

***Senecio vulgaris* L. subsp. *denticulatus* (O. F. Muell.) P. D. Sell and *S. vulgaris* subsp. *vulgaris* var. *vulgaris* on Jersey (Channel Islands)**

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ABSTRACT

Evidence obtained from comparative cultivation confirms that *Senecio vulgaris* subsp. *denticulatus* (Asteraceae) and its presumed derivative var. *vulgaris* differ consistently in a number of morphological and life history characters. Field studies on Jersey revealed that both taxa are also ecologically distinct. Subsp. *denticulatus* is only known from coastal areas of dune grassland where it occurs on soils which have large amounts of carbonate and low amounts of mineral nutrients. Its associates include other winter-annuals and species of Mediterranean affinity. Results obtained from soil analyses do not provide any meaningful clue to the unusual and disjunct distribution of subsp. *denticulatus* and several community associates within one of its natural maritime habitats (Les Quennevais). Some observations on the pollination strategy, seed production and predation damage of subsp. *denticulatus* are reported. In contrast to subsp. *denticulatus*, var. *vulgaris* occurs in man-disturbed inland and coastal localities throughout the island. Both taxa seem to interact along an extensive coastal hybrid zone, particularly in the disturbed area north of Les Quennevais. Progeny-analyses of both short ligulate and discoid phenotypes from Les Quennevais showed them to produce patterns of germination, phenological and leaf shape characteristics typical of subsp. *denticulatus*. It is concluded that the low nutrient-supplying power of the Quennevais area is a factor of importance in limiting the distribution of the var. *vulgaris* genotypes to areas outside Les Quennevais. Information on the former distribution of subsp. *denticulatus* on Jersey suggests that its habitat is seriously endangered from progressive destruction by man.

KEYWORDS: *Senecio vulgaris* subsp. *vulgaris* var. *hibernicus*, ecological variation, hybrid zone, adaptation.

INTRODUCTION

Senecio vulgaris L. ($2n = 40$) is subdivided into two subspecies, namely the type subspecies with two varieties and subsp. *denticulatus* (O. F. Muell.) P. D. Sell†. Subspecies *vulgaris* var. *hibernicus* Syme, which is distributed sympatrically with var. *vulgaris* and in its distribution largely limited to the British Isles and Ireland, appears very likely to be a recently evolved stabilized introgressant between var. *vulgaris* and *S. squalidus* ($2n = 20$) (e.g. Abbott 1992). This taxon will not be considered here further. Thus all comparisons reported in this paper are between *Senecio vulgaris* subsp. *denticulatus* and *Senecio vulgaris* subsp. *vulgaris* var. *vulgaris*.

Information available from cultivation experiments (Kadereit 1984a; Gilmer & Kadereit 1989) and extensive herbarium surveys (Allen 1967; Perring & Sell 1968; Kadereit 1984a) indicates that subsp. *denticulatus* and var. *vulgaris* differ conspicuously with regard to germination behaviour, life cycle, morphology and reproductive output, but also geographical distribution and habitat preference. Although no unambiguous native habitat can be delineated for the cosmopolitan weed var. *vulgaris* (Kadereit 1984a), subsp. *denticulatus* is restricted either to natural maritime habitats (dunes, sandy fields and cliffs) along the coasts of N.W. Europe, i.e. from W. France, the Channel Islands, W. and S.W. Britain, to the S. and E. coasts of Sweden (Allen 1967), or can be found in the Mediterranean area, mainly in the mountains of S. Spain and Sicily (Kadereit 1984a). In the British

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†Nomenclature follows Stace (1991) for vascular plant species.

Isles only records from Ainsdale (Merseyside) and the Channel Islands have been confirmed in recent years (Ashton 1990; Harris & Ingram 1992). Rather surprisingly, no detailed ecological study of the natural habitat of subsp. *denticulatus* is available.

The present account provides some field data on the distribution, habitat and pollination strategy of subsp. *denticulatus* in a maritime site on Jersey, Channel Islands. As var. *vulgaris* is reported to be common on Jersey (e.g. Le Sueur 1984), another objective of the present study was to investigate whether the two taxa are isolated through habitat differentiation, or whether they co-occur and hybridize.

The most conspicuous morphological character of subsp. *denticulatus*, and certainly its most reliable diagnostic character in the field, is the presence of ray florets 2.3–3.0 mm long. Ray florets are absent in var. *vulgaris*. The presence of the ray florets is under simple genetic control of the 'ray floret locus', with subsp. *denticulatus* homozygous for the R allele, discoid plants of var. *vulgaris* homozygous for the r allele and short ligulate hybrids between both taxa heterozygous (Trow 1912; Comes 1994). Other less reliable field characters are the rather dense arachnoid indumentum, leaf shape characteristics (Allen 1967) and an irregular achene indumentum (Gilmer & Kadereit 1989). Plants of subsp. *denticulatus* differ further from var. *vulgaris* in showing pronounced seed dormancy, which also seems to be regulated by one major gene (Kadereit 1984a). Recently, however, Ren & Abbott (1991) reported the presence of innate seed dormancy in var. *vulgaris* from the Mediterranean area. The authors concluded that this feature probably evolved in adaptation to the climatic conditions of heavy winter rains and severe summer drought, and enables this taxon to grow as a 'typical Mediterranean' winter annual. Given the putative Mediterranean origin of subsp. *denticulatus* (Kadereit 1984b), the same explanation was previously put forward by Kadereit (1984a) to account for the presence of both these characters, seed dormancy and winter annual life cycle, in subsp. *denticulatus*. The distinctness of subsp. *denticulatus* from var. *vulgaris* is further emphasized by its substantially prolonged time of vegetative growth, first noticed by Trow (1912, 1916) and later by Kadereit (1984a), and its potentially smaller reproductive output under standard conditions in the greenhouse (Kadereit 1984a).

