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Capsella bursa-pastoris (L.) Medikus (*Thlaspi bursa-pastoris* L., *Bursa bursa-pastoris* (L.) Shull, *Bursa pastoris* (L.) Weber)

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A small, erect, annual herb. Stems simple or branched from the base, 3–(10–40)–103 cm high, pale green to straw-coloured, angled and striate, glabrous or sparsely hairy, hairs simple or branched. Stem leaves alternate, basal leaves forming a rosette; leaves oblanceolate, narrowed into a stalk, varying from very deeply pinnatifid to entire, with a large terminal lobe. Stem leaves also very variable in shape and lobing but always clasping the stem with acute basal auricles. Flowers in long, terminal racemes, the rachis and pedicel elongating as the seeds ripen; the calyx pinkish or green; the corolla white; the four petals are obovate, 2–2.2 mm long. Petals up to twice as long as the hairy sepals. The fruit a two-valved silicula, separated centrally by the replum. Dimensions of the silicula vary between 3.6 and 8.8 mm width and 5.0–9.2 mm length; the silicula is triangular–obcordate, emarginate above, on a spreading stalk 5–20 mm long. It is notched at the apex of the two valves, which fall at maturity leaving the small seeds attached to the thin, membranous, elliptical septum. The seeds oblong and flattened, dark reddish or yellowish brown, with two longitudinal grooves separating the seed face into three almost equal parts, and minutely roughened; up to 39 seeds per capsule. Seed dry weights vary between 0.139 and 0.164 mg, with a mean of 0.150 mg ($n = 60$, SE = 0.004). The root system consists of a tap-root, which often forks after about 10 cm, and a few secondary roots.

Native. Two subspecies of *C. bursa-pastoris* are recorded in *Flora Europaea*; ssp. *bursa-pastoris* which occurs throughout the range of the species and ssp. *thracica* (Velen.) Stoj. & Stefanov which is recorded from southern Bulgaria.

World-wide, the species is extremely variable in size, fruit, and leaf form, but it can be distinguished by its long, terminal racemose inflorescences, its triangular seed pods which are flattened at right angles to the stem, its small white flowers, and by the toothed leaves of the rosette (Holm *et al.* 1977).

Various authors have recognized widely different numbers of biotypes of *C. bursa-pastoris* based on morphological criteria in the field (Almquist 1907, 1923, 1929; Shull 1909; Neuffer 1989). Much variation is probably from phenotypic plasticity, a common feature in annual weeds of cultivated land (Kay 1994). Shull (1909) and Neuffer (1989) divided the species into four biotypes according to leaf shape: A (simplex), B (rhomboidea), C (heteris) and D (tenuis); these four biotypes have been recorded in Britain (Aksoy 1996).

I. Geographical and altitudinal distribution

The centre of distribution of the genus *Capsella* appears to be West Asia and Europe. *Capsella bursa-pastoris* is common throughout the British Isles and is recorded from all vice-counties, on a wide range of disturbed, artificial and fertile habitats, although less common in the north (Fig. 1).

Capsella bursa-pastoris is cosmopolitan, being widely distributed throughout Europe, Asia, America, Australasia and Africa (Holm *et al.* 1979). It is found to 65°N in Iceland and to 71°N in Norway. The species is found at 4°N in Colombia and on the equator in Kenya. However, in Colombia it occurs in the cooler highlands and in Kenya at an elevation between 1600 and 2300 m (Holm *et al.* 1977).

In England *C. bursa-pastoris* has an altitudinal range from sea level to 366 m in North Yorkshire, and to 466 m in Durham, and in Ireland from sea level to 381 m near Dublin (Alt. Range Brit. Pl.). It was recorded from Scotland at 900 m (Mukherjee *et al.* 1984). Thus, it occurs from sea-level to 900 m in the British Isles, but is more common in lowland areas.

In Turkey *C. bursa-pastoris* occurs from sea-level to 2000 m (Davis 1965); in Italy from sea-level to 2700 m (Aldo 1955); from sea-level in northern France to about 1850 m in the Pyrenees, from sea-level to 2091 m in Scandinavia (Neuffer 1990) and to around 3000 m in the Alps (Aldo 1955). It also occurs from

* Abbreviated references are used for standard works; see *Journal of Ecology* (1975), **63**, 335–344. Nomenclature of vascular plants follows *Flora Europea* and, where different, Stace (1991).

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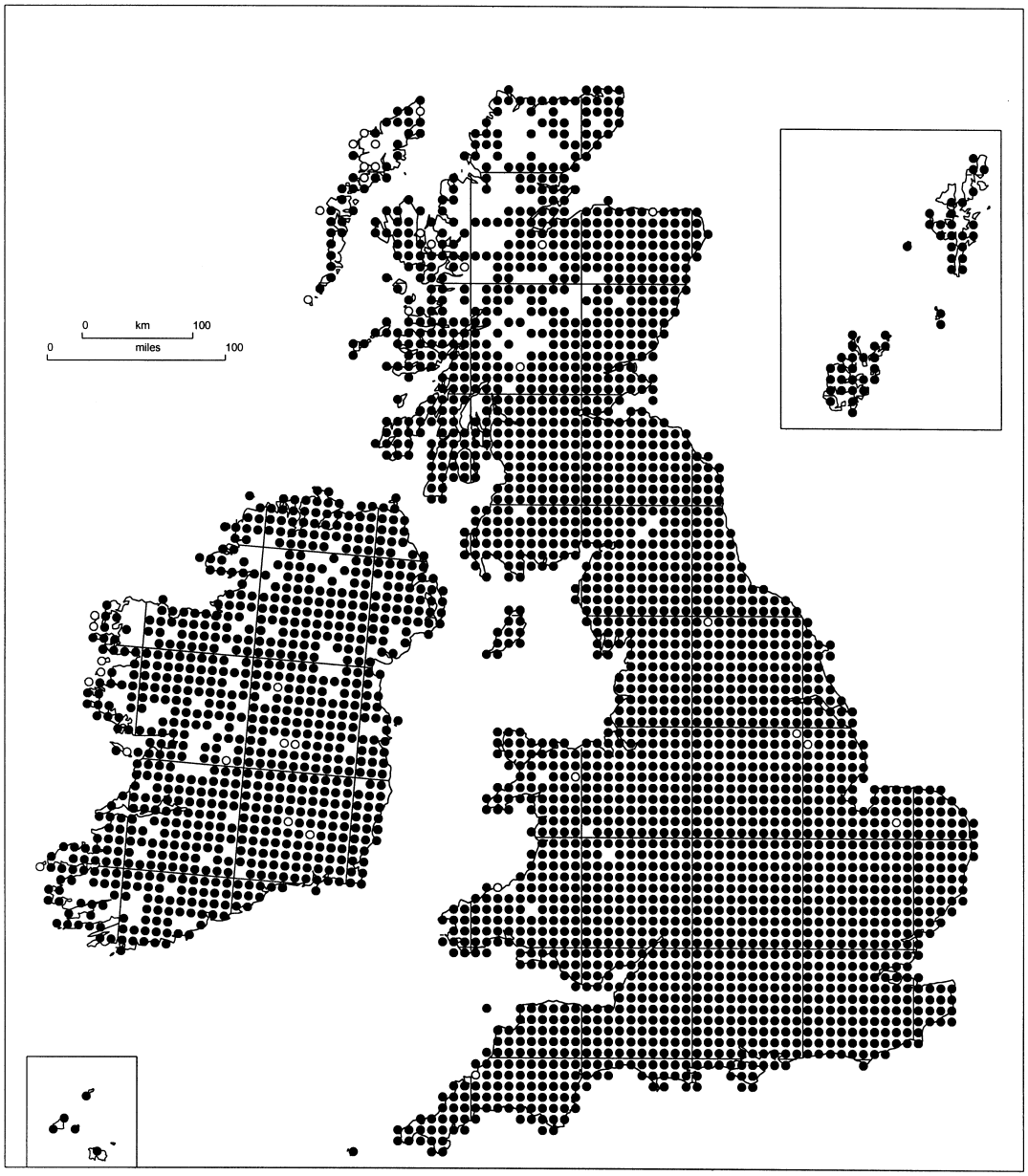


Fig. 1 The distribution of *Capsella bursa-pastoris* in the British Isles. Each dot represents one or more records in a 10-km square of the National Grid. (O) Pre-1950; (●) 1950 onwards. Mapped by the Biological Records Centre, Institute of Terrestrial Ecology, using Dr A. Morton's DMAP program, mainly from data collected by members of the Botanical Society of the British Isles.

