

Towards a simplified taxonomy of *Capsella bursa-pastoris* (L.) Medik. (Brassicaceae)

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ABSTRACT

Capsella bursa-pastoris (L.) Medik. is a species with a cosmopolitan distribution which shows considerable morphological variation. Numerous authors have recognised widely differing numbers of varieties, microspecies or other infraspecific subdivisions (segregates) of this species. In an attempt to clarify this situation, we grew British material of the species under controlled conditions through to the F₃ generation to remove environmental variation, and assessed the plants on the basis of a range of morphological criteria, namely leaf shape, capsule size and also length of time taken to flower. Analysis of these characteristics consistently produced four basic groups, which had been previously described. Herbarium specimens could also nearly always be assigned to one of these groups. Limited chromosome counts suggest that two of these groups are diploid and two are tetraploid. We suggest this fourfold division into broad groups reflects the major genetic separations within the species, but that there is also considerable phenotypic plasticity shown by *C. bursa-pastoris* in response to factors such as shade or trampling. These four groups appear to differ in their geographical distribution in Britain.

KEYWORDS: Shepherd's Purse, morphological variation, leaf characters, capsule characters, chromosome counts, infraspecific groupings.

INTRODUCTION

Capsella bursa-pastoris (L.) Medik. (Shepherd's Purse) (Brassicaceae) has a cosmopolitan distribution, and is a colonising species of disturbed ground. Being found in a broad range of conditions, up to 5900 m (Wilson 1949; Mani 1978) and in almost all countries of the world from tropical to subarctic habitats (Holm *et al.* 1979), the species is known to exhibit considerable morphological variation.

Capsella bursa-pastoris has been described by numerous authors since the late 19th century, and has been divided taxonomically into many species, subspecies, varieties, microspecies and segregates. Jordan (1864), one of the earliest workers, described five species in France, namely *Capsella agrestis*, *C. virgata*, *C. ruderalis*, *C. sabulosa* and *C. praecox*, none of which are recognised today. Hopkirk (1869) considered the variation in Belgium to consist of subspecies derived from one common type, and he went on to describe six subspecies based primarily on the character of the capsule. Mott (1885) described eight varieties for Leicestershire and Rouy & Foucaud (1893) listed seven varieties and four subspecies based on the fruit characteristics in France. Almquist (1907) described 70 elementary species and later (Almquist 1921) examined British *Capsella bursa-pastoris* and listed 16 species. His descriptions were based on fine distinctions of leaf and capsule shape and size. Two years later, Almquist (1923) had recorded twelve classes of *Capsella* containing almost 200 microspecies. His microspecies were again based on minute differences in capsule shape and size, differing leaf shapes and position of leaf lobes. More recently, but only in Cyprus, Meikle (1977) recognized two species based on capsule size whilst Clapham *et al.* (1987) record *Capsella bursa-pastoris* as "very variable with a strong tendency for distinctive populations to arise because of self-pollination. Many of these have been named", but they do not specify any of these. The first edition of *Flora Europaea* (Chater 1964) comments that numerous variants have been described by Almquist, whilst the second edition (Chater 1993) states that "there is extreme

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polymorphism within the four species listed" and that "*Capsella bursa-pastoris* is especially polymorphic and its variants incorporate many of the characteristics of the other three species". Most recently, Stace (1997) describes *C. bursa-pastoris* "as extremely variable in leaf and fruit shape; c. 25 segregates have been recognized in the British Isles". No details of these are given, nor is any information on them provided by the specialist *Crucifers of Great Britain and Ireland* (Rich 1991).