On Jersey, field studies were primarily focused on the sand dune system of St Ouen's Bay at the western end of the island, and in particular on the widest part of the dunes in the south, known as Les Quennevais. In this area, initial observations revealed that subsp. *denticulatus* becomes exceedingly rare c. 200 m away from the shore, but is present again 1,000 m or more farther inland. Since the Quennevais area is well-known for remarkable changes in soil pH and carbonate values (Böcher 1954; Ranwell 1975), a study was designed to investigate the distribution of subsp. *denticulatus* and its associated vegetation in relation to soil types along a transect, roughly coinciding with Ranwell's (1975) main study transect. Soil samples from outside this area were also analysed.

As I encountered discoid plants within the habitat of subsp. *denticulatus* which could not be assigned to either taxon using morphological criteria, a comparative cultivation experiment was designed to determine whether these variants exhibit (i) innate seed dormancy, (ii) a substantially slower speed of development and (iii) a smaller reproductive capacity than typical plants of var. *vulgaris* from Jersey and, as a control, var. *vulgaris* from the Botanic Garden, Mainz University (Germany).

MATERIALS AND METHODS

FIELD WORK

Studies on Jersey were carried out between 13 and 19 May 1992. Following Ranwell's terminology (1975), the transect area on Les Quennevais (Fig. 1a), ranging from the seawall south of the slipway at Le Braye to the inland limit of the dune system south of the enclosed valley below Ville des Quennevais (c. 1.6 km), was classified into four zones of landscape structure according to distance from the shore: 1, the coastal dune area (0–c. 100 m); 2, the dune plain (100–700 m); 3, the plateau scarp (700–1000 m); and 4, the plateau dunes including the crestline (1000–1600 m). Within 300 m distance from the shore, the number of plants of *S. vulgaris* was determined in 2 m × 2 m sampling areas at regular 2 m intervals. Beyond 300 m inland, only plants were counted that were found by walking over the terrain towards the plateau scarp, and to the plateau height (c. 1025 m inland).

Along the transect, it was impossible to distinguish between subsp. *denticulatus* and short ligulate

plants identified as probable hybrids between subsp. *denticulatus* and var. *vulgaris*. Any attempt to quantify differences in ray floret length certainly would have resulted in confusing putative hybrids with small individuals of subsp. *denticulatus* bearing small ray florets. Accordingly, all radiate plants have been referred to as subsp. *denticulatus*. At various patches near the transect, however, in particular adjacent to rabbit faeces, plants grew larger. In those places, therefore, individuals could be classified according to their ray floret length as subsp. *denticulatus* (> 2 mm) and putative hybrids (< 2 mm).

Seven soil samples were taken along the transect (sites 1–7), and five samples were collected from surrounding localities (sites 8–12) by removing soil to a depth of c. 6 cm (Fig. 1a,b). Soil samples were allowed to air dry, and subjected to chemical analysis by the Landwirtschaftliche Untersuchungs- und Forschungsanstalt at Speyer (Germany). The pH, percent organic matter, free carbonate, total nitrogen and extractable forms of magnesium (Mg) were determined for all samples, while extractable forms of phosphorus (P_2O_5), potassium (K_2O) and boron (B) were only analysed for samples 1–5. At all sites along the transect records of associated vegetation were made.

OBSERVATION OF PUTATIVE POLLINATORS

Observation of insects was carried out in two natural stands at St Ouen's Bay: stand 1 was situated in a mobile Marram (*Ammophila arenaria*) dune just behind the sea wall south of Le Braye slipway (near site 1 in Fig. 1a), and the other, stand 2, next to the bunker at La Tête du Nièr Côte (at site 10). Stand 1 was monomorphic for *Senecio vulgaris* subsp. *denticulatus*, while stand 2 contained a few short ligulate plants which appeared to be hybrids. Stand 1 consisted of 156 plants which were evenly scattered throughout the observation area. Plants were (5–)9–12(–18) cm tall and mostly had one to three open capitula. Stand 2 included much larger (up to 20 cm), often basally branched individuals with up to 30(–40) open capitula. Approximately 70 individuals (20–30 individuals/m²) were distributed in several patches. On 18 May 1992, the flight sequences of all insect pollinators entering the observation area were recorded between 12.30 p.m. and 2.00 p.m. (stand 1) and 3.30 p.m. and 5.30 p.m. (stand 2).