3000 m up to elevations of almost 5900 m in north-west Himalaya (Mani 1978).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Capsella bursa-pastoris occurs in cool temperate zones (oceanic, suboceanic, subcontinental and humid steppe climates) and in warm temperature subtropical zones (dry-summer Mediterrannean climates with humid winters and dry-summer steppe climates with humid winters). *Capsella bursa-pastoris* is recorded from the Nile Valley which receives only an average of 20 mm precipitation during spring and has a mean May temperature of $\approx 27\,^{\circ}C$. As an overwintering rosette in Germany it survives temperatures as low as $-12\,^{\circ}C$.

Capsella bursa-pastoris is more a species of the temperate zone than of the tropics; where present in the tropics or subtropics, it is usually more abundant at higher elevations (Holm *et al.* 1977). It is predominantly a species of flat or gently sloping land and is favoured by south-facing slopes (Grime *et al.* 1988).

Capsella bursa-pastoris is a species of both urban and rural wastelands, of cultivated land, particularly as a weed of vegetable crops and as a garden weed, in

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bare patches in damp to dry grassland and on path sides. It has been recorded as a winter annual on rock outcrops (Grime *et al.* 1988).

Damage owing to wind or insolation has not been noted. The species has been recorded from some very dry areas in parts of its range, such as the Isthmic desert in Egypt (Hassib 1951), but it has not been found in permanently wet conditions.

(B) SUBSTRATUM

In Britain, *C. bursa-pastoris* is widespread on brown earths of neutral pH and in man-made habitats, which may be shallow and somewhat stony, or compacted and clayey. It also occurs on brown calcareous earths of higher pH developed over calcareous bedrock, and grows well on builders' rubble with a high mortar content. It is especially frequent on fertile soils in areas of intensive arable agriculture (Rodwell 1992).

Capsella bursa-pastoris is found predominantly on soils ranging from clay to sandy loam and with pH in the range 5.0–8.0. Soil analyses (methods according to Chem. Anal.) from sites supporting *C. bursa-pastoris* gave a range for total nitrogen of 0.10% to 0.43%. Phosphorus ranged from 3.8 to 31.7 mg 100 g^{-1} and exchangeable potassium, calcium and magnesium, extracted with M ammonium acetate (pH 9.0), ranged from 4.3 to 32.5 mg 100 g^{-1}, 178–1978 mg 100 g^{-1} and 4–12 mg 100 g^{-1}, respectively. Soil depths ranged from 14 to about 40 cm (Aksoy 1996).

Capsella bursa-pastoris occurs on serpentine in the southern Urals (Brooks 1987), and is also found on loess in the Lublin in Poland (Lipecki 1989). It is recorded from a sandy loam soil, which is alkaline but rather low in calcium carbonate and sulphates and relatively high in chlorides and organic matter, in the Isthmic desert and Nile valley in Egypt (El-Habibi & Youssef 1981), and from a sandy loam rich in calcium carbonate in the Aegean region of Turkey (Aksoy & Gemici 1993). It has been recorded on humus-rich wet soil in Korea (Kang 1983).

III. Communities

Capsella bursa-pastoris is most frequent as a weed of arable crops, and as a colonizer of open ruderal communities, disturbed habitats and trampled sites.

After effective ploughs were introduced into farming, the proportion of short-lived species in arable weed communities was noted to have gradually increased, especially species such as *C. bursa-pastoris* and *Thlaspi arvense* which can germinate at any time of the year (Ellenberg 1988). This capacity of *C. bursa-pastoris* to ripen seeds and complete its life cycle early in the season in a dense crop (Andreasen *et al.* 1996) has contributed to its being one of the dominating species in the weed flora. However, these latter authors studied the changes in the weed flora of arable fields in Denmark over a 20-year interval and concluded that although it was still one of the dominating species, *C. bursa-pastoris* had declined in abundance since the last survey in all crop types except grass ley, probably owing to the continuing use of herbicides. Some other species which had previously been common had declined to almost no representation. Other species which were still dominant weed species, besides *C. bursa-pastoris*, were *Chenopodium album*, *Elytrigia repens*, *Fallopia convolvulus*, *Myosotis arvensis*, *Persicaria maculosa*, *Poa annua*, *Polygonum aviculare*, *Stellaria media*, *Taraxacum officinale* agg., *Veronica arvensis*, *V. persica* and *Viola arvensis*. Examples of the occurrence and associated species of *C. bursa-pastoris* in British arable sites, bearing weed vegetation from calcicole to calcifuge in character, are given by Kay (1994).

The National Vegetation Classification (NVC) includes *Capsella bursa-pastoris* in several communities, mainly of the ruderal and disturbed communities classified under the heading 'Other Vegetation'. There are two communities and two subcommunities in which *C. bursa-pastoris* is a dominant species with a constancy value of IV or V, namely the *Stellaria media – Capsella bursa-pastoris* (OV13) and the *Stellaria media – Urtica urens* (OV14) communities, and the *Plantago major* subcommunity of the *Polygonum aviculare – Matricaria discoidea* (OV18b) community, and the *Fallopia convolvulus – Veronica persica* subcommunity (OV9d) of the *Stellaria media – Polygonum aviculare* community. Table 1 includes a list of the characteristic species for these communities, with a constancy value greater than III.

In addition, *Capsella bursa-pastoris* has a constancy of III in the following NVC communities: OV3 (*Papaver rhoeas – Viola arvensis*), OV4 (*Chrysanthemum segetum – Spergula arvensis*), OV5 (*Digitaria ischaemum – Erodium cicutarium*), OV7 (*Veronica persica – Veronica polita*), OV8 (*Veronica persica – Alopecurus myosuroides*), OV10 (*Poa annua – Senecio vulgaris*) and OV19 (*Poa annua – Matricaria discoidea*). It is also a minor component, with a constancy of only I or II, in the following communities or typical subcommunities: OV6 (*Cerastium glomeratum – Fumaria muralis boraei*), OV11 (*Poa annua – Stachys arvensis*), OV16 (*Papaver rhoeas – Silene noctiflora*), OV17 (*Reseda lutea – Polygonum aviculare*), OV20 (*Poa annua – Sagina procumbens*), OV21 (*Poa annua – Plantago major*), OV22 (*Poa annua – Taraxacum officinale* agg.) and OV25 (*Urtica dioica – Cirsium arvense*), together with two communities from the mesotrophic grassland classification, MG1 (*Arrhenatherum elatius* grassland) and MG7 (*Lolium perenne* leys and related grassland) (Rodwell 1992).

Rodwell (1994) has recorded that, in West Yorkshire, the *Stellaria media – Capsella bursa-pastoris* (OV13; listed as WE14) community could be found in arable fields and gardens, particularly where soils had been limed, giving rise to this somewhat richer

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Table 1 National Vegetation Classification communities, and distinctively different subcommunities, in which *Capsella bursa-pastoris* is a dominant, together with other species with a constancy of IV or V

Species	OV9d	OV13	OV14	OV18b
Agrostis stolonifera	IV			
Capsella bursa-pastoris	IV	V	V	IV
Chenopodium album	IV	IV	IV	
Elytrigia repens	IV			
Fallopia convolvulus	V			
Lolium perenne				V
Matricaria discoidea	IV			V
Plantago major				IV
Poa annua	IV		V	IV
Polygonum aviculare	V	IV		V
Senecio vulgaris		V	V	
Stellaria media	IV	V	V	
Trifolium repens	IV			
Tripleurospermum maritimum	IV			
Urtica urens			V	
Veronica persica	IV			

community than some of the other associations listed above. Rodwell (1994) also notes that, in situations such as field gateways or earth paths, mixtures of short-lived plants and perennials can survive by being resistant to trampling; species such as *C. bursa-pastoris* and *Poa annua* are mixed with *Matricaria discoidea*, *Plantago major* or *Taraxacum officinale* agg., for example (the renumbered OV18, 21 and 22 communities).