The problems of taxonomy at the infraspecific level, relevant to a very variable species such as *C. bursa-pastoris* which is largely inbreeding yet has many phenotypic variations, are discussed, for example, by Stace (1989). This author notes that such phenotypic modifications would not be given taxonomic status by most taxonomists and that when such variations are recognised as phenotypic, they are relegated to synonymy. *Capsella bursa-pastoris* certainly shows phenotypic variation as a direct result of a wide range of environmental factors including temperature, shading, altitude, latitude and season; for example, Almquist (1923) found that leaves developing in autumn and spring were mostly lobed, whereas mid-summer leaves tend to be poorly lobed or entire. Hurka (1990) found pronounced ecotypic variation in time to flowering between early Scandinavian and late Alpine populations; he also found early and late ecotypes in North America. Aksoy (1996) observed the effects of shading on leaf shape, Steinmayer *et al.* (1985) recorded correlations between leaf form and temperature and rainfall, and Neuffer (1989) investigated the effects of temperature on variables such as leaf shape and flowering times. However, it is possible that not all the complex variations observed in this species can be reduced to phenotypic variation superimposed on one single species complex.

Shull (1909) collected seeds of *C. bursa-pastoris* from different sites in North America, where the species is introduced but now widely naturalized, and grew these under standard conditions for several generations, by self-pollination. He found that the majority of his plants could be fitted into four basic groups based on the characters of the rosette leaf shape. He referred to these four groupings ("biotypes" *sensu* Shull) as *Capsella bursa-pastoris* and used these names for them: rhomboidea, simplex, heteris and tenuis.

Steinmayer *et al.* (1985) examined 29 populations of *C. bursa-pastoris* from the Alps to northern Scandinavia, from Iceland and also a population from the Hindu Kush Mountains in Afghanistan, while Neuffer (1989) worked with populations of *C. bursa-pastoris* collected from southern to northern Europe (including three from Britain), two populations from Egypt and one from Israel. Their populations were grown under standard conditions either in glasshouses or in field trials for varying periods of time. Analyses of leaf shapes and capsule size allowed the authors to classify most of their plants into one of the four basic groups proposed by Shull (1909).

This paper seeks to expand on the work of Neuffer (1989) by examining populations of *C. bursa-pastoris* from a variety of habitats and geographical areas in Britain, to determine how well Shull's four basic groups are generally recognizable in the field, and from herbarium specimens; to germinate and grow seed from the different populations under standard conditions, and to observe whether, when environmental variation is removed, the plants can be classified according to Shull's groups; and, finally, to determine whether or not this classification is maintained in their progeny.

If Shull's groupings are substantiated then a step will have been made towards simplifying the taxonomic classification of *C. bursa-pastoris* from 200 microspecies, or 25 segregates, or no attempt at all to sub-divide this variable species, to producing four useful groups, which can be recognized as having a distinct genetic basis underlying the environmentally modified phenotype.

Although Shull's work was concerned only with examining leaf morphology, other workers, mentioned above, have used capsule size and shape as identifying characters and these have also been examined in the present paper; chromosome numbers have also been assessed. Chromosome numbers are usually tetraploid with $2n = 32$ (Davis 1965; Löve & Löve 1956; Svensson 1983; Clapham *et al.* 1987). Chater (1993) records both $2n = 32$ and also $2n = 16$; Svensson (1983) also records diploid specimens with $2n = 16$ from Greece.

MATERIALS AND METHODS

Seed samples from locally available populations were collected from 20 different habitats in Bradford and district, and from 14 other locations throughout Britain, between April and July 1993.

These were germinated in potting compost in a glasshouse and grown on until they set seed. Cross pollination was assumed to be prevented by keeping each of the populations in a different place in the glasshouse, with sliding separating doors to aid isolation, and by the fact that the species is primarily adapted for self-pollination. Subsequent seed collection and growing was continued through to the F_3 generation.

In each generation the rosette leaf shape was assessed for 15 plants, randomly selected from each population, according to a four-fold categorisation on the basis of Shull (1909) as follows:

Capsella bursa-pastoris group A ("simplex" sensu Shull (1909))

Leaves with mostly simple, rounded or triangular, acutish lobes.

Capsella bursa-pastoris group B ("rhomboidea" sensu Shull (1909))

Leaves divided to the midrib; possessing a more or less rhombic terminal lobe, set off by deep sinuses from the nearest lateral lobes.