COMPARATIVE CULTIVATION

Seed material (achenes) for comparative cultivation, including a germination experiment, was derived from each of eight individuals of subsp. *denticulatus* (in the following referred to as A1–A8), seven individuals of unidentified discoid plants (B1–B7), three individuals of short ligulate plants identified as probable hybrids between the two taxa (C1–C3) and eight individuals of var. *vulgaris* (D1–D8) collected in various locations around the coastal plain at St Ouen's Bay, the neighbouring Ouaisné Common, as well as interior waste ground or agricultural sites at the eastern landward edge of St Ouen's Bay. Between 14 and 19 May 1992 seed material was either directly harvested in the field, or, at the end of May, carefully removed from fruiting plants which had been pressed as herbarium specimens. In addition, achenes were collected from eight individuals of var. *vulgaris* (E1–E8) in the Botanic Garden, Mainz University, on 31 May 1992. Collecting codes of seed parents are used throughout the text to refer to their respective greenhouse progenies and are listed in Table 1. Collecting sites are also included, and their numbers refer to locations illustrated in Fig. 1a,b.

For a test of seed dormancy, samples of five achenes per seed parent were sown on five dates between 31 May and 8 September 1992 in 5 cm plastic pots filled with Frühlstorfer Erde, Typ P, and were kept moist during the entire experiment. Germination was recorded daily over a period of 160 days from first sowing.

At 27, 50 and 72 days following first sowing, a variable number of seedlings (as available) from each of the five accessions (A–E) were transplanted individually into 8 cm diameter plastic pots filled with sterilized compost. On any one day, only samples that had germinated during the previous 20 days were transferred. A total of 154 plants, representing between one and nine offspring from each of the seed parents listed in Table 1 except A2, A5, A6, A8 and C3, were grown to first fruiting under a natural light regime in an unheated greenhouse at the Botanic Garden, Mainz University. As the experiment approached the winter period, plants were transferred to a heated greenhouse with supplemental lighting provided by incandescent lamps (16 hour day), and temperatures at 20 °C day / 15 °C night. Conditions were maintained this way until the end of the experiment on 21 January 1993.

