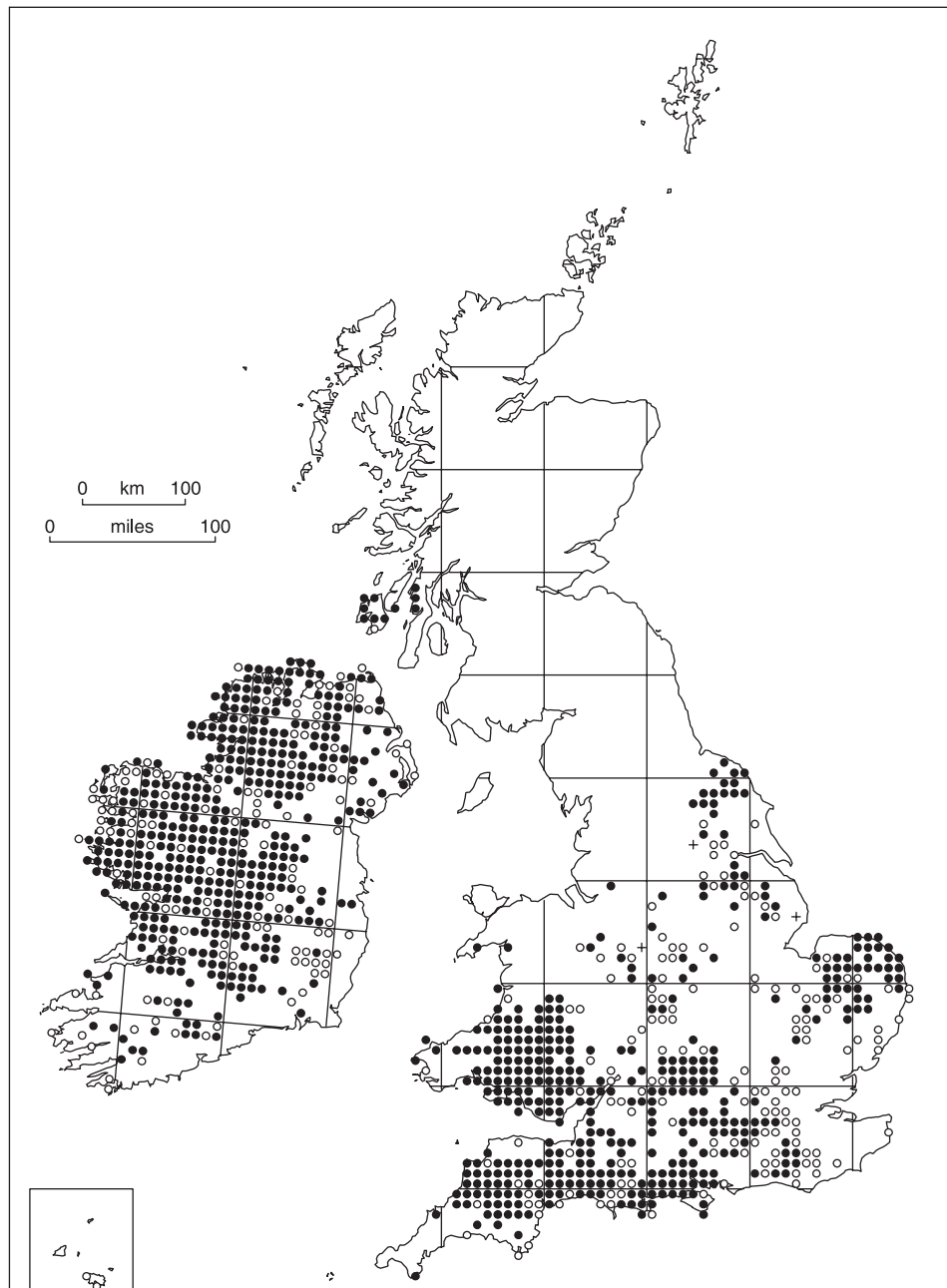


Fig. 1 The distribution of *Cirsium dissectum* in the British Isles. Each dot represents at least one record in a 10 km square of the National Grid. Native: (●) 1970 onwards, (○) pre 1970, (+) introduced. Mapped by H.R. Arnold, using Dr A. Morton's DMAP software, Biological Records Centre, Centre for Ecology & Hydrology, Monks Wood, mainly from data collected by members of the Botanical Society of the British Isles.

mixture of fen meadow, rush pasture and wet heath, often occurring in a mosaic. In Wales these habitats are situated over a wide range of strata ranging from sedimentary and igneous Lower Palaeozoic rocks to Old Red Sandstone, Coal Measures and Carboniferous Limestone of Upper Palaeozoic age (Blackstock *et al.* 1998). In Devon and Cornwall rhos pastures are characteristically found on the Culm Measures, sandstones and shales of late Carboniferous age (Durrance & Lamming 1982) that cover much of mid-Devon through to north-east Cornwall. Soil types include poorly draining surface-water gleys with non-humose, humose or peaty topsoils and peats (Blackstock

et al. 1998; Ross 1999). *Cirsium dissectum* also occurs on sand dune slacks on typical sand-pararendzinas (Ross 1999). In Ireland it extends onto the limestone plateau of the Burren, occurring in the east Burren fens where drainage is impeded (D'Arcy & Hayward 1997).

Mineral nutrient status is typically characterized by particularly low phosphorus and non-limiting concentrations of potassium. Calcium is often abundant in *C. dissectum* sites where it may result from calcareous spring-fed ground water (Wheeler & Shaw 1987). Total nitrogen and organic matter vary considerably from the low concentrations found in sand dunes to high levels in peaty sites (Table 1; de Vere 2007).

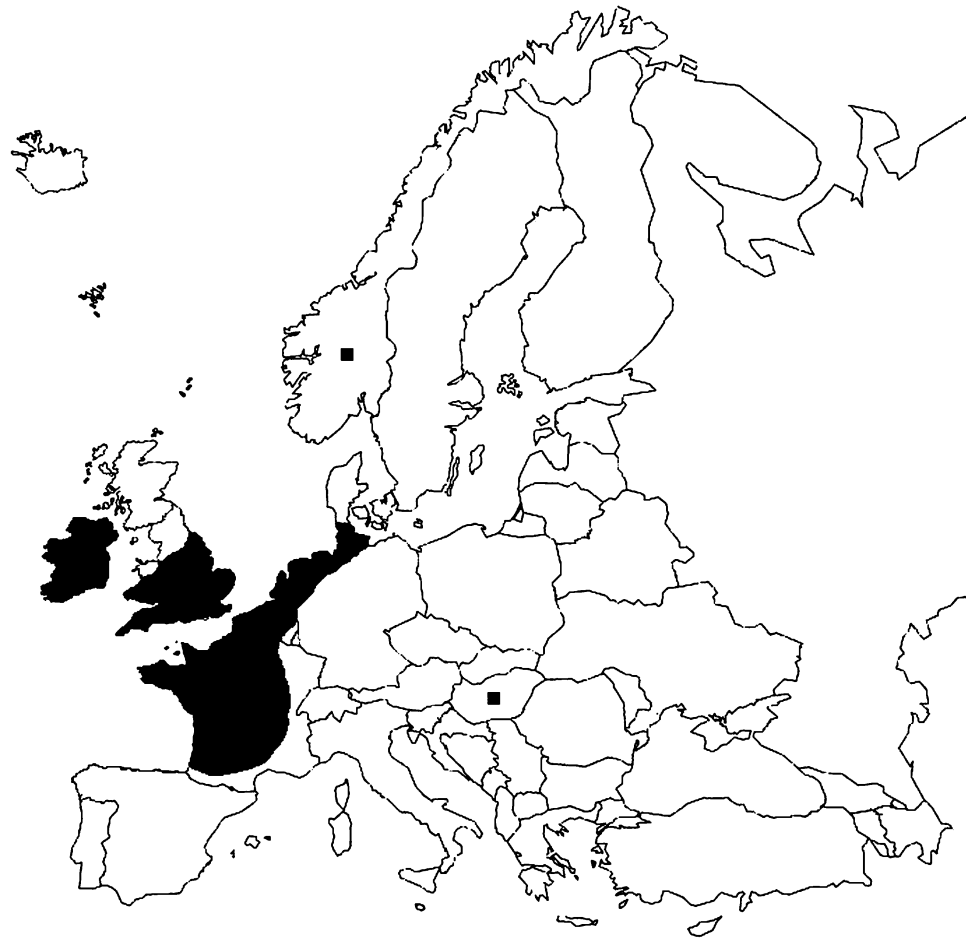


Fig. 2 European range of *Cirsium dissectum* (black shading) based on records in the literature (Fl. Eur. 4; Hegi Fl. ed. 6, 4; Vergl. Chor.; Bonnier (1851–1922); Haeupler & Schonfelder (1989); Van Rompaey & Delvosalle (1972)). Squares represent countries where it is naturalized.