Capsella bursa-pastoris group C ("heteris" sensu Shull (1909))

Leaves divided to the midrib; the terminal lobe usually separated from the nearest lateral lobes by deep, clean-cut incisions.

Capsella bursa-pastoris group D ("tenuis" sensu Shull (1909))

Sinuses relatively shallow, rarely extending to the midrib; the terminal lobe is not separated from lateral lobes by deep incisions; lateral lobes are generally slender, elongated and acute.

The original parent plants had also been evaluated on this categorisation. While most of these could be fitted to one of the groups a number were of intermediate status and could not be classified at the time of collecting.

For each of the F_3 plants, the lengths and widths of 30 seed capsules were measured to provide an indication of shape. The number of days elapsed between germination and the production of the first flower by each plant was recorded for each group.

The somatic chromosome number was determined for 15 plants of the F_3 generation of each group from root-tip squashes. The root tips were pretreated for 2 hours in a solution of 0.1% colchicine and 2 mM 8-oxychinoline (1:1), fixed in Carnoy's fluid and stained in aceto-orcein.

In addition to the fresh material collected during this study, herbarium material from The Natural History Museum, London (BM) was consulted to obtain further information on the relative frequencies and geographical distribution of the groups in Britain, wherever the groups could be recognized from herbarium specimens. Two hundred specimens were examined, of which 189 could be allocated to one of Shull's four basic groups.

RESULTS

Although the field populations showed phenotypic variation, the F_1 generation, produced by self-pollination, gave rise to F_2 and F_3 generations which exhibited no phenotypic variability from the F_1 generation. Observations and measurements from the F_3 generation are presented in Figs 1 & 2 and Table 1, divided into the leaf morphology groups shown consistently from the F_1 generation.

The chromosome studies reported in this paper indicate that there are diploid as well as tetraploid populations of *C. bursa-pastoris* in Britain. Groups A and B (simplex and rhomboidea) are tetraploid while groups C and D (heteris and tenuis) are diploid. The results indicate that the rate of growth was greater for the tetraploid groups, which produced larger capsules (Fig. 2). Capsule

TABLE 1. MEASUREMENTS OF VARIOUS PARAMETERS (MEAN \pm STANDARD ERRORS) FOR THE DIFFERENT GROUPS (A-D) (SENSU SHULL (1909)) OF *CAPSELLA BURSA-PASTORIS* GROWN UNDER STANDARD GREENHOUSE CONDITIONS

Group	A (simplex)	B (rhomboidea)	C (heteris)	D (tenuis)
Chromosome number	$2n = 4x = 32$	$2n = 4x = 32$	$2n = 16$	$2n = 16$
Capsule length (mm)	7.81 ± 0.15	7.58 ± 0.15	6.56 ± 0.11	6.29 ± 0.11
Capsule width (mm)	7.34 ± 0.11	6.47 ± 0.11	4.85 ± 0.07	4.25 ± 0.06
Days to first flowering	32 ± 4.26	40 ± 5.12	65 ± 6.24	70 ± 7.54

30 capsules from 15 plants for each group were measured.

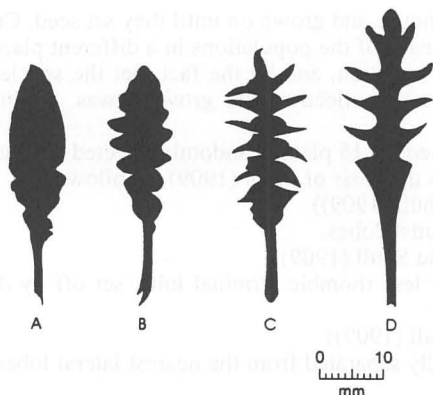


FIGURE 1. Comparison of leaf morphologies for F_3 *Capsella bursa-pastoris* groups A-D, grown under standard conditions: A - simplex; B - rhomboidea; C - heteris; D - tenuis (sensu Shull (1909)).