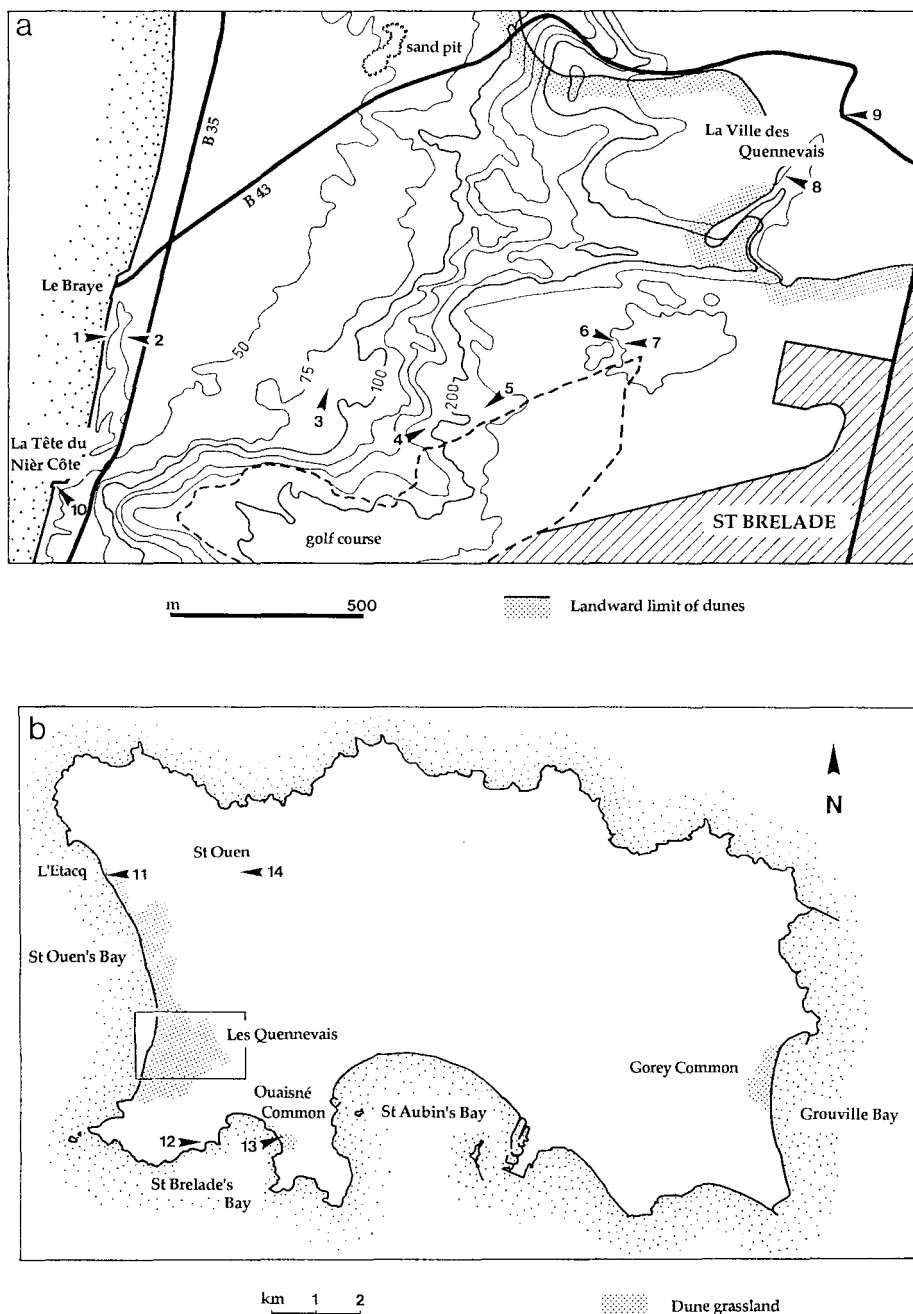


FIGURE 1. a. Topographic location of study sites on Les Quennevais (sites 1–7) and adjacent areas (sites 8–10). Based on the 1:25,000 States of Jersey Official Map, 1988; additional information on contours and sand pit outline compiled from the 1:25,000 Geological Survey Map, Jersey, 1982. Heights are in feet above M.S.L. based on a bench mark at St Helier Harbour, Jersey, of 29.9 feet (= 9.1 m). Built-up area hatched. b. Map of Jersey showing the location of four study sites (11–14) outside the research area (outlined). The distribution of extant dune grassland (Le Sueur 1984) is indicated.

TABLE 1. COLLECTING SITES AND COLLECTING CODES OF SEED PARENTS OF *SENECIO VULGARIS* FROM WHICH EXPERIMENTAL PROGENIES WERE GROWN

Collecting site	Subsp. <i>denticulatus</i>	Unidentified discoid plants	Putative hybrids	Var. <i>vulgaris</i>
COASTAL PLAIN AT ST OUEN'S BAY, JERSEY				
Dune behind seawall, near waste ground, L'Etacq (11)		B1*, B2*		
Les Quennevais, coastal dune and dune plain south of slipway at Le Braye, 10– 100 m inland from the shore (1/2)	A1*, A2, A3*, A4*, A5	B3*, B4*	C1*	
Les Quennevais, plateau dunes, c. 1320 m inland from the shore (6)	A6	B5*, B6*	C2*	
On sandy soil near bunker, La Tête du Nièr Côte (10)	A7*		C3	D1*
OUAISNÉ COMMON, JERSEY				
Coastal dune belt, Ouaisné Common (13)	A8	B7*		
INTERIOR SITES AT THE LANDWARD EDGE OF ST OUEN'S BAY, JERSEY				
Wayside in the valley below Ville des Quennevais (8)				D2*
Arable field, St Brelade (9)				D3*
Waste ground, St Ouen (14)				D4*–D8*
BOTANIC GARDEN, MAINZ UNIVERSITY, GERMANY				
				E1*–E8*

* Seed parents used both in the germination and the comparative cultivation experiment; numbers in brackets refer to locations in Fig. 1.

STATISTICAL ANALYSES

During the experiment, plants were examined for the phenological, vegetative and reproductive characters listed in Table 2. Means and standard errors for each character were computed. Multiple comparisons of group means were made using Tukey's test (VMS Version of SAS Release 6.07), considered appropriate for unequal sample sizes (Sokal & Rohlf 1981; SAS Institute Inc. 1988), and were evaluated at the 1% significance level. In order to represent interrelationships among groups graphically, the data were also subjected to canonical variate analysis (C.V.A.) (Reyment *et al.* 1984; Reyment 1991). Character LRAY (length of ray floret) was excluded from the C.V.A. because the character was known a priori to distinguish some of the accessions. The C.V.A. was carried out using the SAS procedure CANDISC (VMS Version of SAS Release 6.07). This procedure also computes both Hotelling's multivariate T^2 -test, which tests the hypothesis that the canonical means of the groups are equal, and Mahalanobis' distances (D^2) between canonical means of groups.

RESULTS

DISTRIBUTION AND HABITAT

Senecio vulgaris subsp. *denticulatus* was only found in Jersey on two dune systems, namely Ouaisné Common and the coastal stretch along St Ouen's Bay with the largest and deepest dune system in the south, known as Les Quennevais (Fig. 1a,b). Jersey's third area of dune grassland, Gorey Common, at the eastern end of the island, was not visited. All populations seen in inland areas were var. *vulgaris*. By contrast, plants of subsp. *denticulatus*, putative hybrids, unidentified discoid plants

TABLE 2. CHARACTERS SCORED IN THE COMPARATIVE CULTIVATION EXPERIMENT OF *SENECIO VULGARIS*

Character	Abbreviations
Determined by the daily inspection of all plants:	
1. Days from germination to formation of first buds	BUD
2. Days from first buds to first anthesis	BA
3. Days from germination to first anthesis	ANTH
4. Days from anthesis to first fruiting	AF
5. Days from germination to first fruiting	FRUIT
Measured at the time of first fruiting:	
6. Stem height (cm) from soil surface to base of apical capitulum	STH
7. Number of capitula and buds	NCAP
8. Length (mm) of ray floret ^a	LRAY
9. Number of achenes per apical capitulum	NACH
10. Number of unfertilized ovules per apical capitulum	NUNFO
11. Number of florets per apical capitulum	NFLORET (=NACH+NUNFO)
12. Reproductive potential	REPRO (=NCAP×NACH)

^aOnly subsp. *denticulatus* and putative hybrid progenies.

and var. *vulgaris* grew in mixtures of varying composition in various places in the man-disturbed area north of Les Quennevais. This area, however, was not explored extensively. Near to plants of subsp. *denticulatus* found on Ouaisné Common was an extensive population of var. *vulgaris* growing at a building site. However, no putative hybrids were found in the latter location.