III. Communities

In Europe, *Cirsium dissectum* is a defining species in the Cirsio-Molinietum Siss. et De Vries 1942. This association has been recorded in Britain (Wheeler 1980) and in Ireland (White & Doyle 1982). These are grasslands dominated by *Molinia caerulea* with *Carex panicea*, *Carex hostiana*, *Carex pulicaris*, *Gymnadenia conopsea*,

Potentilla erecta and *Succisa pratensis*. In Ireland *C. dissectum* has a wide synecology (O’Criodain & Doyle 1997). White & Doyle (1982) describe it as a characteristic species of the Junco Conglomerati-Molinion Westhoff 1968 and state that most of the wet grasslands in western Ireland belong to this alliance.

Braun-Blanquet & Tüxen (Ir. Pfl.) defined a Cirsio dissecti-Schoenetum nigricantis association that was

Table 1 Soil nutrient characteristics for 22 *Cirsium dissectum* sites throughout the British Isles, sampled in July 2004. Mean with standard deviation in brackets is given along with minimum and maximum values with site name and grid reference

Nutrient	Mean (SD) <i>n</i> = 22	Minimum (site, National Grid reference)	Maximum (site, National Grid reference)
Total N (%)	0.7 (0.6)	0.1 (Kenfig, Wales, SS784816)	2.4 (Wicken Fen, England, TL562705)
Extractable P (mg kg ⁻¹)	2.7 (2.4)	0.2 (Doagh Lough, Ireland, H079526)	7.8 (Lough Corrib, Ireland, M170434)
Exchangeable K ⁺ (mg kg ⁻¹)	119 (107)	18 (Lough Talt, Ireland, G397161)	529 (Giant’s Causeway, Ireland, C944445)
Exchangeable Ca ²⁺ (mg kg ⁻¹)	3185 (3583)	248 (Mambury Moor, England, SS385171)	12112 (Bleach Lough, Ireland, R441557)
Organic matter (%)	31 (26)	6 (Kenfig, Wales, SS784816)	87 (Lough Corrib, Ireland, M170434)
pH	5.2 (0.5)	4.5 (Rans Wood, England, SU362031)	6.1 (Lough Bunny, Ireland, R382979)

For each of the 22 sites, five topsoil samples (depth 15 cm, diameter 3 cm) were taken with an auger and air-dried. pH was determined electrometrically after mixing air-dried soil with distilled water. Organic matter was determined using loss on ignition (2 h at 800 °C). Total (Kjeldahl) nitrogen was determined using the Kjeltec system 1002 (Tecator, Sweden) and extractable phosphorus using Olsen’s method (Allen *et al.* 1989). Calcium was extracted using 1.0 M ammonium acetate with lanthanum chloride, and potassium with 1 M ammonium nitrate; these elements were then determined using air-acetylene flame absorption in an atomic absorption spectrophotometer (Varian Spectra AA 50, Varian, UK).

unique to Ireland, the characteristic species being *Schoenus nigricans*, *Cirsium dissectum*, *Anagallis tenella* and *Hydrocotyle vulgaris*. White & Doyle (1982) describe the association as widespread throughout Ireland and Ivimey-Cook & Proctor (1966) found it to be the most widespread and characteristic fen type in the Burren, especially in the low-lying limestone country in the eastern part of the area. The most constant species were: *Agrostis stolonifera*, *Carex hostiana*, *Carex panicea*, *Cirsium dissectum*, *Mentha aquatica*, *Molinia caerulea*, *Potentilla erecta*, *Schoenus nigricans*, *Succisa pratensis*, *Aneura pinguis*, *Campyllum stellatum*, *Drepanocladus revolvens sensu lato*, *Fissidens adianthoides* and *Scorpidium scorpioides*. O'Cruidain & Doyle (1997) do not support the *Cirsium dissectum*-*Schoenus nigricans* association as defined by Braun-Blanquet & Tüxen (Ir. Pfl.) and place this community in Ireland within the *Schoenus nigricans* Allorge 1922. They define a new sub association, the *Cirsietosum dissecti*, that comprises vegetation from the driest of habitats for *Schoenus nigricans*.

In Ireland, *Cirsium dissectum* is sometimes found on the edges of turloughs, growing with *Carex panicea*, *Carex hostiana*, *Carex flacca*, *Molinia caerulea* and *Succisa pratensis* on nutrient poor fens, often on skeletal limestone, or with *Schoenus nigricans*, *Molinia caerulea*, *Achillea ptarmica* and *Parnassia palustris* in areas where a layer of fen peat is usually present (Goodwillie 2003); it is not, however, a characteristic turlough species.

de Vere (2007) surveyed 11 sites in England and Wales to examine the range of communities in which *C. dissectum* was found. Sites were chosen that appeared to represent the greatest amount of variation in community type. Ten 2 × 2 m quadrats were surveyed at each site during July or August, and MAVIS Plot Analyser v. 1 (Smart 2000) and Rodwell (1991, 1995, 2000) used to assign the sites to National Vegetation Classification (NVC) communities (Table 2). Detrended Correspondence Analysis (DCA) was carried out (Fig. 3) to examine the relationships between quadrats and sites using the program DECORANA within the Community Analysis Package 2.15 (Pisces Conservation, 2003). Three broad groups emerged when all 11 sites were included in the analysis: (i) SD14b and SD14d (*Salix repens*-*Campyllum stellatum* dune-slack, *Rubus caesius*-*Galium palustre* and *Festuca rubra* subcommunities), (ii) S24c (*Phragmites australis*-*Peucedanum palustre* tall-herb fen, *Symphytum officinale* subcommunity) and (iii) the remainder of sites that consisted of M16b (*Erica tetralix*-*Sphagnum compactum* wet heath, *Succisa pratensis*-*Carex panicea* subcommunity) and M24c (*Molinia caerulea*-*Cirsium dissectum* fen meadow, *Juncus acutiflorus*-*Erica tetralix* subcommunity). When the dune-slack and tall-herb fen communities were removed, the M16b and M24c sites showed some differentiation but still overlapped within the ordination plot. Rodwell (1991, 1995, 2000) does not include *Cirsium dissectum* within the SD14 community and, in addition to the M24, M16 and S24 communities, includes *C. dissectum* within the M21 *Narthecium ossifragum*-

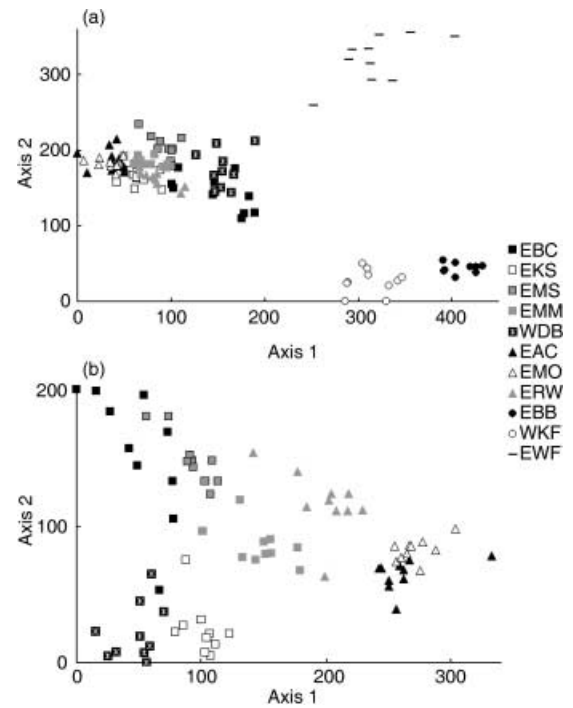


Fig. 3 Detrended Correspondence Analysis of sites where *Cirsium dissectum* is present. Each point represents a single quadrat. See Table 2 for a description of the 3 letter site codes shown. The shape of each point represents a National Vegetation Classification community: squares M24c; squares containing a star M24; triangles M16b; closed circles SD14b; open circles SD14d; dashes S24c. (a) Analysis of all 11 sites surveyed. (b) The same analysis with the SD14b, SD14d and S24c communities removed.

Sphagnum papillosum valley mire, M22 *Juncus subnodulosus*-*Cirsium palustre* fen-meadow, M13 *Schoenus nigricans*-*Juncus subnodulosus* mire and M29 *Hypericum elodes*-*Potamogeton polygonifolius* soakway communities and subcommunities.