In Ireland, *C. bursa-pastoris* occurs in the Veronica-Lamietum hybridi association within the suballiance Eu-Polygono-Chenopodenion. This community is widespread and grows on nutrient-rich loamy soils of around neutral pH (White 1982). Diagnostic species are *C. bursa-pastoris*, *Galium aparine*, *Lamium purpureum*, *Sonchus oleraceus* and *Veronica persica*. *Capsella bursa-pastoris* also occurs in the Lolio-Plantaginetum association in Ireland. Characteristic species are *C. bursa-pastoris*, *Lolium perenne*, *Plantago major*, *Poa annua*, *Polygonum aviculare* and *Taraxacum officinale* agg.

In Central Europe *C. bursa-pastoris* is a member of the community of waste ground and related arable and garden weeds, of the class Chenopodietea, listed by Ellenberg (1988) as including the following characteristic species: *Aethusa cynapium*, *Amaranthus albus*, *A. blitoides*, *A. hybridus*, *A. retroflexus*, *Atriplex hortensis*, *A. tatarica*, *Chenopodium album*, *C. bonus-henricus*, *C. chenopodioides*, *C. ficifolium*, *C. foliosum*, *C. murale*, *C. vulvaria*, *Corrigiola litoralis*, *Datura stramonium*, *Diplotaxis muralis*, *Echinochloa crus-galli*, *Eragrostis minor*, *Geranium rotundifolium*, *Linaria vulgaris*, *Panicum capillare*, *Phleum paniculatum*, *Portulaca oleracea*, *Senecio vulgaris*, *Solanum nigrum*, *S. villosum*, *Sonchus oleraceus*, *Stellaria media*, *Tripleurospermum inodorum*, and *Urtica urens*. This dry habitat ruderal vegetation of the community Chenopodietea is found on building rubble, rubbish tips, roadside and relatively dry habitats heavily dependent on man (Ellenberg 1988).

Ellenberg (1988) also refers to *C. bursa-pastoris* as being a species frequently found with plants characteristic of trampled areas of the Polygonion avicularis alliance, along with species such as *Agrostis capillaris*, *Leontodon autumnalis*, *Lolium perenne*, *Matricaria discoidea*, *Plantago major*, *Poa annua*, *Polygonum aviculare*, *Taraxacum officinale* agg. and *Trifolium repens*.

However, Oberdorfer (1979) distinguishes a community of weeds of summer crops (class Chenopodietea), including *C. bursa-pastoris* among other species which are found almost as frequently in the winter cereals as in the summer crops, with all of the species listed being nutrient-demanding ones, often nitrogen indicators.

Knapp & Knapp (1953) indicated that *C. bursa-pastoris* is found as a characteristic species in two chalk-loving ruderal associations in central Europe. The first occurs mainly on south-facing dolomite cliffs in the Austrian Tirol, at an altitude of 1050–1300 m, with a soil pH of 6.5–7.0 in montane–subalpine spruce stands (Table 2). The second is from montane, central alpine pine–spruce stands on stony terraces or on morainic deposits with deeper soil, of pH 6.3–7.0, at 800–1000 m altitude, where the climate is warmer and drier than that of the previous association (Table 2). Knapp & Knapp (1953) described a montane association containing *C. bursa-pastoris* from central Austria, the Panico-Chenopodietum (Table 2) occurring on rich, dry, permeable soils in a warmer area than the previously described chalk-loving ruderal associations, and also an alpine association with *C. bursa-pastoris*, the Delphinietum consolidae.

Capsella bursa-pastoris is recorded from the Arrhenatheretum elatioris in the herb-rich meadows of the Polish western Carpathians, between 250 and

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Table 2 Characteristic species from Central European associations described by Knapp & Knapp (1953) in which *Capsella bursa-pastoris* is found: (a) from spruce stands, (b) from pine-spruce stands and (c) from the Panico-Chenopodietum association. See text for further details

Species	(a)	(b)	(c)
Achillea millefolium	+	+	
Aegopodium podagraria	+	+	
Anagallis arvensis	+	+	+
Anchusa arvensis	+		
Apera spica-venti		+	
Arenaria serpyllifolia	+	+	+
Campanula rapunculoides	+		
Capsella bursa-pastoris	+	+	+
Centaurea cyanus		+	
Chenopodium album	+	+	+
Convolvulus arvensis		+	+
Conyza canadensis			+
Echinochloa crus-galli			+
Euphorbia helioscopia	+	+	+
Fallopia convolvulus	+	+	+
Galeopsis tetrahit	+	+	
Galinsoga parviflora			+
Galium spurium	+	+	+
Geranium pusillum		+	
Legousia speculum-veneris		+	
Lithospermum arvense		+	
Myosotis arvensis	+	+	+
Neslia paniculata	+		
Persicaria maculosa			+
Polygonum aviculare	+	+	+
Setaria pumila			+
Setaria viridis			+
Sinapis arvensis	+		
Solanum nigrum			+
Stellaria media		+	
Thlaspi arvense		+	
Valerianella dentata	+		
Vicia cracca	+	+	+
Vicia hirsuta		+	
Viola tricolor	+	+	+

350 m altitude (Stuchlikowa 1967). Two herb communities are described; a taller one, attaining 60–160 cm height and a shorter one of up to 50 cm. *Capsella bursa-pastoris* occurs in the latter, which is mown twice yearly. Characteristic species include *Ajuga reptans*, *Arabis arenosa*, *Bromopsis erecta*, *Convolvulus arvensis*, *Elytrigia repens*, *Euphorbia cyparissias*, *Euphrasia rostkoviana*, *Galeopsis tetrahit*, *Galium aparine*, *G. verum*, *Glechoma hederacea*, *Holcus mollis*, *Linaria vulgaris*, *Lolium perenne*, *Medicago lupulina*, *Myosotis arvensis*, *Phleum pratense*, *Polygala vulgaris* ssp. *collina*, *Polygonum maculosa*, *Rorippa sylvestris*, *Sanguisorba officinalis* and *Tragopogon pratensis* ssp. *orientalis*.

Kliment (1991) recorded the association of Capsello bursae-pastoris-Poëtum annuae from the Velká Fatra mountain chain in Slovakia; it occurred on flat to gently sloping ground (5°), with east, west and south orientations, at altitudes between 900 and 1280 m, on humic soils with pH ranging from 4.9 to 7.3.

IV. Response to biotic factors

(A) GRAZING

Capsella bursa-pastoris is grazed by cattle, horses, yaks, sheep and rabbits (Disp. Pl.; Crawley 1990). Its leaves are also eaten by slugs (Dirzo & Harper 1980). These latter authors noted that slug-grazing rarely, if ever, killed the plants; the effect was to change the size of plants but not their density, as mortality owing to slugs was offset by reduced self-thinning. This species appears to be highly palatable to slugs in experimental trials, with the hairiness of the leaves not deterring their being eaten (e.g. Cook *et al.* 1996). The shape of the leaves does not appear to influence feeding preference by insect herbivores in any consistent way (Rivero-Lynch *et al.* 1996).

(B) COMPETITION

Capsella bursa-pastoris is a pioneer of disturbed ground and as such it is an opportunist species. When established in open places it will grow quickly and tends to have a high percentage cover initially. However, after perennial grass species enter the succession, it declines in abundance and soon disappears (Aksoy 1996). As a common weed it might compete with crops, but a study of its effects on the growth of radish (*Raphanus sativus*) found that it competed poorly and posed little threat to the crop yield (Perera & Ayres 1992).