Particular attention was paid to the Quennevais area, where subsp. *denticulatus* characteristically grows either on seaward facing slopes of mobile coastal dunes dominated by Marram, and additionally characterized by *Phleum arenarium*, or grows abundantly as a component of an open turf vegetation, called fixed calcareous dune vegetation by Böcher (1954), which follows a little farther away from the coastal dune area. Common associates here are bryophytes and small herbaceous plants like *Myosotis ramosissima* and *Saxifraga tridactylites*, and plants of essentially Mediterranean affinity like *Lagurus ovatus*, *Mibora minima* and *Viola kitaibeliana*.

RELATIONSHIP OF PLANT FREQUENCIES TO SOIL PARAMETERS AND ASSOCIATED VEGETATION

The frequency distribution of plants of *Senecio vulgaris* subsp. *denticulatus*, including six unidentified discoid plants, in relation to the (approximate) topographic location of study sites 1–7 is illustrated in Fig. 2. It is evident that the frequency of plants of subsp. *denticulatus* declines dramatically beyond 200 m distance from the coast, with plants becoming extremely rare over most part of the dune plain and along the plateau scarp, an area c. 800 m wide. Surprisingly, plants of subsp. *denticulatus*, short ligulate hybrids and unidentified discoid plants were abundant again on the plateau dunes (beyond c. 1025 m inland from the shore), extending as far as the inland limit of the dune system. This observation, however, was not documented in detail. Abundance of *S. vulgaris* on the plateau dunes, nonetheless, might be exemplified by 97 individuals recorded in one subjectively chosen 1 m² quadrat at c. 1345 m distance from the shore (site 7, Fig. 1a), comprising 53 plants of subsp. *denticulatus*, 32 short ligulate hybrids and twelve unidentified discoid plants. This exceeded the density of plants found in the coastal dune area, where in a 3 m × 2 m sampling unit outside the transect area, c. 50 m inland from the shore, 105 radiate, eight intermediate and two discoid plants were counted among a total of 115 plants.

Soils of all sites from Les Quennevais have high pH and also high carbonate values (Table 3). In general, they are low in organic matter, total nitrogen, and, as far as analysed, all minerals including boron, magnesium, phosphorus and potassium. Also, it is evident that soil pH is largely similar in all soil samples analysed. One of the plateau dune sites (7), where vegetation cover of subsp. *denticulatus* was exceptionally high (see above), is more similar to the densely covered coastal open turf site (2) than to any other site analysed, including the second plateau site (6) nearest to it. This

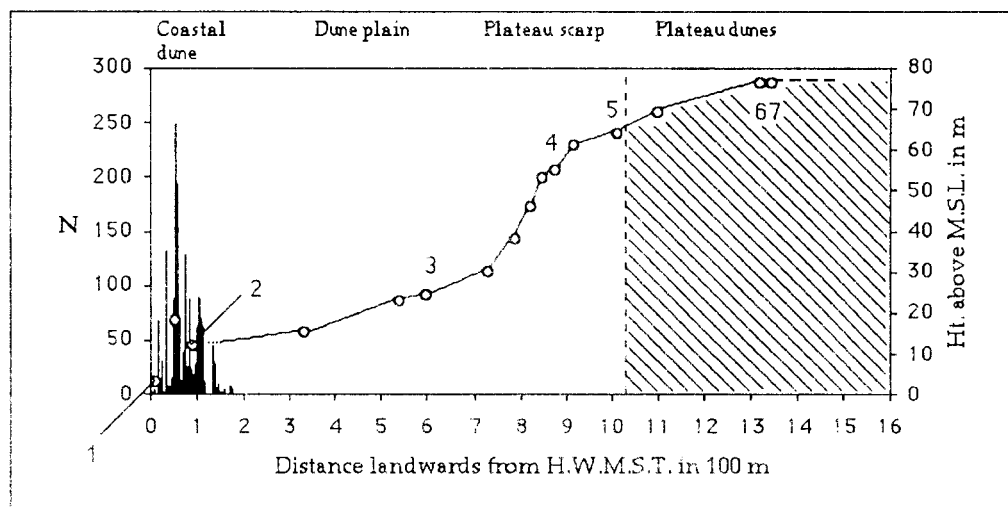


FIGURE 2. Frequency distribution of subsp. *denticulatus* (including six unidentified discoid plants) in relation to the approximate topographic location of study sites 1–7 on Les Quennevais. Note that the area c. 1025 m and more farther inland from the shore (hatched) harbours large populations of subsp. *denticulatus*, short ligulate hybrid, and unidentified discoid plants (not mapped in detail). Numbers correspond to sampling sites shown in Fig. 1a. N = number of individuals.

relates to higher amounts of organic matter and total nitrogen, as well as to lower levels of carbonate content, indicating a great amount of small scale variation of these edaphic factors across the transect zone. The results from the soil analyses reveal no distinct signs of leaching on the plateau dunes farthest east, thus confirming previous results obtained by Ranwell (1975).