Blackstock *et al.* (1998) surveyed 50 wet grassland sites in lowland Wales and examined edaphic and floristic characteristics within them. They suggested an additional subcommunity called the Welsh nodum (M24x) within the M24 community to cover stands that had a poor representation of preferentials for the existing subcommunity types. Three variants of M24x were described with *C. dissectum* occurring in two of these. When Yeo *et al.* (1998) surveyed 114 remnant stands of neutral and acidic dry grasslands and wet pastures in mid-Wales, *Cirsium dissectum* was most frequent in M24b *Molinia caerulea*-*Cirsium dissectum* fen meadow, typical subcommunity, M24c and M24x, but small populations were also recorded from a range of other community types.

IV. Response to biotic factors

(A) GRAZING

Cirsium dissectum has soft prickles on its leaves but these do not form an effective grazing deterrent:

Table 2 Species frequency and abundance data for 11 sites containing *Cirsium dissectum* in Britain

Site Code NVC Community	EBC M24c	EKS M24c	EMS M24c	EMM M24c	WDB M24	EAC M16b	EMO M16b	ERW M16b	EBB SD14b	WKF SD14d	EWf S24c
<i>Achillea ptarmica</i>	V (1–4)	I (1)	IV (1)	II (1)	–	–	–	–	–	–	–
<i>Agrostis canina canina</i>	V (5–9)	V (2–8)	V (3–6)	V (4–6)	I (1–4)	–	IV (1–2)	V (4–8)	–	–	–
<i>Agrostis capillaris</i>	III (2–8)	–	–	–	–	–	–	II (1–4)	–	–	–
<i>Agrostis curtisii</i>	–	–	–	–	–	III (2–8)	V (1–7)	IV (4–5)	–	–	–
<i>Agrostis gigantea</i>	–	–	II (1–8)	–	–	–	–	–	–	–	–
<i>Agrostis stolonifera</i>	II (2–6)	–	–	–	III (1–7)	–	–	–	V (8–9)	IV (1–4)	III (4–7)
<i>Anagallis tenella</i>	–	I (1)	–	–	I (1)	–	I (1)	–	–	III (1–3)	–
<i>Angelica sylvestris</i>	–	–	–	–	I (1)	–	–	–	–	–	IV (1–6)
<i>Anthoxanthum odoratum</i>	I (1)	III (1–3)	III (1)	III (1–2)	IV (1–6)	–	–	–	–	I (1)	–
<i>Asperula cynanchica</i>	II (1–4)	–	–	–	V (1–4)	–	I (1)	I (1)	IV (1)	IV (1–3)	–
<i>Betula pendula</i> seedling	III (1)	–	–	–	–	–	–	II (1)	–	–	–
<i>Betula pubescens</i> seedling	–	–	–	–	–	I (1)	I (1)	–	–	–	–
<i>Briza media</i>	–	–	–	–	I (1)	–	–	–	–	IV (1–8)	–
<i>Calluna vulgaris</i>	I (1)	I (1)	I (2)	III (2–5)	–	V (4–7)	V (2–6)	IV (1–5)	–	–	–
<i>Calystegia sepium</i>	–	–	–	–	–	–	–	–	–	–	II (1)
<i>Carex viridula oedocarpa</i>	–	–	I (1)	IV (1)	–	II (3–4)	V (1–5)	V (1–7)	–	–	–
<i>Carex echinata</i>	–	V (1–3)	I (1)	–	–	–	–	–	–	–	–
<i>Carex flacca</i>	–	–	II (1–5)	I (1–2)	III (1)	–	–	–	–	I (1)	–
<i>Carex hostiana</i>	–	–	–	IV (1–5)	IV (1–4)	–	–	–	–	–	–
<i>Carex nigra</i>	I (1)	–	–	–	II (1)	–	–	–	V (2–8)	IV (1–8)	–
<i>Carex ovalis</i>	III (1–5)	–	–	–	–	–	–	–	–	–	–
<i>Carex panicea</i>	III (1–5)	V (3–5)	IV (1–5)	V (4–7)	IV (1–5)	IV (1–5)	V (3–7)	V (1–6)	III (2–3)	V (1–6)	IV (1–8)
<i>Carex pulicaris</i>	–	I (1)	–	IV (1)	IV (1–3)	I (1)	I (1)	–	–	–	–
<i>Centaurea nigra</i>	–	–	–	–	II (1)	–	–	–	–	I (1)	–
<i>Cirsium dissectum</i>	IV (4–9)	V (1–6)	V (1–6)	V (3–8)	V (1–8)	IV (1–4)	V (3–5)	V (2–6)	III (3–9)	V (3–8)	II (1–5)
<i>Cirsium palustre</i>	II (1–4)	II (1–5)	V (1–5)	I (1)	IV (1)	–	–	–	–	I (4)	III (1–5)
<i>Cynosurus cristatus</i>	–	–	–	–	II (1)	–	–	–	–	–	–
<i>Dactylorhiza maculata</i>	–	IV (1)	–	V (1)	II (1)	–	–	–	–	–	–
<i>Dactylorhiza</i> sp.	–	–	–	–	–	–	–	–	I (1)	II (1)	–
<i>Danthonia decumbens</i>	I (2)	IV (1–3)	–	V (1–3)	III (1–5)	–	V (1–3)	V (1–4)	–	I (1–3)	–
<i>Deschampsia cespitosa</i>	–	–	–	–	–	–	–	–	–	–	I (4)
<i>Eleocharis palustris</i>	–	–	–	–	–	–	–	–	–	I (9)	–
<i>Epilobium hirsutum</i>	–	–	–	–	–	–	–	–	–	–	I (1)
<i>Epilobium palustre</i>	I (1)	I (1)	I (1)	–	II (1)	–	–	–	–	–	–
<i>Epipactis palustris</i>	–	–	–	–	–	–	–	–	IV (1–3)	V (1–3)	–
<i>Equisetum palustre</i>	–	–	–	–	II (1)	–	–	–	V (1–3)	IV (1–4)	–
<i>Erica cinerea</i>	–	–	–	–	–	II (1–5)	III (1–4)	I (1)	–	–	–

Table 2 Continued

Site Code NVC Community	EBC M24c	EKS M24c	EMS M24c	EMM M24c	WDB M24	EAC M16b	EMO M16b	ERW M16b	EBB SD14b	WKF SD14d	EWf S24c
<i>Erica tetralix</i>	I (1)	V (4–6)	–	IV (4–6)	–	V (4–7)	V (1–7)	II (1–4)	–	–	–
<i>Eriophorum angustifolium</i>	–	–	–	–	–	–	–	–	–	I (1)	–
<i>Euphrasia nemorosa</i>	–	–	–	–	–	–	–	–	–	I (1)	–
<i>Festuca rubra</i>	–	IV (4–7)	–	–	V (1–8)	–	–	–	–	–	–
<i>Filipendula ulmaria</i>	–	–	–	–	II (1–4)	–	–	–	I (1)	–	V (1–7)
<i>Fragaria vesca</i>	–	–	–	–	–	–	–	–	–	I (1)	–
<i>Fraxinus excelsior</i> seedling	–	–	–	–	I (1)	–	–	–	–	–	–
<i>Galium uliginosum</i>	–	–	–	–	–	–	–	–	–	–	III (1–4)
<i>Holcus lanatus</i>	IV (1–8)	IV (1–4)	III (1–2)	II (1–3)	V (1–6)	–	–	–	I (1)	III (1–3)	I (1)
<i>Hydrocotyle vulgaris</i>	I (4)	II (1–3)	–	–	–	–	–	I (3)	V (1–9)	V (4–8)	III (3–7)
<i>Iris pseudoacorus</i>	–	–	–	–	–	–	–	–	–	–	IV (1–2)
<i>Juncus acutiflorus</i>	IV (1–7)	V (1–8)	IV (1–4)	III (1–8)	V (1–8)	II (1–3)	–	II (1–6)	–	III (1–4)	–
<i>Juncus articulatus</i>	–	–	–	–	–	–	–	–	II (1)	–	–
<i>Juncus conglomeratus</i>	–	III (1–5)	III (1–7)	IV (1–5)	III (1–8)	III (2–8)	–	–	–	–	–
<i>Juncus effusus</i>	I (1)	I (1)	V (1–7)	I (5–7)	–	II (1)	–	–	–	–	–
<i>Juncus squarrosus</i>	–	–	–	–	–	–	III (1–4)	–	–	–	–
<i>Juncus subnodulosus</i>	–	–	–	–	–	–	–	–	–	–	V (3–9)
<i>Lactuca serriola</i>	–	–	–	–	–	–	–	–	–	I (1)	–
<i>Lathyrus palustris</i>	–	–	–	–	–	–	–	–	–	–	I (1–3)
<i>Lathyrus</i> sp.	–	–	I (1)	–	–	–	I (1)	–	–	–	–
<i>Leontodon autumnalis</i>	–	–	–	–	–	–	–	–	–	II (1–2)	–
<i>Leontodon hispidus</i>	–	–	–	–	–	–	–	–	–	I (2)	–
<i>Leontodon saxatilis</i>	I (2)	–	–	–	–	–	–	–	–	–	–
<i>Lotus corniculatus</i>	–	–	–	–	–	–	–	–	IV (1–4)	IV (1–4)	–
<i>Lotus pedunculatus</i>	V (1–9)	II (1–4)	V (2–6)	IV (1–3)	V (1–4)	–	–	–	–	–	–
<i>Luzula multiflora</i>	I (4)	II (1–3)	I (1)	III (1)	IV (1–3)	–	–	I (1)	–	–	–
<i>Lychmis flos-cuculi</i>	–	–	–	–	III (1)	–	–	–	–	I (1)	I (1)
<i>Lycopus europaeus</i>	I (1)	–	–	–	–	–	–	–	–	I (1)	–
<i>Lysimachia vulgaris</i>	–	–	–	–	–	–	–	–	–	–	III (1–5)
<i>Lythrum salicaria</i>	–	–	–	–	–	–	–	–	–	–	III (1–4)
<i>Melilotus officinalis</i>	–	–	–	–	–	–	–	–	V (1–7)	–	–
<i>Mentha aquatica</i>	II (1–4)	–	–	–	–	–	–	–	V (1–5)	IV (1–4)	II (1–3)
<i>Molinia caerulea</i>	V (4–7)	V (9–9)	V (8–9)	V (7–9)	V (7–9)	V (6–9)	V (6–9)	V (5–8)	–	III (4–5)	IV (7–9)
<i>Myrica gale</i>	–	–	–	–	–	–	–	I (6)	–	–	–
<i>Narthecium ossifragum</i>	–	V (3–8)	–	–	–	–	–	–	–	–	–
<i>Odontites vernus</i>	–	–	–	–	–	–	–	–	I (1)	–	–
<i>Oenanthe lachenalii</i>	–	–	–	–	–	–	–	–	V (1–3)	–	–