(C) TRAMPLING

Ellenberg (1988) included *Capsella bursa-pastoris* as one of the species frequently found with plants characteristic of trampled areas, and notes that such species withstand a high degree of trampling owing to their small size, the fact that they branch close to the ground, that the tissues are tough and elastic, and that there is rapid regeneration of their vegetative organs.

Plants from seeds collected from moderately trampled areas produced a rosette with more leaves, but a smaller plant which flowered later and produced smaller seed capsules containing fewer seeds, compared to plants grown from seeds collected from arable fields (Neuffer & Meyer-Walf 1996). Ellenberg (1988) noted that where there is very heavy treading the plants do not produce seed at all.

Capsella bursa-pastoris occurs in moderately trampled sites in urban areas. Whereas most perennial species quickly disappear from trampled sites, seed of *C. bursa-pastoris* is easily dispersed, germinates quickly and establishes on trampled land. In this habitat, plants of *C. bursa-pastoris* are short and have

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small rosettes with less dissected leaves and fewer flowers. However, an appreciable number of plants (16–70%) may die on trampled sites during the growing period (Aksoy 1996).

(D) CHEMICAL

Control of *C. bursa-pastoris* can be effected by spraying with MCPA or 2,4-D at the rate of 1.1–1.4 kg in 1100 L per hectare (1–1.25 lb per 100 gallons per acre), preferably applied in the early stages of development (Salisbury 1961) and by application of the isopropylamine salt of *n*-(phosphonomethyl) glycine in an aqueous dilution of 10 mL L^{-1} per 20 m^2. Treatment with rimsulphuron at up to 35 g per ha achieved 85% control of this species (Eberlein *et al.* 1994), and 2,4-DB ester has also been found effective (Cudney *et al.* 1993). A range of weedkillers has been reported to be effective for controlling *C. bursa-pastoris* by Evans (1962); of those tested the species appeared resistant only to propham (IPC). Cousens & Mortimer (1995), however, refer to some evidence of the development of tolerance of the species to the ethametsulphuran methyl herbicide. Flame weeding using liquefied petroleum gas (propane) can be used to control weeds in organic farming, but species such as *C. bursa-pastoris* with protected growing points can be completely killed only in the early stages of growth (Ascard 1995).

V. Response to environment

(A) GREGARIOUSNESS

After initial colonization, *C. bursa-pastoris* occurs most frequently in small scattered groups of plants. Occasionally large colonies (containing >35 plants m^{-2}) have been recorded from urban sites on builders' rubble (Aksoy 1996).

(B) PERFORMANCE IN DIFFERENT HABITATS

Both vegetative and reproductive structures of *C. bursa-pastoris* are very variable in different habitats. Mean plant dry weight yield, plant height, number of capsules, number of seeds per capsule and seed weights of *C. bursa-pastoris* are given in Table 3 for a range of habitats. Plants were mainly isolated individuals, or in the case of waste land the plants were numerous but so small that they did not touch each other, and density will probably not have affected plant size. The variation in the above features may be associated with the mineral nutrients which are relatively high in garden and arable land soil and low in grassland, wasteland and trampled sites. As well as varying with habitat, the number of seeds per capsule and seed weights vary according to the position of the capsules on the plant. The number of seeds is highest in capsules located on the middle of the stem while seed weight increases from top to bottom.

Germination of plants grown under standard conditions from seed collected along an altitudinal transect in the Alps (Neuffer & Bartelheim 1989) showed no relationship to the place of origin. However, time to flowering, plant height, rosette diameter and leaf forms all varied in a manner related to altitude; Neuffer & Hurka (1986a,b) have also related these features, particularly development time until flowering, to latitude. These results suggest that the variation in these features is primarily genetically based and is often of adaptive value, correlated with habitat; although, on a smaller geographical scale, Paoletti *et al.* (1991) argue that such characters vary owing to phenotypic plasticity.

(C) EFFECTS OF FROST, DROUGHT AND WATERLOGGING

Capsella bursa-pastoris can produce over-wintering rosettes, and is described by King (1966) as a winter annual and by Baskin & Baskin (1989) as a facultative winter annual. Göppert (1881) observed that *C. bursa-pastoris* survived low winter temperatures of down to $-12\,^{\circ}C$ in Germany. However, its ability to survive over winter depends, partly on weather severity, but also on plant size (Debaeke 1988); this author recorded mortalities ranging from 30 to 100%.

The species has been found from semihumid to dry habitats, usually on fairly dry places in the U.K. In general it occurs most frequently in dry habitats, being very rare in wet soil in Europe (Ellenberg 1988). *Capsella bursa-pastoris* can be classed a mesophyte, its growth being adversely affected by both drought and excess of water (Aksoy 1996). Ellenberg (1988) records that in Central Europe it was only moderately

Table 3 Mean ($\pm$SE) plant dry weight yield, height, number of capsules, number of seeds per capsule and seed air-dry weights of *C. bursa-pastoris* growing in different habitats in West Yorkshire

Habitat	Garden	Arable land	Grassland	Waste land	Trampled
Dry weight (g)	17.7 $\pm$ 2.3	9.7 $\pm$ 1.1	6.9 $\pm$ 1.0	4.2 $\pm$ 0.6	1.6 $\pm$ 0.3
Plant height (cm)	75.4 $\pm$ 7.3	58.7 $\pm$ 8.5	48.4 $\pm$ 5.2	37.2 $\pm$ 9.1	18.3 $\pm$ 10.2
No. of capsules	985 $\pm$ 38	765 $\pm$ 25	425 $\pm$ 21	206 $\pm$ 14	58 $\pm$ 18
No. of seeds per capsule	27.3 $\pm$ 1.8	25.2 $\pm$ 1.4	22.3 $\pm$ 1.5	20.6 $\pm$ 1.0	17.4 $\pm$ 1.5
Seed weight (mg)	0.160 $\pm$ 0.01	0.155 $\pm$ 0.02	0.150 $\pm$ 0.01	0.147 $\pm$ 0.02	0.149 $\pm$ 0.02

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affected by a dry summer, with up to a 30% reduction in numbers compared to the previous year. However, in Britain, during the extraordinarily dry summer of 1995, our observations in West Yorkshire indicated that most plants of *C. bursa-pastoris* died because of a water deficit. Those plants which survived produced only very small rosettes.

Capsella bursa-pastoris grown under dry conditions in the laboratory shows some adaptability to droughting, such as the formation of thick waxy cuticles (plants collected from an urban park had 13 mg dm^{-2} cuticular wax), leaf rolling habit and an increase in leaf pubescence. When grown in waterlogged soil, the reproductive and vegetative potential of *C. bursa-pastoris* is low and in extremely waterlogged soil the plant does not survive (Aksoy 1996).

VI. Structure and physiology

(A) MORPHOLOGY

The root system consists of a single white tap-root, but often this forks after about 10 cm to produce a thinner secondary root. The diameter of the proximal portion of the unbranched root in well-developed plants is about 5 mm. In deep, uncompacted soil the rooting depth is to around 33 cm, but in compacted, trampled soil the tap-roots become twisted and shorter. A network of fibrous roots, with third order laterals, arises from the tap-roots, which sometimes branch again towards the distal region. The network of lateral roots is more dense in the proximal than distal region of the tap-roots.

Leaf shape varies from entire to deeply lobed (e.g. Steinmeyer *et al.* 1985), although more deeply lobed leaves may tend to appear later in a plant's life (Rivero-Lynch *et al.* 1996). The dimensions of rosette leaves are dependent on habitat and can vary between 3 and 33 cm in length and 1.5–8.6 cm in width. Stomatal counts, from three regions of 27 different leaves from an urban park population in West Yorkshire, gave a mean of $137.4 \pm 5.7\ mm^{-2}$ for the adaxial surface and $211.9 \pm 6.9\ mm^{-2}$ for the abaxial surface.