Table 4 lists the species recorded in the area around the seven soil sampling sites on Les Quennevais. Among those plant species which were found to show a disjunct pattern of distribution along the transect similar to that observed in subsp. *denticulatus*, i.e. being present in the coastal area (sites 1 and 2) and on the plateau dunes (6 and 7), but virtually absent from most parts of the dune plain and the plateau escarpment (3–5), were *Honkenya pepioides*, *Phicum arenarium*, *Saxifraga tridactylites* and *Viola kitaibetana*. In contrast, other taxa, for example *Euphorbia portlandica*, *Mibora minima* and *Myosotis ramosissima*, were present along the entire transect. Chemical analysis, however, makes clear that the remarkable pattern of disjunct distribution exhibited both by *Senecio vulgaris* subsp. *denticulatus* and its four community associates is not reflected by the soil parameters (Table 3).

As regards the surrounding localities (Fig. 1a,b), the bunker site at La Tête du Nièr Côte (10), closest to Les Quennevais, harboured plants of subsp. *denticulatus* and putative hybrids, but also a single individual of var. *vulgaris* in a sheltered and shaded place nearby. This site is edaphically most similar to Les Quennevais, except for the lack of carbonate (Table 3), and, apart from *Armeria maritima*, has a rather similar set of species associates (not recorded in detail). In contrast, the seawall site near waste ground at L'Étaq (11), where scattered unidentified discoid plants of *Senecio vulgaris* were found, is the most unusual of all sites at St Ouen's Bay because it has relatively high amounts of organic matter, nitrogen and carbonate, and extremely high amounts of magnesium. Both localities are of high pH, similar to values found on Les Quennevais. The two interior sites (8 and 9), typical for var. *vulgaris*, are characterized by lower pH values than all sites at St Ouen's Bay, and have relatively high amounts of organic matter and nitrogen, but these values are lower than those found at L'Étaq. Carbonate is absent from both of these interior sites. In the maritime site at Beau Port (12) *S. sylvaticus* occurred profusely, but no plants of *S. vulgaris* were found. This certainly reflects an edaphic composition which is virtually intolerable for the latter species with respect to high levels of soil acidity, soil compactness, and, probably, nitrogen content (Table 3).

TABLE 3. RESULTS OF SOIL ANALYSES AND LOCATION OF SOIL SAMPLES COLLECTED BETWEEN 16 AND 18 MAY 1992 ON LES QU'ENNEVAIS (1-7) AND SURROUNDING LOCALITIES (8-12) ON JERSEY (CHANNEL ISLANDS)

Topographic location/ soil components	1 Coastal dune, south of Le Braye, mobile seaward facing slope	2 Coastal dune, south of Le Braye, open turf	3 Dune plain, stable landward site	4 Plateau scarp, semi stable slope dunes	5 Plateau scarp, footpath in low/medium shrub	6 Plateau stable dunes
Distance from H.W.M.S.T. (m)	10	50	595	875	1010	1320
Elevation (m above M.S.L.)	3	12	24	55	64	76
Presence of <i>S. vulgaris</i>	d	d,h	—	—	(d rare)	d,h,u
pH H ₂ O/CaCl ₂	7·7/6·9	7·5/6·9	7·3/7·0	7·4/7·0	7·4/7·0	7·7/7·1
% OR	0·28	1·43	0·64	0·58	0·28	0·34
CaCO ₃ (%)	3·3	2·7	3·1	3·3	3·3	4·2
N (%)	0·00	0·04	0·00	0·01	0·00	0·00
B	0·16	0·28	0·28	0·34	0·38	—
Mg	4/A	4/A	4/A	2/A	2/A	3/A
P ₂ O ₅	3/A	3/A	2/A	2/A	4/A	—
K ₂ O	4/A	7/A	5/A	4/A	5/A	—

TABLE 3. *Continued.*

Topographic location/ soil components	7 Plateau stable dunes	8 Wayside in the valley below Ville des Quennevais, woodland	9 Arable field, St Brelade	10 On sandy soil nr. bunker, La Tête du Nièr Côte	11 Dune behind sea wall, adjacent to waste ground, L'Étaq	12 Maritime rocks, Le Beau Port
Distance from H.W.M.S.T. (m)	1345	1625	1740	0	0	50
Elevation (m above M.S.L.)	76	68	73	12	6	30
Presence of <i>S. vulgaris</i>	d,h,u	v	v	d,h, (v rare)	u	—
pH H ₂ O/CaCl ₂	7.3/6.8	6.9/5.9	6.6/6.0	7.5/6.6	7.5/7.0	5.8/3.6
% OR	1.34	3.22	3.82	1.07	9.46	31.72
CaCO ₃ (%)	2.2	0.0	0.0	0.0	15.9	0.0
N (%)	0.05	0.13	0.23	0.00	0.23	1.06
B	—	—	—	—	—	—
Mg	4/A	15/C	9/B	6/B	36/D	28/D
P ₂ O ₅	—	—	—	—	—	—
K ₂ O	—	—	—	—	—	—

Notes: Letters indicate the presence of *Senecio vulgaris* as follows: d – subsp. *denticulatus*; v – var. *vulgaris*; h – putative hybrids; and u – unidentified discoid plants. Numbers of collecting sites correspond to numbers shown in Fig. 1. Soil parameters abbreviations as follows: percentage organic matter (% OR); percentage calcium carbonate (CaCO₃); total soil nitrogen (N); boron (B) in mg/kg dry weight soil; magnesium (Mg), phosphorus (as P₂O₅) and potassium (as K₂O) in mg/100 g dry weight soil. Content abbreviations: A = low, B = medium, C = very high, D = extremely high.