Table 2 Continued

Site Code NVC Community	EBC M24c	EKS M24c	EMS M24c	EMM M24c	WDB M24	EAC M16b	EMO M16b	ERW M16b	EBB SD14b	WKF SD14d	EWf S24c
<i>Trifolium dubium</i>	–	–	–	–	–	–	–	–	–	I (1)	–
<i>Trifolium fragiferum</i>	–	–	–	–	–	–	–	–	IV (1–5)	III (1–5)	–
<i>Trifolium pratense</i>	–	–	–	–	I (1–4)	–	–	–	III (1–5)	V (1–5)	–
<i>Trifolium repens</i>	II (1–4)	–	–	–	II (1–5)	–	–	–	IV (1–5)	II (1)	–
<i>Ulex gallii</i>	–	–	–	II (4–6)	–	V (6–8)	–	–	–	–	–
<i>Ulex minor</i>	–	–	–	–	–	–	V (1–5)	I (1)	–	–	–
<i>Veronica scutellata</i>	I (1)	–	–	–	–	–	–	–	–	–	–
<i>Viola canina</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Viola palustris</i>	–	II (1–2)	–	–	V (1–4)	–	IV (1–2)	–	–	–	–

Ten 2 × 2 m quadrats were surveyed at each of 11 sites; in each quadrat all species were identified and abundance estimated using the Domin scale. Roman numerals indicate species frequency (the number of quadrats a species occurs within): I, 1–20%; II, 21–40%; III, 41–60%; IV, 61–80%; V, 81–100%. The numbers in brackets are the Domin range across the quadrats. Site codes: EKS (Knowstone Moor), EMM (Mambury Moor) and EMS (Meshaw Moor) are rhos pasture sites in Devon; WDB (Drostre Bank) is a rhos pasture in Wales; EAC (Aylesbeare Common) is a heath in Devon and EBC (Baddesley Common), EMO (Marlpitt Oak) and ERW (Rans Wood) are New Forest heaths. EBB (Braunton Burrows) is a dune slack in Devon and WKF (Kenfig) a dune slack in Wales. EWf is within Wicken Fen, Cambridgeshire. Sites were assigned to NVC communities using MAVIS Plot Analyser v. 1 (Rodwell 1991, 1995, 2000; Smart 2000).

defoliated plants are seen frequently in cattle-grazed sites. In a growth-room experiment Ross (1999) discovered that *C. dissectum* is reasonably robust in its ability to withstand defoliation. Defoliated plants (with all of the leaves removed) showed a 35% decrease in root relative growth rate (RGR) and a 63% increase in shoot RGR; this allowed leaf biomass to be replaced in less than 8 weeks. Replacement of the leaves depended on adequate nitrogen supply but was not particularly sensitive to low concentrations of phosphorus.

(B) OTHER PLANTS

Cirsium dissectum is susceptible to being out-competed by plants that are able to increase biomass more rapidly, especially when nutrient levels are increased through the effects of fertiliser addition or natural succession (see section V(B) below). In an open greenhouse experiment where *C. dissectum* plants were grown with and without a grass competitor (*Agrostis capillaris*), the below-ground presence of the grass reduced the average biomass of *C. dissectum* by a factor of 5.8 (Jongejans 2004).

V. Responses to the environment

(A) GREGARIOUSNESS

Cirsium dissectum can be locally abundant in sites with suitable conditions. It reproduces vegetatively via long rhizomes and typically forms dense patches within all habitat types. In the British Isles, density varied from 4 rosettes m⁻² in a Welsh rhos pasture to 24 rosettes m⁻² in a sand dune slack at Braunton Burrows, Devon. Jongejans (2004) recorded higher densities for plants in the Netherlands: in five grasslands density varied from 18 to 133 rosettes m⁻².

Figure 4 illustrates the patches of rosettes found within a small population at Wicken Fen, Cambs. The size of each patch was measured and the genetic identity of 35 plants throughout the population was determined using 8 microsatellite loci. Plants with the same multilocus genotype belong to the same clone. Each patch generally contains more than one multilocus genotype suggesting that patches often contain more than one clone (de Vere 2007).

(B) PERFORMANCE IN VARIOUS HABITATS

Table 3 compares morphological variation in plants growing in three different community types. The differences between the populations are due to phenotypic plasticity and genetic differentiation (de Vere 2007). There is considerable variation in the proportion of plants that flower at different sites; de Vere (2007) showed a significant positive relationship between the proportion of *C. dissectum* rosettes that flower and the mean vegetation height within the community ($r^2 = 0.544$, $\beta = 0.753$, $t = 4.99$, $P < 0.001$).

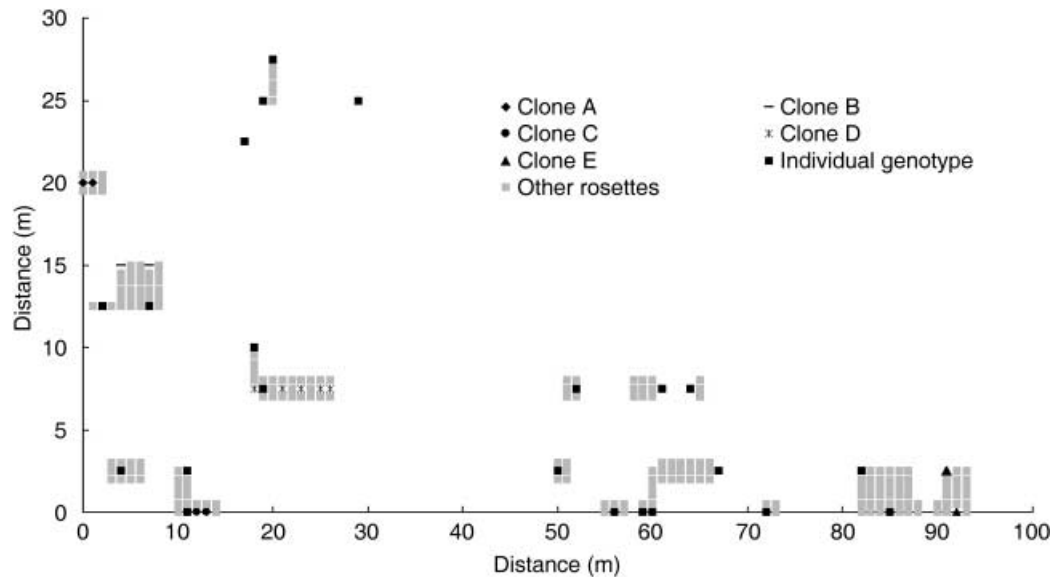


Fig. 4 Schematic representation of a *Cirsium dissectum* population at Wicken Fen, Cambridgeshire. Grey boxes represent the positions of patches of *C. dissectum* rosettes. Black symbols represent individual rosettes that have been genotyped using eight microsatellite loci. Black squares represent rosettes with different multilocus genotypes. Rosettes with the same multilocus genotype are represented with the same symbol (de Vere 2007).