(B) MYCORRHIZA

Ruderal species that colonize disturbed ground are generally non-mycorrhizal (e.g. Reeves *et al.* 1979; Medve 1984), and *C. bursa-pastoris* might accordingly be expected not to form mycorrhizal associations. Also, Brassicaceae has traditionally been regarded as a non-mycorrhizal family; however, one-third of the British species examined have been recorded as sometimes being mycorrhizal, but not consistently in any species (Harley & Harley 1987). This is the case for *C. bursa-pastoris*, which has had vesicular-arbuscular mycorrhizas recorded at very low percentages by some authors (e.g. Kruckelmann 1975 reported 1% infection) but reported as absent by others. Results rather at variance with this (DeMars & Boerner 1994, 1995) have been reported of 15% and even 35% infection when in the presence of a mycorrhizal matrix from surrounding species, although no arbuscules were observed, and these authors suggested that the mycorrhizas may be non-functional.

A study was made of the mycorrhizal status of *C. bursa-pastoris* in Britain in August 1997 (R. Francis and D. J. Read, personal communication) in plants sampled from a range of sites. No infection was seen in plants from a layby in Ayrshire, Scotland, the sea front, Rhyll, Clywd, a farmyard entrance in Cumbria and edges of rural paths in Eldwick, West Yorkshire and near Kidderminster, Hereford and Worcester. However, samples from a fairly bare lawn, associated with *Taraxacum officinale* agg., and from the edges of paths in the University of Bradford campus, West Yorkshire, were found to have a patchy distribution of abundant mycorrhizal infection. Roots detached from mature plants (carefully teased out) from these sites showed clear arbuscules in inner layers of the cortex; several entry points through root hairs were also seen. These results support the patchily higher infection levels recorded by DeMars & Boerner (1994, 1995), but suggest that the mycorrhizas may be functional.

(C) PERENNATION: REPRODUCTION

Capsella bursa-pastoris is a summer or winter annual, semi-rosette therophyte. Reproduction is entirely by seeds. Three generations have been observed in a year from plants which germinate in early spring, although Evans (1962) gives a typical pattern involving two periods of germination and Cousens & Mortimer (1995) show a bimodal pattern of seedling emergence with peaks in March and September. The species forms a persistent seed bank in the soil (Hurka & Haase 1982; Grime *et al.* 1988), seed germinating from the seed bank in numbers up to $75\ m^{-2}$ of soil to 10 cm depth (Ellenberg 1988), and viable seed has been recorded after a dormancy of at least 35 years (Kivilaan & Bandurski 1981), although a notable decline in number of viable seeds was recorded after about 5 years' burial by Conn & Deck (1995). The half-life of seeds in the soil is ≈ 5 years; but this falls to about 1 year if the soil is disturbed annually through cultivation, when the rate of loss of seeds was found to be about 52% per year (Roberts & Feast 1973). This is presumably because seeds germinate and the seedlings are then killed during cultivation, rather than owing to an increase in seed mortality in the seed bank.

(D) CHROMOSOMES

Chromosome numbers are usually tetraploid with $2n = 32$ (Shull 1929; Chr. Atl.; Löve & Löve 1956; Davis 1965; Raj 1965; Hsu 1968; Svensson 1983; Hurka 1984). In *Flora Europaea* the chromosome

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number is recorded as $2n = 32$ and also $2n = 16$. In addition, Svensson (1983) records diploid specimens with $2n = 16$ from Greece.

Greater levels of genetic heterogeneity have been recorded for European populations of *C. bursa-pastoris* that were sampled from more intensively disturbed sites, that had been recently cultivated, than from non-cultivated sites (Bosbach & Hurka 1981), suggesting a positive relationship between the degree of environmental variability and genetic variation.

(E) PHYSIOLOGICAL DATA

The mean relative growth rate of seedlings of *C. bursa-pastoris* was determined over a 4-week period, with a day temperature of 20 °C, night temperature of 15 °C and an 18-h day. The photon flux density was relatively low (fluorescent lighting) at 140 μmol m^{-2} s^{-1} and the relative humidity 60%. Twelve plants for each of two harvests were grown in sand, and watered every other day with 20 mL of Long Ashton solution (Hewitt 1966). The value obtained for R_{max} was 1.27 $week^{-1}$. The seed was gathered from a population in Bradford, West Yorkshire.

Thirty-two 1–2 cm tall seedlings of *C. bursa-pastoris* were planted out in a garden loam, together with equal numbers which received an NPK (7:7:7) fertilizer addition of either 50 g m^{-2} or 150 g m^{-2}. The plants were grown on to the fruiting stage and then harvested. The mean dry weights (± 1 SE) of roots, of the rosette leaves and of the remainder of the shoot material, comprising the stem, its leaves and the inflorescence, are given in Table 4. In the unfertilized plot, the roots constituted 5.4%, the rosette leaves 14.5% and the rest of the shoot material 80.1% of the total weight. With the fertilized plants the root weight and rosette leaf weight increased correspondingly, but their percentage of the total weight generally decreased (Table 4) while the stem/leaf/inflorescence weights increased proportionately more. The mean number of capsules per plant was much higher for the high fertilizer regimes (Table 4). *Capsella bursa-pastoris* thus partitioned its resources in a typical ruderal strategy, allocating most to the flowering stem and inflorescence, with a low allocation to rosette leaves and a very low allocation to roots, regardless of soil fertility.

Capsella bursa-pastoris occurs in open, dry communities throughout Central Europe on wasteland ruderal sites, and is also recorded from partial shade (Ellenberg 1988). It has been reported from shaded habitats in Korea (Kang 1983), and although it occurs most frequently in open habitats throughout the British Isles, it has been observed under deciduous tree canopies in Bradford, West Yorkshire. Pot-grown specimens under artificial neutral screens, with a reduction in light flux to 39, 25 and 20% of ambient, produced shorter leaves (means of 18.0 ± 1.7, 16.1 ± 1.4, and 12.5 ± 1.2 cm, respectively, compared with 21.7 ± 2.1 cm unshaded). Plant dry weight, leaf width, numbers of inflorescences, the ratio of chlorophyll a:b and total chlorophyll were all significantly reduced with reduced light flux. However, even under a light flux of only 20% ambient the species set seed: 20% germination was obtained from this.

Calcium, phosphorus, potassium and nitrogen requirements were investigated in sand culture experiments carried out in a growth cabinet, with a flux density of 102 μmol m^{-2} s^{-1} over a 14-h day and with a day temperature of 25 °C and night temperature of 15 °C. The solutions used were modified (Aksoy 1996) from Hewitt (1966); calcium was supplied (as $CaCl_2$) at 5, 15, 50 and 200 μg mL^{-1} and nitrogen at 140 μg mL^{-1} (as $NaNO_3$). Total dry weight increased markedly from 5 to 200 μg mL^{-1} calcium. Shoot dry weight increased by a factor of 25 and root weight by a factor of 40 between 5 and 200 μg mL^{-1}. At concentrations of 5 and 15 μg mL^{-1} many rosette leaves became curled, suggesting symptoms of calcium deficiency (Fageria *et al.* 1991). The response to increasing levels of calcium is consistent with the distribution of *C. bursa-pastoris* on circumneutral soils with moderate to high base status.