TABLE 4. VEGETATION ASSOCIATED WITH *SENECIO VULGARIS* AT SITES 1-7 IN JERSEY (CHANNEL ISLANDS)

Records from the adjacent sites 6 and 7 are pooled for comparison.

Taxa	Sites					
	1	2	3	4	5	6 and 7
<i>Ammophila arenaria</i>	+	+		+	+	+
<i>Bellis perennis</i>		+				
<i>Calystegia soldanella</i>	+					
<i>Cerastium</i> sp.						+
<i>Cerastium diffusum</i>		+		+		
<i>Cerastium semidecandrum</i>	+					
<i>Cladonia rangiformis</i>			+	+		
<i>Claytonia perfoliata</i>					+	
<i>Crataegus monogyna</i>					+	
<i>Dactylis glomerata</i>					+	
<i>Eryngium maritimum</i>	+					
<i>Euphorbia portlandica</i>		+	+	+		+
<i>Fumaria muralis</i>					+	
<i>Galium verum</i>						+
<i>Geranium</i> sp.					+	
<i>Geranium molle</i>		+				
<i>Honkenya peploides</i> [†]	-					+
<i>Juncus</i> sp.		+				
<i>Lagurus ovatus</i> [†]	+	+				
<i>Mibora minima</i> [†]		+	+	+		+
<i>Myosotis ramosissima</i>	+	+	+			+
<i>Oenothera stricta</i>				+		
<i>Phleum arenarium</i> [†]	+					+
<i>Plantago maritima</i>		+				
<i>Pinus pinaster</i>				+		
<i>Quercus ilex</i> [†]				+	+	
<i>Quercus robur</i>						+
<i>Ranunculus bulbosus</i>		+		+		
<i>Rosa pimpinellifolia</i>		+	+	+		+
<i>Rubus fruticosus</i> agg.	+					
<i>Saxifraga tridactylites</i> [†]	+	+				+
<i>Senecio vulgaris</i> subsp. <i>denticulatus</i> [†]	+	+			(+)	+
<i>Silene nutans</i>			+	+		+
<i>Trifolium occidentale</i>		+				
<i>Ulex europaeus</i>			+			-
<i>Vicia sativa</i>		+	+		+	+
<i>Viola knaibelliana</i> [†]		+				+

Notes: Taxa are indicated as + = present or (+) = rare. Taxa of Mediterranean affinity are marked [†] and those showing a pattern of disjunct distribution along the transect are indicated by ‡.

OBSERVATION OF PUTATIVE POLLINATORS

Within each of the two natural stands at St Ouen's Bay, flies were the most frequent visitors of subsp. *denticulatus* during the observation periods. Members of the family Sarcophagidae (*Sarcophaga dissimilis* Meigen) were caught and identified within stand 1. These flies showed a remarkable preference for the ray florets: systematically manipulating these florets one after the other possibly for nectar extraction, they often moved in a circle on the capitulum, largely neglecting the inner disc florets. Flies of the family Anthomyiidae were taken from stand 2. Though specimens attracted by the decaying *Fucus* tidal litter on the nearby shore were also members of the same family (Anthomyiidae), they were clearly a different species (P. Kirby, pers. comm., 1993).

Table 5 gives the number and the flight movements of insects in terms of number of plants visited during a flight sequence recorded within each of the two stands. The total number of insects

TABLE 5. OBSERVED NUMBER OF PUTATIVE POLLINATORS VISITING ONE TO FIVE DIFFERENT PLANTS OF *SENECIO VULGARIS* SUBSP. *DENTICULATUS* IN TWO NATURAL STANDS AT ST OUEEN'S BAY, JERSEY

Stand	No. of plants visited during flight sequence				
	1	2	3	4	5
1	4	10	0	2	1
2	3 ^a	2 ^b	0	0	0

^a Including one unidentified syrphid fly.

^b Flights between long rayed plants.

Stand 2 harboured several short ligulate hybrids.

(including one syrphid fly) visiting stand 1 and stand 2 was 17 and 5, respectively. Mean number of plants visited per putative pollinator was 2.2 (stand 1) and 1.4 (stand 2).

Discrimination by flies in favour of the long rayed plants of *Senecio vulgaris* subsp. *denticulatus* in comparison to short ligulate hybrids was observed in stand 2, where both transitory flights occurred between long rayed individuals. The observation that long rayed plants were more attractive to insects than intermediate and discoid plants, was also made in a 12 m² mixed stand on the plateau dunes that was observed on 14 May 1992 for a windy one-hour period (2.30 p.m.–3.30 p.m.). This stand also comprised unequal numbers of radiate, intermediate and discoid plants of nearly equal height ((7–)17–21 cm) in an approximate ratio of 5:3:1. During this time, one unknown insect visited preferentially three long rayed plants during a flight sequence.

Outside observation periods, *Psilothrix viridicoeruleus* Fourcroy, a small beetle of the Melyridae family, was frequently seen visiting the capitula of *Senecio vulgaris* subsp. *denticulatus* in the dunes, not only foraging on pollen but probably also feeding on the ray florets, which often showed marked signs of damage.