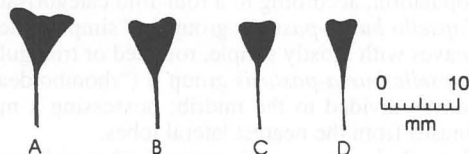


FIGURE 2. Comparison of capsule size and shape for F_3 *Capsella bursa-pastoris* groups A-D, grown under standard conditions: A - simplex; B - rhomboidea; C - heteris; D - tenuis (sensu Shull (1909)).

lengths for groups A (simplex) and B (rhomboidea), the tetraploids, were significantly different based on t-tests (at $p < 0.001$) from those of group C (heteris) and D (tenuis), the diploids. Capsule lengths were not significantly different between A and B nor between C and D. However, capsule widths were significantly different (at $p < 0.001$) between all four groups. Days to flowering was also examined and, as for capsule length, the differences between A and B were not significant, nor those between C and D, but the differences between the tetraploids and diploids were significant, based on t-tests, at $p < 0.001$ with the tetraploids flowering earlier (Table 1). Observations, however, suggest that the diploid groups tended to flower over a more extended period and to survive longer than the tetraploids.

From observations of 289 individual plants (both herbarium and fresh) from Britain, the relative frequencies of the four groups were found to be: A (simplex) 23%; B (rhomboidea) 39%; C (heteris) 33% and D (tenuis) 5%. Based on this relatively restricted sample, the distribution of the four groups appears to vary geographically (Fig. 3); from the material (fresh and herbarium) available, groups B and C were found throughout Britain but group A was not recorded from northern Scotland and group D (based on a small percentage of records overall) was only found in material from England.

DISCUSSION AND CONCLUSIONS

The classification of *C. bursa-pastoris* in the field has been hampered by the polymorphic variation in leaf shape and size resulting from gene-environment interactions, particularly as the species is of such widespread geographical and altitudinal distribution and is found in a wide variety of habitats. Neuffer (1989), working with a large number of populations of *C. bursa-pastoris*, showed that the genotypes defining leaf type are easily modified by environmental parameters and that the degree of phenotypic plasticity varies from provenance to provenance. This variation has led to widely differing attempts to classify *C. bursa-pastoris* in terms of microspecies based on either leaf shapes and/or capsule shape and size.

If systematic botany relies solely on descriptions of plants in the field then the problems of classifying polymorphic species such as *C. bursa-pastoris* will remain. However, if collateral cultivation methods are adopted in lieu of comparative field morphology, as has been carried out in this study, then a useful step forward may be made.

Because genotype-environment interactions are very pronounced then the use of herbarium specimens in classifying *C. bursa-pastoris*, although also of considerable value, may have limitations owing to the presence of intermediate leaf shapes. It is not always possible to classify these into the basic groups, although in the current work only 5% of the herbarium specimens