Table 3 Morphological variation in leaves and flowering stems of *Cirsium dissectum* plants from 3 sites in Devon: Knowstone Moor (EKS), Aylesbeare Common (EAC) and Braunton Burrows (EBB). Leaf characters were measured on vegetative rosettes and flowering stem height on flowering rosettes. Means (SD in parentheses) are given, along with the results of one-way ANOVAs followed by *post hoc* Tukey tests. Mean squares, *F*-ratios and *P*-values are shown. Sites that do not share a letter are significantly different

	Knowstone Moor (EKS) (<i>n</i> = 30)	Aylesbeare Common (EAC) (<i>n</i> = 30)	Braunton Burrows (EBB) (<i>n</i> = 30)	MS	<i>F</i>	<i>P</i>
Number of leaves per rosette	3.1 (1.1)a	3.6 (1.4)ab	3.9 (1.3)b	5.3	3.4	0.037
Leaf length (cm)	10.4 (2.3)a	8.2 (4.1)a	16.2 (6.0)b	514.4	25.7	< 0.001
Leaf width (cm)	2.3 (1.6)ab	1.9 (0.6)a	2.7 (0.7)b	5.3	4.5	0.014
Petiole length (cm)	6.4 (3.3)a	2.7 (2.5)b	5.6 (3.2)a	117.4	13.1	< 0.001
Length of flowering stem (cm)	63.7 (12.0)a	64.9 (24.5)a	50.5 (11.6)b	1896.8	6.3	0.003

Jongejans *et al.* (2006a) examined the effect of increasing productivity on *C. dissectum* in a garden experiment. Individual rosettes of *C. dissectum* were surrounded by *Molinia caerulea* plants and the effect of nutrient enrichment (equivalent of 120 kg N ha⁻¹ year⁻¹) examined. The biomass of *M. caerulea* tripled in the nutrient-enriched plots and the increased competition caused a decrease in *C. dissectum* survival from 90% in un-enriched plots to 33% in enriched plots. Nutrient enrichment did not increase the total biomass of *C. dissectum* but did increase the percentage of rosettes that flowered from 2.3% in un-enriched plots to 19% in the enriched plots. The turnover rate of plants was also increased, partly due to the increased flowering, but also due to an increase in rosettes that died without flowering. The increased allocation to sexual reproduction in enriched plots was due to the reduced cost of producing flowers and seeds when more nutrients were available and also through a reduction in the root–shoot ratio (Jongejans *et al.* 2006a). The latter is presumably an adaptive response to the

need to compete for light rather than nutrients. It therefore appears that in more productive sites, flowering is greater, but *C. dissectum* will become out-competed.

Soons & Heil (2002) investigated the effect of population size and site productivity on the ability of *C. dissectum* to colonize new areas in the Netherlands. Productivity was assessed by clipping three 20 × 20 cm vegetation plots at each site and determining the mean dry mass. Colonization ability consisted of seed production, dispersal ability and germination. Dispersal ability was represented by the relative height that seeds were released (the height of the capitulum above the soil surface minus the height at which the horizontal wind speed was zero) and the terminal velocity of seeds (greater terminal velocity decreased the possibility of long distance dispersal). Smaller populations were found to have lower colonization capacity as they produced fewer seeds per capitulum, had lower percentage germination (under greenhouse conditions) and a narrower range of seed dispersal distances. Sites with

greater productivity had higher seed production and percentage germination was greater under greenhouse conditions. These factors should allow greater colonization capacity of nearby sites but this will only be possible if there are safe sites for seedling establishment; other research suggests that this is very rarely the case (see sections VI(C) and VIII(D)). Seed dispersal ability decreased with greater productivity, reducing the possibility of longer distance dispersal.

(C) EFFECT OF FROST, DROUGHT, ETC.

Cirsium dissectum is found in moist habitats, although some of its sites such as the heaths of the New Forest, Culm grasslands of south-west England, well-drained *Schoenus* fens on limestone and sand-dune slacks will dry out to an extent during the summer. Ross (1999) showed that plants grown in growth-room conditions were able to survive more than 32 h but less than 64 h in a post-wilting state but that this had a negative impact on relative growth rate (see section VI(E)(ii)). It therefore seems likely that *C. dissectum* can survive limited periods of summer drought even though it will affect subsequent growth.

VI. Structure and physiology

(A) MORPHOLOGY

Cirsium dissectum has a hemi-cryptophyte basal rosette growth form. It typically produces new rosettes at the end of long rhizomes but new rosettes can also be formed at the base of existing ones. Rhizomes are a pale straw colour and smooth, with small brown scales at the nodes. Rhizome lengths vary, from close to the parent plant to up to 40 cm, and they grow in a downward curve through the soil, seemingly unaffected by roots or tussocks of other species or soil type (Jongejans 2004). After 2 years, plants have produced a large caudex, approximately 10 × 2 cm (de Vere 2007). Jongejans (2004) investigated the relationships between rosette size, flowering probability, rhizome formation and site characteristics within five grasslands in the Netherlands. The number of rhizomes produced by a plant varied from 0 to 5 and was generally positively correlated with its caudex weight; caudex weight in turn was positively correlated with site productivity. The most productive grassland had the greatest percentage of rosettes that flowered; flowering rosettes had heavier caudices than vegetative rosettes and produced more rhizomes. Rhizome length and depth did not differ systematically between sites.

(B) MYCORRHIZA

Arbuscular mycorrhizas are found, with the youngest fine roots being the most heavily colonized and older roots having very little detectable arbuscule development (Ross 1999).

(C) PERENNATION: REPRODUCTION

Cirsium dissectum is a long-lived perennial; in productive sites it can flower in its second year at the earliest. Rosettes die after flowering, but generally plants reproduce vegetatively before this.

Survival and growth of seedlings in the field is very rare and clonal propagation is the dominant form of reproduction (Jongejans 2004; Jongejans *et al.* 2006b). In a 5-year study of three grasslands in the Netherlands, Jongejans (2004) found only three seedlings. Similarly Kay & John (1994) and de Vere (2007) found no seedlings in their surveys of populations in the British Isles. The low number of seedlings is caused primarily by very low establishment rates in vegetation stands (Jongejans *et al.* 2006b; de Vere 2007), as seedlings are more abundant in restoration areas where the top soil has been removed near *C. dissectum* populations (Jongejans 2004).

(D) CHROMOSOMES

Material from Port Ellen, Islay was found to be $2n = 34$ (Morton 1977).

(E) PHYSIOLOGICAL DATA

(i) Response to shade

Ross (1999) compared relative growth rate in *C. dissectum* and *Helianthus annuus* at two light levels, 350 and 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photon flux density, in a growth room with a 16 h day at 22 °C and 15 °C night. Plants were grown in conical flasks containing Rorison nutrient solution. The mean relative growth rate was 0.063 $\text{g g}^{-1} \text{day}^{-1}$ for *C. dissectum* and 0.125 $\text{g g}^{-1} \text{day}^{-1}$ for *H. annuus* at the higher light, and 0.055 $\text{g g}^{-1} \text{day}^{-1}$ for *C. dissectum* and 0.105 $\text{g g}^{-1} \text{day}^{-1}$ for *H. annuus* at the lower light; Ross (1999) concluded that *C. dissectum* was relatively tolerant of shade. Ellenberg (1988) gave *C. dissectum* a light indicator value of 7, representing a species of well-lit places that also occurs in partial shade, but Hill *et al.* (1999) gave *C. dissectum* within Britain a light indicator value of 8, representing a light-loving plant rarely found where relative illumination in summer is less than 40%.

(ii) Water relations

Ross (1999) investigated water uptake and water-use efficiency using a gravimetric method; plants were grown in conical flasks containing Rorison nutrient solution and the use of water determined by weighing the plants and the conical flasks containing the solutions at regular intervals. *Helianthus annuus* was also grown so that the water use of this mesophytic species could be compared to *C. dissectum*. The experiment was carried out in a growth room with a 16 h day at 22 °C and 15 °C night with day-time light

supplied at $350 \mu\text{mol m}^{-2} \text{s}^{-1}$ photon flux density. The mean relative water uptake (RWU) was 0.41 g mm^{-2} leaf area for *C. dissectum* and 0.28 g mm^{-2} leaf area for *H. annuus*. The mean water use efficiency (measured as dry matter/water used in transpiration) was 0.394 dry mass gain g g^{-1} water used for *C. dissectum* and 0.397 dry mass gain g g^{-1} water used for *H. annuus*. *Cirsium dissectum* thus appears to have a relatively high water use but similar levels of water use efficiency compared to a mesophytic species. Ross (1999) went on to investigate the response of *C. dissectum* to dehydration by growing plants in pots of sand until wilting point was reached and then examining the effects of increasing the number of hours before plants were re-watered. Plants were allowed to reach wilting point (when all leaves were visibly flaccid at the beginning of a day-time cycle); these were then watered for the next 6 weeks to allow a recovery period, and harvested. There was a significant, negative, linear relationship between the number of hours that water was withheld after the wilting point had been reached and subsequent relative growth rate ($r^2 = 0.41$, $P < 0.001$). Plant survival was 100% for plants left for up to 32 h after wilting before being watered but at 64 h all of the plants died (no intervals between were measured).