Phosphorus was supplied as NaH_2PO_4 at 4, 8, 16, 32 and 64 μg mL^{-1}. Both root and shoot dry weights increased from 4 μg mL^{-1} to give a maximum at 16 μg mL^{-1}, and then decreased sharply, with the yield at 64 μg mL^{-1} being only slightly greater than that at 4 μg mL^{-1}. This result is not unexpected, as other ruderal species such as *Stellaria media* (Sobey 1981)

Table 4 Mean dry weight values (g) ± 1 SE and percentages of the total weight for different parts of *C. bursa-pastoris* plants, together with the mean ($\pm$SE) number of seed capsules, grown under three fertilizer regimes: (a) unfertilized, (b) fertilized at 50 g m^{-2} NPK and (c) fertilized at 150 g m^{-2}. See text for further details

	(a) Dry wt (g)	%	(b) Dry wt (g)	%	(c) Dry wt (g)	%
Roots	0.92 ± 0.08	5.4	1.90 ± 0.03	7.1	1.39 ± 0.03	3.3
Rosette leaves	2.45 ± 0.03	14.5	2.55 ± 0.40	9.5	4.00 ± 0.45	9.4
Stem, stem leaves and inflorescence	13.55 ± 1.00	80.1	22.45 ± 1.40	83.5	37.0 ± 1.50	87.3
No. of capsules	475 ± 30		700 ± 30		1125 ± 70	

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have not shown an increased response to high levels of phosphorus unless accompanied by a high concentration of nitrogen. However, when *C. bursa-pastoris* was grown in an untreated garden loam and with inorganic fertilizer containing 7% P_2O_5 and 7% N applied at half the recommended rate and at twice the recommended rate, the dry weight yield was significantly higher with the latter treatment (Aksoy 1996).

Nitrogen was supplied at 3, 9, 27, 81 and 243 μg mL^{-1} as $NaNO_3$ and the total dry weight of *C. bursa-pastoris* increased up to 81 μg mL^{-1} but with a significant decline at 243 μg mL^{-1}. Ellenberg (1988) describes *C. bursa-pastoris* as occurring in habitats with average nitrogen availability (but nonetheless a nitrogen-loving weed), although the plant is regarded by Gilbert (1991) as a ruderal species of nitrogen-rich habitats. In a fertilizer experiment, described above for P requirement, the highest yield for *C. bursa-pastoris* was where N at 7% (in addition to P and K) was applied at twice the recommended rate.

Gilbert (1991) reported that *C. bursa-pastoris* occurs in cultivated and roadside soils, which in Britain are high in potassium. Potassium was supplied as K_2SO_4 at 16, 32, 64, 128 and 256 μg mL^{-1}. Total dry weight increased with potassium concentration up to 32 μg mL^{-1} but then declined.

Seedlings of *C. bursa-pastoris* were grown for 5 weeks in modified Hewitt's solution (Hewitt 1966; Aksoy 1996) containing NH_4-N at 81 μg mL^{-1} as $(NH_4)_2SO_4$, or NO_3-N at 81 μg mL^{-1} as $NaNO_3$, at pH values of 4, 5, 6 and 7, with a day temperature of 25 °C, night 15 °C and 14-h day. The dry weight of *C. bursa-pastoris* was significantly greater with NO_3-N than NH_4-N at all pH values. With increasing pH and NO_3-N, there was a significant increase in weight up to pH 6, and a significant decrease at pH 7. However, in the case of NH_4-N, there was an increase in dry weight with increasing pH through to pH 7. The yield at all pH values was significantly greater with NO_3-N than NH_4-N, but all seedlings survived in all treatments, suggesting that although *C. bursa-pastoris* responds preferentially to NO_3-N, as a cosmopolitan species of varied habitats it can also utilize NH_4-N.

The performance of *C. bursa-pastoris* under fluctuating soil water stress was examined in a sand culture experiment. The plants were divided into five groups and watered 2, 4, 6, 8 and 10 consecutive days out of 14; the experiment was run for 8 weeks.

The highest total dry weight was obtained under the relatively harsh regime of watering only 4 consecutive days out of 14. The yields for plants watered 6, 8 and 10 consecutive days were significantly lower than that for the harshest regime of watering only 2 consecutive days out of every 14.

Excised leaves of *C. bursa-pastoris* grown under 'dry' conditions (watered sparingly every 10 days) exhibited a water deficit of only 36% of that shown by leaves from plants watered every 4 days. The leaves of sparsely watered plants were distinctly more hairy, stomatal closure was more rapid and the leaves were thicker and more inrolled than those of plants watered regularly. The results of these experiments support the observations in the literature that although *C. bursa-pastoris* can be generally considered a mesophyte, it is more commonly found in drier habitats than wet ones and shows some adaptability to moderate droughts.

Low temperature photosynthesis in successional winter annuals, including *C. bursa-pastoris*, has been studied in the United States by Regehr & Bazzaz (1976). They reported measurements of photosynthesis in *C. bursa-pastoris* at different temperatures at different times of the year. The maximum photosynthetic rate in March at 15 °C was 22 mg CO_2 dm^{-2} h^{-1}, while photosynthetic rate in May at 25 °C was 20 mg CO_2 dm^{-2} h^{-1} and in October at 25 °C was 16 mg CO_2 dm^{-2} h^{-1}.

(f) Biochemical data

The biochemistry of *C. bursa-pastoris* seeds in Egypt has been studied by El-Habibi & Youssef (1981) who found that the chromatographic separation of the saponifiable fraction of oil reveals the presence of oleic acid (21.2%), linoleic acid (9.2%), stearic acid (52.3%) and palmitic acid (17.1%).

Garcia Marquina *et al.* (1955) reported the presence of bursolic and citric acid and galacturonic acid, a constituent of pectin; a triterpene compound; and also the presence of arabinose, mannose, xylose and pentose, but not hexose, sugars. Only a trace of tannins has been found, and although alkaloids had previously been reported as being present, their absence was claimed by the above authors. The liquid extract has reportedly been used as an antihaemorrhaging agent and for urinary tract illness (Garcia Marquina *et al.* 1955).

Capsella bursa-pastoris is cultivated for salad use in the United States of America (Spencer 1968); the leaves are also used as a salad and its seeds have some medicinal value in Turkey and China (Usher 1974; Aksoy 1996).

VII. Phenology

Seeds germinate throughout the year, usually with a large peak at the beginning of March and a small peak after August. After germination in March rosettes continue to enlarge until the beginning of June, with the first leaves produced 12–14 days after germination. The first shoots are produced at the beginning of May and the first flowers formed 3–4 days after shoot development commences. The first ripe seeds and capsules are found by late May. The times of flowering and seed production differ depending on the relative position on the scape; when the lower branches have ripe capsules, the upper branches still

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have flowers. Seeds are usually dispersed from June to August.

Although *C. bursa-pastoris* occurs throughout the year, it is found less frequently during autumn and winter; temperatures needed for germination and growth occur mainly during spring and summer, and during autumn and winter the seeds have a low germination potential, and the plants a slow rate of growth. Germination very late in a year tends to result in a small rosette which produces early flowers during the following spring.

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

The species is generally homogamous and the stamens are often reduced or aborted in cold weather. Small insects, particularly flies and small bees, visit the flowers freely (Shull 1909), but these are usually automatically self-pollinated (Fl. Br. Isl.). However, Shull (1929) assumes the small percentage of cross pollination which does occur (1–2%) results from slight protogyny which allows the stigma to be receptive to pollen several hours before the anthers ripen. Using isozyme markers Hurka *et al.* (1989) estimated outcropping rates for different populations of between 2 and 10%. Hurka (1990) considers that cloudy and rainy weather appears to favour self-pollination, while dry and sunny weather favours outcrossing.

(B) HYBRIDS

In the British Isles the only hybrid recorded (Hyb. Br. Isl.) is between *C. bursa-pastoris* and the introduced *C. rubella* (*C. gracilis*). Shull (1909, 1929) has recorded a number of hybrids between *C. bursa-pastoris and* other species of *Capsella* in the United States of America.

(C) SEED PRODUCTION AND DISPERSAL

Seeds of *C. bursa-pastoris* are on average 0.8–1.0 mm long and 0.6–0.8 mm wide. Hurka & Benneweg (1979) reported average seed length of European material to be 0.97 ± 0.07 mm ($n = 20\,000$), but with pronounced variation between different populations. The heaviest seeds are generally produced by the flowers which first open. The number of seeds per capsule (silicula) and number of capsules per plant vary, partly owing to different genotypes, and partly depending on habitat. Estimation of seed production for several plants grown in a cool glasshouse experiment gave a minimum of 7 seeds per capsule and 11 325 seeds per plant and a maximum of 39 seeds per capsule and 58 512 per plant. Hurka & Haase (1982) in a random block experiment recorded a minimum of 5000 seeds and a maximum of 90 000 seeds per plant. The number of seeds and capsules per plant is very variable and depends on the position of the capsule on the scape and also on habitat.