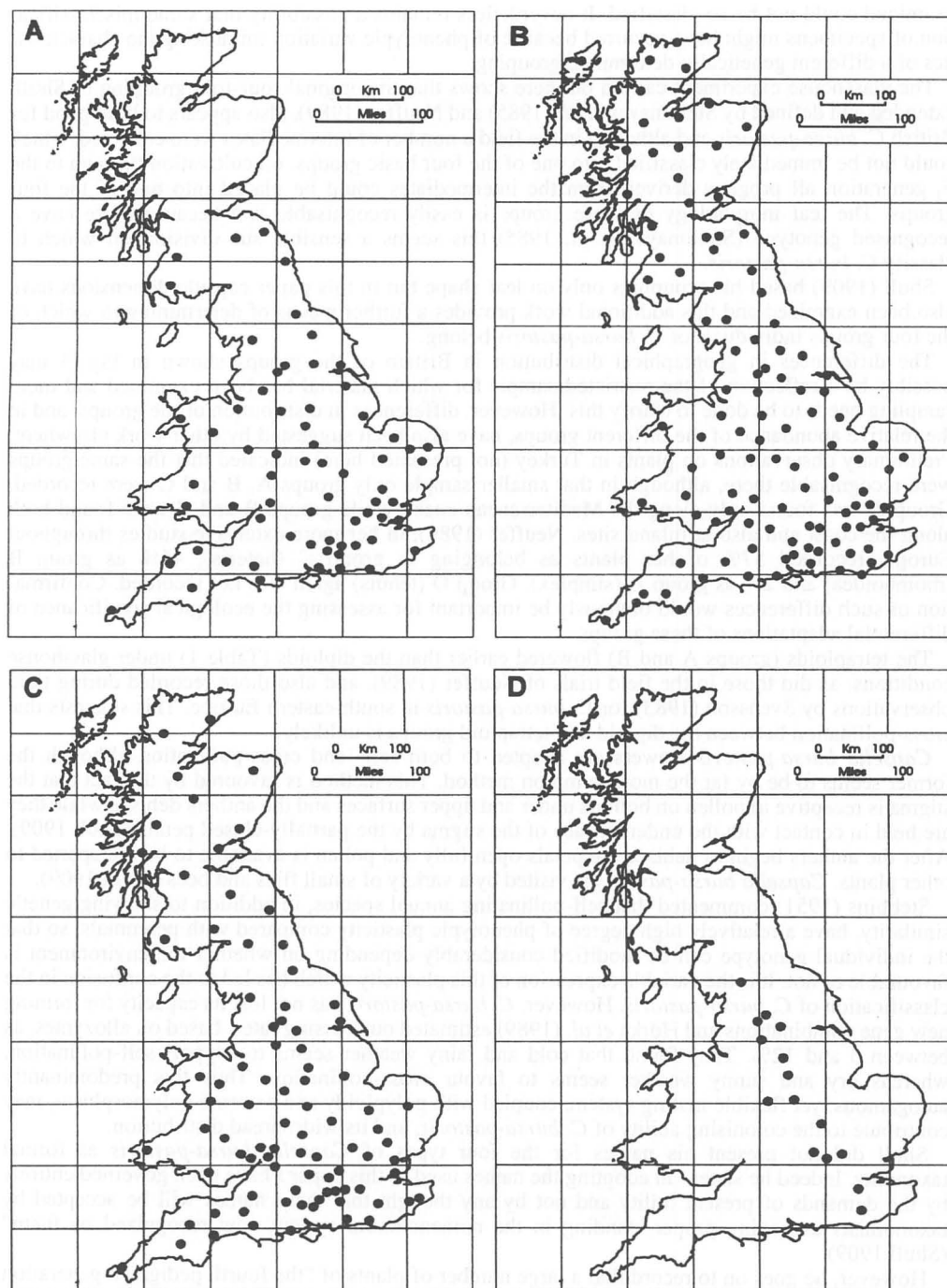


FIGURE 3. Distribution of *Capsella bursa-pastoris* groups A–D in Britain, based on collected samples and herbarium material: A - simplex; B - rhomboidea; C - heteris; D - tenuis (sensu Shull (1909)).

examined could not be so classified. It nevertheless remains a possibility that some misclassification of specimens might have occurred because of phenotypic variation mimicking the characteristics of a different genetically-determined grouping.

The glasshouse experiment carried out here shows that the original four-fold grouping of Shull, extended and defined by Steinmayer *et al.* (1985) and Neuffer (1989), also appears to hold good for British *C. bursa-pastoris* and although in the field a number of intermediates were collected, which could not be immediately classified into one of the four basic groups, on cultivation through to the F_3 generation all progeny derived from the intermediates could be placed into one of the four groups. The leaf morphology of these groups is easily recognisable and because these have a recognised genotype (Steinmayer *et al.* 1985) this seems a sensible sub-division on which to classify *C. bursa-pastoris*.