(iii) Response to nutrients

Pegtel (1983) included *C. dissectum* in a glasshouse pot experiment where plants were watered with nutrient solutions lacking various nutrients. Solutions lacking phosphate and nitrate resulted in plants that showed very little increase in dry mass over time, whilst the absence of sulphate caused little reduction in growth. The absence of potassium slowed down growth after 2 months and symptoms of deficiency became visible as necrotic spots on the leaves. Absence of calcium and magnesium also slowed growth but to a lesser extent than potassium.

Hayati & Proctor (1990) analysed the chemical composition of leaf material collected in June from Aylesbeare Common, Devon, and identified relatively high concentrations of Ca 1.85 (SD 0.41), Mg 0.41 (SD 0.06), K 2.27 (SD 0.19), Na 0.95 (SD 0.21) and P 0.146 (SD 0.071), expressed as percentage dry mass. They also found that plant Ca and Mn was positively correlated with soil Ca and Mn status, while plant Mg and Na were negatively correlated with soil Ca. Hayati & Proctor (1991) investigated plant responses to nutrients (Ca, Mg, N, P and K) added to pots of wet heath peat. This demonstrated that *C. dissectum* showed a strong positive response to calcium carbonate but not to calcium chloride, and to added P but not to N or K.

Cirsium dissectum is not found in very acidic soils and this is likely to be due to toxic effects of raised aluminium and ammonium concentrations in areas with pH lower than 4.5. de Graaf *et al.* (1997) studied the effects of Al concentrations and Al : Ca ratios

on the growth of *C. dissectum* in nutrient solution experiments. Aluminium accumulation in the shoots was seen as Al concentrations in the nutrient solutions were increased and this correlated with a reduction in growth at high Al concentrations ($200\text{--}500 \mu\text{mol L}^{-1}$). Poor root development, yellowish leaves and reduced contents of Mg and P in the plants were observed, all indications of Al toxicity. These negative effects were partially counterbalanced when plants were grown in the same Al concentration but with increased Ca concentrations, resulting in lower Al : Ca ratios.

de Graaf *et al.* (1998) investigated ammonium toxicity in a hydroculture experiment using nutrient solutions that differed both in mineral nitrogen form and in ammonium concentration. It was found that plants performed better using nitrate as a nitrogen source than when ammonium was used, with increasing ammonium concentrations causing a reduction in growth. Lucassen *et al.* (2002) elaborated on the findings of de Graaf *et al.* (1998) by suggesting that ammonium as the sole nitrogen source only had a negative effect on *C. dissectum* when in combination with low pH. Ammonium uptake at a rhizosphere pH of 4 resulted in decreased survival rate and biomass development. At higher pH or when nitrate was the sole nitrogen source these effects were not seen. Similarly, Dorland *et al.* (2003) conducted glasshouse dose-response experiments examining the influence of ammonium on germination and survival: a significant negative correlation of both germination and survival with increasing ammonium addition was found at a pH of 4.3.

Franzaring *et al.* (2000) examined the response of *C. dissectum* to elevated ozone concentrations. After 28 days of ozone levels of $26.3 \mu\text{L L}^{-1}$ (accumulated exposures over a threshold of 40 nL L^{-1}), a significant decrease in root mass and the root:shoot ratio was observed and after 113 days a significant decrease in shoot mass was seen. These results were in marked contrast to *Molinia caerulea*, which showed an increase in growth in response to elevated ozone.

(F) BIOCHEMICAL DATA

No biochemical data are available.

VII. Phenology

The large elliptical-lanceolate leaves of *C. dissectum* die back in winter and are often replaced with much smaller lanceolate leaves. These are hairless and fleshy and persist throughout the winter, often being partially or completely submerged in standing water. The larger, hairy leaves begin to appear again in the British Isles by March with full-sized rosettes present by May. Flowering can start as early as the end of May, with most occurring in June and continuing throughout July. Ripe seed-heads can be found throughout July and August.

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

There are generally 20–160 florets in each capitulum (de Vere 2007). Florets are hermaphrodite; however, Smith (1822) recorded gynodioecy in a population in Ashdown Forest in Sussex but this has not been reported since. The corolla consists of a tube *c.* 9 mm long and a limb of *c.* 11 mm, which divides into 5 irregular lobes of *c.* 5 mm. The corolla tube is white and the limb a deep magenta–purple. Five epipetalous stamens are attached at the junction of the tube and limb of the corolla; the filaments are *c.* 5 mm long and the connate, creamy-white anthers 5.8 mm. The anther tube encloses the central part of the style and ends in five teeth. The style is magenta–purple, *c.* 25 mm (Fig. 5).

The florets have a sweet perfume and produce copious nectar; a range of butterflies, bumblebees and long-tongued dipteran flies visits them. In a small population of *C. dissectum* at Cwm Hydfer, Wales, Kay & John (1994) recorded a mean flight distance between

capitula for the small pearl-bordered fritillary (*Boloria selene* Denis & Shiffermueller) of 2.45 m (*n* = 7) with a maximum distance of 4.8 m and a possibility of occasionally much longer interflight distances of greater than 30 m. The common carder bumblebee (*Bombus pascuorum* Scopoli) flew a mean distance between capitula of 1.33 m (*n* = 11) with a maximum of 3 m.

The pollen grain is circular to three-angled in polar view, with a diameter of *c.* 50 µm; it is echinate and circular to slightly elliptical in meridian view (Fig. 6; de Vere 2007).

(B) HYBRIDS

The hybrid *C. dissectum* × *C. palustre* = *C.* × *forsteri* (Sm.) Loudon is not infrequent where the parents occur and is the commonest hybrid thistle (Stace 1997; Preston *et al.* 2002). It is found throughout the range of *C. dissectum* in the British Isles and has been recorded from France and the Netherlands (Hyb. Br. Isl.). It has discontinuously spiny winged, cottony pubescent stems and intermediate leaves and capitula. *Cirsium*

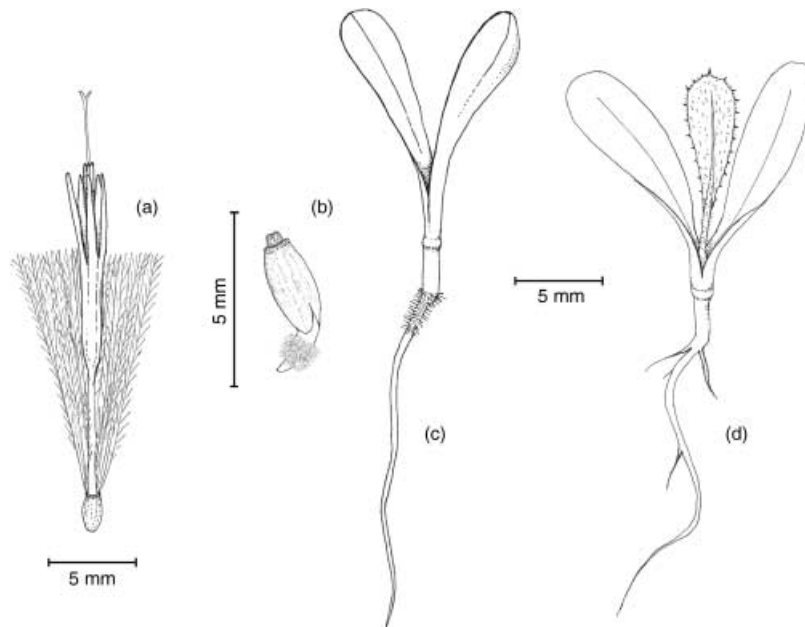


Fig. 5 Floret and seedling development in *Cirsium dissectum*: (a) single floret with part of the pappus removed; (b–d) developing seedling.