Usually the ripe capsules of *Capsella* split along their septa but the seeds do not fall immediately; instead they remain connected to the axis of the fruit by the dried funicle. The seeds are shed by the wind and by rain drops. Wind velocity and atmospheric humidity affect seed shedding, which is delayed when the velocity is low and atmospheric humidity is high owing to the funicle drying out more slowly.

Coquillat (1951) suggested that *C. bursa-pastoris* falls into the category of dispersal associated with disturbed habitats, having seeds with no very obvious morphological adaptations. Salisbury (1961) reported that the seed is dispersed by wind, by rain wash, on the feet of birds, in the droppings of birds (particularly sparrows), on the feet and in the droppings of various mammals, including sheep, cattle, and horses, and also by ants. The seed is also dispersed by yaks and goats (Disp. Pl.).

Experiments examining the dispersal of *C. bursa-pastoris* showed that, with unassisted dispersal in sheltered conditions, all seeds fell within 50 cm of the parent plant, with the majority falling between 15 and 30 cm, while with wind-aided dispersal 80% of the seeds fell within 50 cm of the parent plant and the other 20% was scattered between 50 and 105 cm from the parent. Although the seeds have no special wind-dispersal mechanisms they are small and light, and carriage by wind gives local dispersion (Aksoy 1996).

Hurka & Haase (1982) reported that the seed epidermis of *C. bursa-pastoris* produces a mucilage which, when moistened, becomes sticky. This glues seeds to mud which is then picked up on the feet of birds and can be carried long distances. *Capsella bursa-pastoris* is frequent on roadsides, pathways, the edge of car parks and gardens, and ripe seed may be transported in mud sticking to the feet of humans and to car tyres, providing long-distance dispersal.

(D) VIABILITY OF SEEDS: GERMINATION

Capsella bursa-pastoris germinates at temperatures between 5 and 30 °C. Lowest germination (14%) is obtained at 5 °C and maximum (44%) at 25 °C, falling to 40% at 30 °C (data from Lauer, Fig. 491 (Ellenberg 1988) show somewhat different trends). Seed from a Turkish population, germinated under the same conditions, gave a significantly higher percentage germination at all temperatures. Neuffer & Hurka (1988) reported that the percentage germination of *C. bursa-pastoris* from Scandinavia, Central Europe and the Alps varied between the different locations. Neuffer & Hurka (1988) and El-Habibi & Youssef (1981) found that alternating night/day temperatures of 10/30 °C and 20/30 °C, respectively, enhanced germination. However, we found that a range of alternating temperatures, including 10/30 °C and 20/30 °C, produced a lower percentage germination in both a

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British and a Turkish population of *C. bursa-pastoris* than was obtained at a constant temperature of 25 °C.

Percentage germination is significantly reduced by darkness (to 15%) and the optimum temperature for germination is reduced from 25 to 20 °C (Aksoy 1996). Popay & Roberts (1970a,b) also obtained an optimum of 9% at 20 °C for seed of *C. bursa-pastoris* germinated in darkness. However, Benjamin (1974) found that a temperature of 25 °C produced the highest germination (13%). Thus, *C. bursa-pastoris* has a pronounced light requirement as significantly fewer seeds germinate in darkness, as is common with other ruderal species such as *Chenopodium album* (Benjamin 1974). However, the germination of seeds incubated in darkness under controlled conditions may overestimate the *in situ* germination of buried seeds in the field, as Baskin & Baskin (1989) report values of only 1% and 4% from their experiments with *C. bursa-pastoris*. These authors argue that *C. bursa-pastoris* exhibits annual conditional dormancy/non-dormancy cycles, losing the ability to germinate first at high and then at lower temperatures as they enter conditional dormancy with increasing spring temperatures (Baskin & Baskin 1989).

Freshly harvested seed of *C. bursa-pastoris* is reported to be dormant (Holzner *et al*. 1982; Baskin & Baskin 1986) and to require a period of stratification (imbibed seeds chilled at 4 °C for 2 weeks) before germination will occur (Popay & Roberts 1970a,b). Pre-chilling at 4 °C and freezing at −20 °C for 6 weeks gave 49% and 29% germination, respectively, compared with 44% for an untreated control. As with some other small-seeded pioneer species, dormancy will also be enforced by high CO_2 concentrations and a particular red/far red light ratio, as well as by darkness (Popay & Roberts 1970a,b; Holzner *et al*. 1982).

While maximum germination at 25 °C on filter paper moistened with water was 44%, germination was enhanced when the medium was garden soil (65%) or peat-based compost (71%), and reduced on silica sand (38%). Germination on filter paper moistened with nutrient solution (Hewitt's) produced the highest percentage germination of all tests (98%), and was very rapid, being completed in 6 days, compared with 14 for silica sand, 9 for garden soil and 8 for the compost, reflecting the habitat preference of *C. bursa-pastoris* for nutrient-rich gardens and cultivated arable land. This might be because NO_3^- stimulates germination or breaks dormancy in some ruderal species, including *C. bursa-pastoris* (e.g. Popay & Roberts 1970a; Vincent & Roberts 1977; Roberts & Benjamin 1979; Kleijn & van der Voort 1997).

Seed does not germinate if the soil water content is less than 10%: germination is optimal at about 20% and declines at higher levels (Benjamin 1974). Under waterlogged conditions in distilled water there was only 21% germination.

All germination tests were carried out in a growth cabinet with a flux density of 102 μmol m^{-2} s^{-1} over a 12-h day, at 25 °C when temperature was not being investigated. There were five replicates of 100 seeds, from a bulk gathering collected from West Yorkshire, UK and from Izmir, Turkey during June 1993. Seed stored at ambient temperature and humidity in the laboratory started to lose viability after 6 months, and after 2 years' germination was reduced by 30%. However, Popay & Roberts (1970a) reported that there was no reduction in viability of *C. bursa-pastoris* seed after 2 years' storage at 4 °C.

(E) SEEDLING MORPHOLOGY

Germination is epigeal. After imbibition, and the swelling of the shrivelled floral parts, the radicle emerges from the proximal end of the seed. Radicle emergence takes a minimum of 3 days and the cotyledons appear after 4–5 days. Growth of lateral roots commences after 15 days, the first true leaves appear around 12–14 days, and the second leaves after 14–17 days. Seedling development is shown in Fig. 2.

IX. Herbivory and disease

(A) ANIMAL FEEDERS OR PARASITES

Capsella bursa-pastoris is grazed by cattle, horses, yaks, sheep and rabbits (Disp. Pl.; Crawley 1990).

The following insects are recorded as feeding on *C. bursa-pastoris* (L.K. Ward, personal communication):

Insecta

Hemiptera
Lygaeidae
Drymus sylvaticus (F.): larvae feed on fruits and seeds.
Scolopostethus affinis (Schilling): larvae feed on fruits and seeds.
S. decoratus (Hahn): larvae feed on fruits and seeds.
Stygnocoris fuligineus (Geoffroy in Fourcroy): larvae feed on fruits and seeds.

Aphididae
Aphis euonymi F.: feeds on leaves. Causes leaf curling.
A. fabae Scopoli: larvae and adults feed on flowers and shoots.
A. frangulae Kaltenbach ssp. *capsellae* Kaltenbach: feed on leaves and flowers.
A. nasturtii Kaltenbach: larvae and adults feed on leaves.
Aulacorthum solani (Kaltenbach): feed on flowers, leaves and shoots. Vector of virus diseases.
Brachycaudus (L.) ssp. *lateralis* (Walker): feed on leaves and stems.
Brevicoryne brassicae (L.): larvae and adults feed on flowers and leaves. Mostly attack upper surface of leaves, which become pale, curved and folded.
Lipaphis erysimi (Kaltenbach): feed on shoots and leaves.