Shull (1909) based his groupings only on leaf shape but in this paper capsule dimensions have also been examined and this additional work provides a further means of determining to which of the four groups individuals of *C. bursa-pastoris* belong.

The differences in geographical distribution in Britain of the groups shown in Fig. 3 may possibly be a reflection of the restricted sample for which material has been examined and more sampling needs to be done to clarify this. However, differences in distribution of the groups, and in the relative abundance of the different groups, have also been suggested by other work elsewhere. Preliminary observations on plants in Turkey (not presented here) indicated that the same groups were recognisable there, although in that smaller sample only groups A, B and C were recorded. Group A was found only along the Mediterranean coast, while groups B and C were found both along the coast and also at inland sites. Neuffer (1989), in her more extensive studies throughout Europe, recorded 57% of her plants as belonging to group C (heteris), 41% as group B (rhomboidea) and 2% as group A (simplex). Group D (tenuis) again was not recorded. Confirmation of such differences would obviously be important for assessing the ecological significance of differential adaptations of these groups.

The tetraploids (groups A and B) flowered earlier than the diploids (Table 1) under glasshouse conditions, as did those in the field trials of Neuffer (1989), and also those recorded during field observations by Svensson (1983) for *C. bursa-pastoris* in south-eastern Europe. This suggests that cross-pollination between the diploid and tetraploid groups is unlikely.

Capsella bursa-pastoris flowers are adapted to both self- and cross-pollination although the former seems to be by far the more common method. This method is favoured by the fact that the stigma is receptive to pollen on both its under and upper surfaces and the anthers dehisce while they are held in contact with the under surface of the stigma by the partially-closed petals (Shull 1909). After the anthers begin to dehisce the petals open fully and pollen is available to be transported to other plants. *Capsella bursa-pastoris* is visited by a variety of small flies and bees (Shull 1909).

Stebbins (1951) commented that self-pollinating annual species, in addition to showing genetic similarity, have a relatively high degree of phenotypic plasticity compared with perennials, so that the individual genotype can be modified considerably depending on whether the environment is favourable or not. It is the variable expression of this plasticity which has led to the confusion in the classification of *C. bursa-pastoris*. However, *C. bursa-pastoris* has not lost its capacity for forming new gene combinations and Hurka *et al.* (1989) estimated outcrossing rates, based on allozymes, as between 3 and 12%. They found that cold and rainy weather seems to support self-pollination, whereas dry and sunny weather seems to favour cross-pollination. Thus this predominantly autogamous, yet flexible mating system, coupled with polyploidy and extreme polymorphism, may contribute to the colonising ability of *C. bursa-pastoris*, and its widespread distribution.

Shull did not present his names for the four types of *Capsella bursa-pastoris* as formal taxonomy. Indeed he states "in adopting the names used in this paper I have been governed entirely by the demands of present utility and not by any thought that these names will be accepted by taxonomists as having proper standing in the nomenclatural system now recognized by them" (Shull 1909).

However, he goes on to record that a large number of plants of "the fourth pedigree generation and a few of the fifth under observation" retained "easily recognized differentiating marks, which, except in one form, show no transgression of the characteristic features of any other form studied. These forms are therefore distinct elementary species, or biotypes, each characterized by certain constant features and each with its own range of fluctuating variability." (Shull 1909). Shull

comments that he was at first inclined to use binomial names, leaving the Linnaean species name - *bursa-pastoris* - as the valid name for the aggregation of the infraspecific forms, having the same habit and triangular or obcordate capsules. But the fact that a corresponding series of infraspecific forms may occur in different related species led him to use the trinomial system, and he used the same infraspecific names for the two closely related species *Bursa* (= *Capsella*) *bursa-pastoris* and *Bursa* (= *Capsella*) *heegeri*.

The authors are of the opinion that Shull's (1909) interpretation of this taxon is based on sound characters underlying the complex phenotypic variability, and that consideration might be given to the establishment of subspecific nomenclature to describe these four groups of *C. bursa-pastoris*.

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