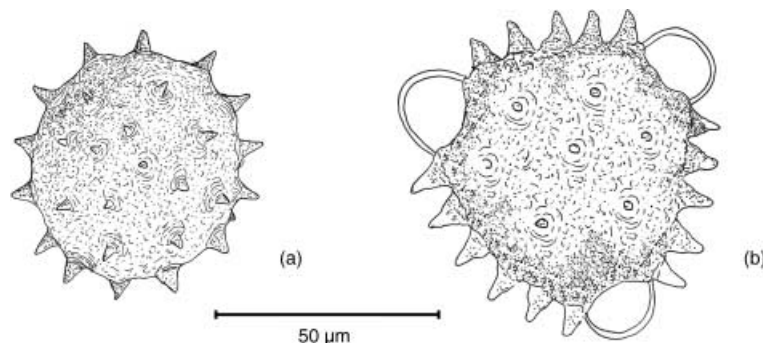


Fig. 6 Pollen grain of *Cirsium dissectum* in (a) meridian and (b) polar view.

dissectum × *C. acaule* = *C. × woodwardii* was known from Pen Hill, Swindon, north Wilts between 1848 and 1952 and recorded at South Lopham Fen, east Norfolk, in 1953 (K. J. Walker, pers. comm.).

(C) SEED PRODUCTION AND DISPERSAL

(i) Seed production

Most commonly, only a single capitulum is produced although most populations contain some plants with two or three capitula. *Cirsium dissectum* is self-compatible but selfed capitula produce fewer seeds. Capitula selfed using a paintbrush showed an 89.4% reduction in the number of seeds produced compared to individuals that were out-crossed using the same method ($n = 119$; de Vere 2007). Within each seed head a number of hollow seeds without embryos is often found alongside those that are filled. de Vere (2007) collected 30 seed heads from each of 22 populations throughout the British Isles to examine seed production. The mean number of seeds within a seed head was highly variable both within and between populations. The lowest mean number of seeds per capitulum was observed to be 6.5 (SD 8.5) at Kenfig Burrows in Wales. The highest was at Aylesbeare Common, Devon, with 82.7 (SD 28.1). The mean air-dry mass per achene (with the pappus removed) varied from 1.32 mg (SD 0.42) at a heathland site in the New Forest to 3.63 (SD 0.99) within a highly productive *Schoenus nigricans* fen on the shores of Lough Corrib, Ireland. The mean air-dry achene mass per population was correlated to the concentration of phosphorus in the soil ($r = 0.42$; $P < 0.05$). Jongejans *et al.* (2006b) recorded a range of 72–94 flowers per capitulum with 0.09–0.49 seeds per flower in unpredated capitula and 0–0.37 seeds per

flower in predated capitula in three grasslands within the Netherlands. Flowering and seed production varied significantly over the 5 years that the grasslands were monitored.

(ii) Seed dispersal

The pappus often becomes detached before the seed is shed from the capitulum. Wind dispersal occurs in dry conditions as the pappi stick together when they are wet. Rosettes die after flowering and the flowering stem generally dries out and thins just below the capitulum causing the stem to bend over and eventually break, releasing the capitulum often close to the parent plant. This appears to be an additional dispersal mechanism for the seeds still trapped inside.

de Vere (2007) measured the distance travelled by seeds with pappus attached over 2 days at Braunton Burrows, Devon. On both days wind speed was approximately 7–8 m s⁻¹ at 10 m height, with occasional stronger gusts. Capitula containing ripe seeds ready for dispersal were located and seeds with pappus attached gently dislodged and tracked. Most of the 110 seeds landed within a few metres of the parent plant with only one seed travelling over 20 m (Fig. 7). Kay & John (1994) investigated seed dispersal at Kenfig, Wales and observed dispersal distances up to 10 m at wind speeds of approximately 2 m s⁻¹ and up to 20 m at speeds of around 3–4 m s⁻¹.

Simulated seed dispersal kernels determined by Soons *et al.* (2005) show high probabilities of dispersal close to the parent plant, with dispersal probability dropping to zero at approximately 13 m. The wind speeds used in the model represented the average wind speed distribution during the dispersal season (June to October) in the interior of the Netherlands. Simulations

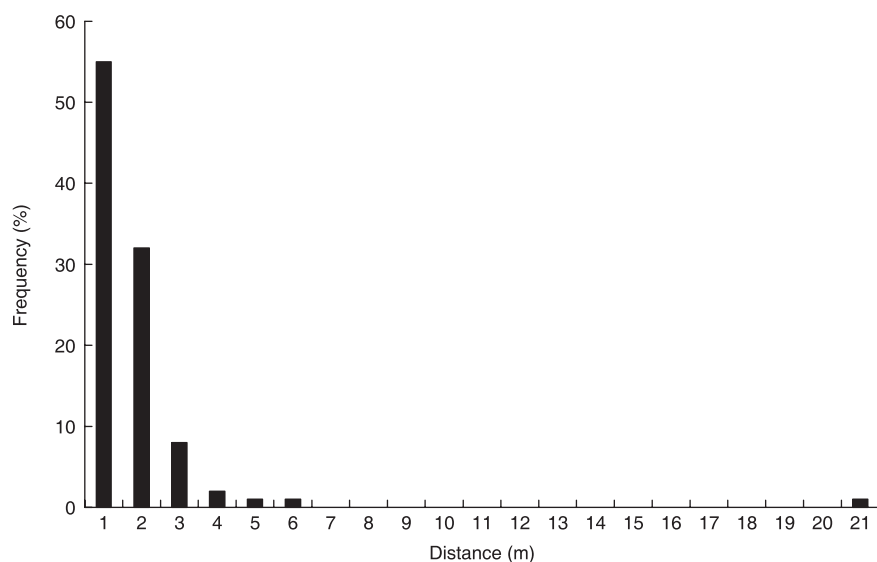


Fig. 7 Dispersal distances for 110 seeds from 11 capitula of *Cirsium dissectum*. Ripe seeds with pappus attached were dislodged from capitula and tracked. If after landing the seed did not move for 2 min, the distance it had travelled was measured. Seed dispersal was measured over 2 days at Braunton Burrows, Devon, with a wind speed of approximately 7–8 m s⁻¹ and occasional stronger gusts.

estimated that 1 in 10 000 seeds would be dispersed over 3.4 km under stormy conditions, with an average horizontal wind speed of 22 m s⁻¹ at 10 m height) (Soons 2006). The dispersal potential of *C. dissectum* therefore appears to be lower than that of *C. vulgare* (Klinkhamer *et al.* 1988) and *C. eriophorum* (Tofts 1999).

(D) VIABILITY OF SEEDS: GERMINATION

J. Ross (unpublished data) investigated germination at 16, 23 and 31 °C for stratified (moist conditions at 5 °C for 6 weeks) and non-stratified (stored dry at 20 °C) seeds in growth conditions of a 16-h day at 43 μmol m⁻² s⁻¹ photon flux density and an 8-h night. Fifty seeds per treatment were germinated in Petri dishes lined with moist filter paper with each treatment having three replicates (Fig. 8). The final percentage germination was higher and the time taken for half of the seeds to germinate (t₅₀) was lower when the temperature was

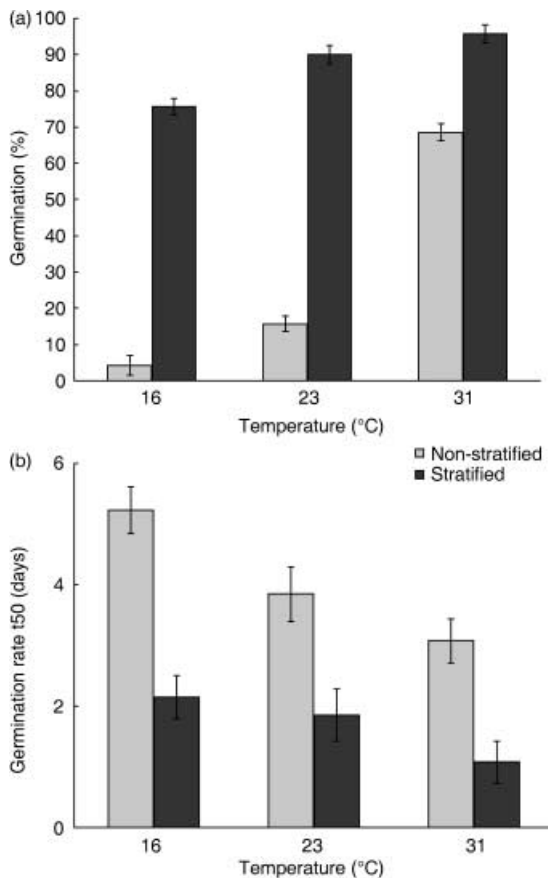


Fig. 8 Germination of stratified and non-stratified seeds of *Cirsium dissectum*. (a) Final percentage germination; (b) germination rate expressed as time taken for 50% of the seeds to germinate (t₅₀). Stratified seeds were stored under moist conditions at 5 °C for 6 weeks, whilst non-stratified seeds were stored dry at 20 °C. Seeds were germinated in a growth room with a 16-h day at 43 μmol m⁻² s⁻¹ photon flux density and an 8-h night. Three replicates of 50 seeds were used per treatment. Germination was carried out in Petri dishes lined with moist filter paper and monitored for 30 days. Adapted from unpublished data of J. Ross.

increased. In all cases stratified seeds germinated better and faster than non-stratified seeds. Seeds were able to germinate in light and dark conditions.