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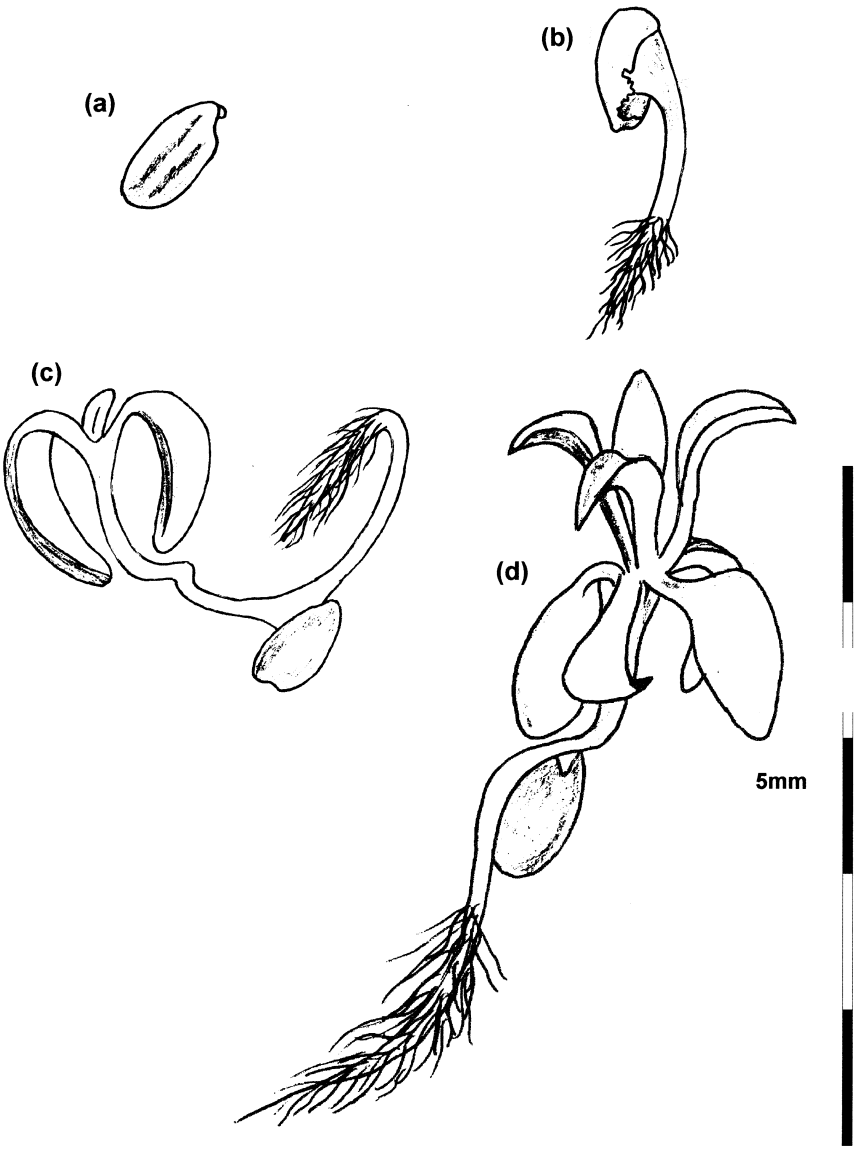


Fig. 2 Seedling establishment of *C. bursa-pastoris*. (a) Seed, (b) after germination for 3 days, (c) after 7 days, and (d) after 15 days. Germination was on moist filter paper, with 12-h days, at 25 °C.

Myzus ascalonicus Doncaster: feed on flowers, leaves and stems.
Myzus certus (Walker): feed on shoots and leaves which roll upwards.
M. persicae (Sulzer): larvae and adults feed on flowers, stems and leaves.

Pemphigidae
Smynthurodes betae Westwood: feed on roots.

Lepidoptera
Pieridea
Anthocharis cardamines (L.): larvae feed on leaves, adults on flowers.
Lithostege griseata (Denis & Schiffermuller): larvae feed on fruits/seeds.

Coleoptera
Chrysomelidae
Phyllotreta nemorum (L.): larvae feed as leaf-miners; found only on glucosinolate-containing species.

Curculionidae
Ceutorhynchus contractus (Marsham): larvae cause galling on stems and mine leaves.
C. erysimi (F.): larvae feed on roots and as leaf-miners.
C. floralis (Paykull): adults.
C. pleurostigma (Marsham): larvae.
C. pumilio (Gyllenhal): adults.
C. sulicollis (Paykull): adults and larvae, which form galls on stems.
C. timidus Weise: larvae cause galling on leaves.

Scarabaeidae
Phyllopertha horticola L.: larvae feed on roots (Gange & Brown 1989).

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Hymenoptera
Tenthredinidae
Athalia bolivari Dusmet: larvae.

Diptera
Cecidomyiidae
Dasineura brassicae Winnertz: larvae cause galling on shoots.

Agromyzidae
Liriomyza strigara (Meigen): larvae mine along midrib, with off-shoots of mines along veins.
Phytomyza horticola Goureau: larvae mine upper and lower surfaces of leaves.

Other invertebrate feeders include:

Arachnida

Acari
Eriophyidae
Aceria drabae (Nalepa): larvae and adults cause galling on leaves, deformation of flowers and form an erineum (L.K. Ward, personal communication).

Mollusca

Agriolimax caruanae Pollonera (Limacidae): feeds on leaves and flowers (Dirzo & Harper 1980). *Capsella bursa-pastoris* appears to be highly acceptable to all mollusc species on which it has been tested, including: *Agriolimax reticulatus* (Duval 1971); *A. columbianus* (Cates & Orians 1975); *Arion ater* (Cates & Orians 1975); and *A. hortensis* (Duval 1973).

(B) PLANT PARASITES AND DISEASES

The leaves, stems and flowers of *C. bursa-pastoris* may be infected with the white rust *Albugo candida* (Pers. ex Hook) Kuntze (Alexander & Burdon 1984); the downy mildew *Peronospora parasitica* (Pers.) ex Fr. (Alexander & Burdon 1984); the powdery mildew *Erysiphe communis* (Wallr.) LK. and the rust *Puccinia trabutii* Roum et Sacc. (Vad. para. Pilze). Paul & Ayres (1990) reported a reduction in the weight of *C. bursa-pastoris*, in mineral-rich soil, when it is infected by the rust *Puccinia lagenophorae* Cooke.

Capsella bursa-pastoris is host to a number of seed-borne viruses (Neergaard 1977). Viruses to which the species is susceptible include beet mild yellowing virus and beet western yellows virus (Stevens *et al*. 1994), the potato spotted wilt virus (Bitterlich & MacDonald 1993) and potato leaf roll virus (Fox *et al*. 1993). *Capsella bursa-pastoris* also sustained moderate galling and supported moderate reproduction of the northern root-knot nematode (*Meloidogyne hapla*) in glasshouse trials (Belair & Benoit 1996).

X. History

Capsella bursa-pastoris probably originated in the East Mediterranean area including Asia Minor. Early Neolithic records of *C. bursa-pastoris* seeds are reported in Turkey between 5850 and 5600 BC, whereas in Central Europe the earliest records date from the Middle and Late Neolithic, from around 4000 BC (Willerding 1986). It seems probable that *C. bursa-pastoris* was brought to Central Europe with the spread of agriculture from the Middle East (Hurka & Neuffer 1991). However, there are two records of *Capsella* seeds from the Pleistocene in Great Britain (Godw. Hist.). Hurka & Neuffer (1991) suggested that *C. bursa-pastoris* may constitute part of the late glacial or preboreal flora. First recorded in Britain by Turner (1548) as '*Bursa pastoris* . . . Shepherdes purse . . . groweth by highwayes almost in every place'.

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