Isselstein *et al.* (2002) investigated seedling establishment by adding *C. dissectum* seeds to a *Cirsio-Molinietum* and a species-poor grassland under treatments including irrigation, cutting of the surrounding vegetation and disturbance of the soil surface. Seedling establishment of *C. dissectum* was consistently higher on the *Cirsio-Molinietum* compared to the species-poor grassland but was still only 15% in the absence of any treatments. Disturbance of the soil and removal of the surrounding vegetation both significantly increased establishment levels. Jongejans *et al.* (2006b) and Soons *et al.* (2005) observed even lower seedling establishment after seed addition in a range of natural *Cirsio-Molinietum* grasslands within the Netherlands, although again establishment was higher in sites where topsoil had been removed as a restoration measure. Smulders *et al.* (2000) recorded seedling establishment of 9–19% when *C. dissectum* seed was added to experimental plots at a restoration site in the Netherlands.

Germination is thus able to occur over a wide range of temperatures and conditions but seedling establishment in experimental field conditions where seeds are added is low and natural establishment is very rarely observed.

(E) SEEDLING MORPHOLOGY

Stages in seedling development are shown in Fig. 5. Cotyledons are obovate with the tip rounded, 12–35 × 5–8 mm. The first true leaves are elliptical–lanceolate to spatulate, having some hairs above and soft prickles, cottony below.

IX. Herbivory and disease

(A) ANIMAL FEEDERS OR PARASITES

Table 4 lists the animal feeders and parasites recorded from *C. dissectum*. de Vere (2007) collected 30 seed heads from 22 populations throughout the British Isles and observed seed predation by Tephritid flies in 13 of these populations. The effects varied from small holes created in some seeds whilst the rest of the seeds in the capitulum were unaffected, to the complete destruction of all the developing seeds. The highest levels of predation were recorded at Lough Bunny in the Burren, Ireland, with 63% of capitula showing some signs of predation by *Chaetostomella cylindrica* (Robineau-Desvoidy). *Chaetostomella cylindrica* was the most widespread species, occurring in seed heads throughout the British Isles, *Terellia ruficauda* (Fabricius) and *Terellia serratulae* (L.) were found only in seed heads from England and Wales, whilst *Tephritis conura* (Loew) was found only in seed heads from Ireland. Floral herbivory was estimated to reduce seed production by 5% in the Netherlands (Jongejans *et al.* 2006b).

Table 4 Invertebrate species recorded from *Cirsium dissectum*

Species	Source	Ecological notes
Araneae		
Philodromidae		
<i>Tibellus oblongus</i> (Walckenaer)	6b	Nesting in capitulum
Coleoptera		
Curculionidae		
<i>Rhinocyllus conicus</i> (Froehlich)	4	Larvae and adults phytophagous, coastal
<i>Sitona</i> sp.	6a	
Diptera		
Agromyzidae		
<i>Phytomyza autumnalis</i> Griffiths	1	Larvae oligophagous. May house puparium. Mining
<i>Liriomyza strigata</i> (Meigen)	1	Larvae polyphagous. Mining
Tephritidae		
<i>Chaetostomella cylindrica</i> (Robineau-Desvoidy)	2, 6a	Larvae feed and pupate within the capitulum
<i>Terellia ruficauda</i> (Fabricius)	2, 6a	Larvae feed and pupate within the capitulum
<i>Terellia serrataulae</i> (Linnaeus)	6a	Larvae feed and pupate within the capitulum
<i>Tephritis conura</i> (Loew)	6a	Larvae feed and pupate within the capitulum
Syrphidae		
<i>Rhingia campestris</i> Meigen	3	Flower visitor
<i>Volucella bombylans</i> (Linnaeus)	3	Flower visitor
<i>Volucella pellucens</i> (Linnaeus)	6b	Flower visitor
Hemiptera		
Cercopidae		
<i>Philaenus spumarius</i> (Linnaeus)	6b	Nymph sucks sap from flowering stem. Polyphagous
Hymenoptera		
Apidae		
<i>Bombus pascuorum</i> (Scopoli)	3	Flower visitor
Lepidoptera		
Nymphalidae		
<i>Eurodryas aurinia</i> (Rottemburg)	6b	Flower visitor
<i>Boloria selene</i> (Denis & Shiffermueller)	3	Flower visitor
<i>Argynnis aglaja</i> (Linnaeus)	6b	Flower visitor
Pieridae		
<i>Pieris napi</i> Linnaeus	3	Flower visitor
<i>Gonepteryx rhamni</i> Linnaeus	6b	Flower visitor
Papilionidae		
<i>Papilio machaon britannicus</i> (Seitz)	5	Flower visitor
Zygaenidae		
<i>Zygaena trifolii</i> (Esper)	6b	Flower visitor

Sources: 1, Spencer (1972); 2, White (1988); 3, Kay & John (1994); 4, Zwölfer & Harris (1984); 5, Borsje (2005); 6a, N. de Vere, pers. observ.: insects reared from capitula, identified by C. Woolley; 6b, N. de Vere, pers. observ.: insects observed on wild plants.

(B) PLANT PARASITES

Ellis & Ellis (1985) state that the rust *Puccinia calcitrapae* DC. (Basidiomycota: Uredinales) occasionally occurs on the leaves and stem, and the smut *Thecaphora trailii* Cooke (Basidiomycota: Ustilaginales) occasionally affects the flowers, fruits and seeds.

(C) PLANT DISEASES

See section (B) above.

X. History

Cirsium dissectum was first recorded by M. de Lobel in 1576 'Cirsium anglicum ... provenit in pratis C. viri D. Nicolai Pointz equis praefecturae Glostriensis in villa vernacule Acton nomine.' (First Rec.)

XI. Conservation

Cirsium dissectum is generally found in moist, nutrient deficient grasslands and heathlands, habitats that have declined throughout Europe (HMSO 1995; Buck-Sorlin & Weeda 2000). It has been lost from many sites in the British Isles as a result of drainage and succession (Fojt & Harding 1995; Preston *et al.* 2002). *Cirsium dissectum* is listed as Least Concern in the UK by Cheffings *et al.* 2005) but there is a reasonable chance that the UK holds more than 25% of the European population, so may have an international responsibility to protect this species.

In Germany and the Netherlands, drainage, acidification, atmospheric nitrogen deposition, fertilizer use and succession have caused large losses in *C. dissectum*, and remaining sites are often small and fragmented (Buck-Sorlin 1993; Jansen *et al.* 1996; Buck-Sorlin &

Weeda 2000; Jongejans 2004; van den Berg *et al.* 2005). Soons *et al.* (2005) related seed dispersal ability to the availability of suitable habitat within an area of the Netherlands to investigate habitat connectivity. The remaining grasslands containing *C. dissectum* were found to be practically isolated from each other in terms of seed dispersal with the regional survival of the species being completely dependent on a few large populations in nature reserves. Due to these factors, *C. dissectum* is now on the Dutch Red List of endangered species (Rossenaar & Groen 2003; Jongejans *et al.* 2006a).

Research has been conducted in the Netherlands (Berendse *et al.* 1992; Jansen & Roelofs 1996; Jansen *et al.* 1996; Beltman *et al.* 2001) and the UK (Tallowin & Smith 2001) into the best methods for restoring Cirsio-Molinietum fen meadows. Topsoil removal to decrease soil fertility in areas with a suitable hydrological regime has proved to be the most successful approach. The UK Biodiversity Action Plan lists purple moor grass and rush pasture as a priority habitat with plans to recreate this habitat on land adjacent to or nearby existing sites (HMSO 1995) and van Soest (2001) has developed a methodology for the identification of suitable restoration sites in south-west England.

Smulders *et al.* (2000) used AFLP to investigate genetic diversity between source and reintroduced populations of *C. dissectum* in the Netherlands. Source populations showed small but significant genetic differences (Φ_{ST} 0.108). The first generation of reintroduced plants showed less genetic variation than their source populations and were also genetically differentiated, but assignment tests showed that reintroduced populations still resembled their source populations. Calculations showed that reintroduction from more than one source population introduced significantly more genetic variation and Smulders *et al.* (2000) suggested that this might be the best strategy for plants in the Netherlands. Only a small number of populations was studied, however, with a maximum distance between them of 200 km. de Vere (2007) found greater levels of differentiation between populations in the British Isles (G_{ST} 0.276).

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