A fly seen visiting var. *vulgaris* in the valley below Ville des Quennevais was *Siphona geniculata* De Geer (Tachinidae) which is a well-known and often abundant flower-visiting fly, with a strong preference for yellow composites (P. Kirby, pers. comm., 1993). Evidently it does not belong to the most frequently observed species of flies visiting *Senecio vulgaris* subsp. *denticulatus* at St Ouen's Bay.

SEED PRODUCTION AND PREDATION DAMAGE

The percentage seed set of subsp. *denticulatus* was recorded in a sample of 17 individuals chosen randomly from the area south of the slipway at Le Braye. Care was taken to collect capitula that had not shed their achenes. The proportion of well-developed achenes found within one capitulum of each plant examined averaged 88.6% and ranged between 48.8 and 98.2%. In the field, there was no indication of any impediment for setting seed under natural conditions, including plants identified as putative hybrids.

As indicated by decapitated, fruiting capitula which were often found lying near the base of the parent plant, achenes of subsp. *denticulatus* seem to be predated even before the time of seed dispersal. Birds are likely to be the predators, as small flocks of goldfinches have been reported to feed on subsp. *denticulatus* (Le Sueur 1976). In addition, subsp. *denticulatus* obviously suffers from grazing by herbivores (probably rabbits) which clip the main axis of the plants and thus affect their branching pattern by inducing the growth of lateral shoots from near the base.

GERMINATION BEHAVIOUR AND COMPARATIVE CULTIVATION

In the course of comparative cultivation, including the germination experiment, it became strikingly evident that in regard to the offspring of discoid plants only progeny of the unidentified discoid parent individuals from the Quennevais area (B3–B6) showed characteristics typical of subsp. *denticulatus*, while offspring of discoid plants from outside this area (B1, B2 from L'Etacq and B7 from Ouaisné Common) proved to be typical var. *vulgaris*. Taking account of the distinctiveness of progenies B1, B2 and B7 on the one hand, and B3–B6 on the other, as will be demonstrated below,

results are presented separately. For all groups analysed, data were pooled over families for comparison.

The results of the seed dormancy experiment are illustrated in Fig. 3. Rather unexpectedly, no pronounced dormancy pattern was recorded for achenes of subsp. *denticulatus* from Les Quennevais, La Tête du Nièr Côte and Ouaisné Common. The minimum time required for germination was only 23 days after first sowing in this taxon. This was followed, however, by a period of continuous germination, which extended over 79 days. Thus, although a few achenes (all produced by parent individuals A1 and A3) germinated within four weeks from first sowing, a greater proportion of subsp. *denticulatus* achenes exhibited a pattern markedly skewed towards later germination, thus showing various degrees of dormancy. While cumulative percentages of total germination largely remained constant over all five successive dates of sowing, time to initial germination and time to final germination decreased from 23 (27) to 10 days and from 102 to 30 days after sowing, respectively. Hence, partial seed dormancy, though obviously present in subsp. *denticulatus*, had been completely lost by the last date of sowing (8 September 1992), i.e. after 14 week's storage at room temperature. There was no seed dormancy in var. *vulgaris* from the coastal site at La Tête du Nièr Côte and interior inland sites of Jersey, as well as from Mainz Botanic Garden. Independent of the date of sowing, the majority of seedlings emerged within 10 days (Fig. 3e,f). Of the achenes of unidentified discoid parent individuals, accessions from L'Étacq (B1 and B2) and the dune grassland on Ouaisné Common (B7) showed a pattern similar to var. *vulgaris*, although synchronization was less apparent during the first two dates of sowing (Fig. 3b). In contrast, achenes produced by unidentified discoid plants from Les Quennevais (B3–B6) and putative hybrids from the same location and La Tête du Nièr Côte (C1–C3) largely followed the germination pattern of subsp. *denticulatus* (Fig. 3c,d). Both differed from subsp. *denticulatus*, however, in that the discoid plants from the Quennevais showed a more rapid initial germination within the first four weeks following first sowing (mainly caused by achenes produced by parent individuals B3 and B4), while, in the case of the putative hybrids, storage at room temperature for 14 weeks was less effective in inducing more rapid and synchronizing germination.

Turning to the results of the cultivation experiment (Table 6), it was evident that subsp. *denticulatus* differed significantly (at the 1% level) from both accessions of var. *vulgaris* in taking a substantially longer time for each developmental stage analysed, and producing more florets per capitulum containing more unfertilized ovules. Number of achenes per capitulum and potential reproductive output, however, were not significantly different for the three groups. With regard to the two vegetative characters stem height and number of capitula (including buds), it was evident that only plants of var. *vulgaris* from Jersey performed similarly to subsp. *denticulatus*.

The two accessions of var. *vulgaris* also differed from each other in several phenological and vegetative characters. Plants from Jersey took approximately eleven days longer to complete their life cycle due to differences in the time from germination to first buds, were taller in stature, and – as was indicated by complete leaf collections of representative plants – produced more leaves along the main stem than var. *vulgaris* from Germany. The major morphological difference between both populations was leaf shape. Fig. 4c,d illustrates that the middle and upper cauline leaves of var. *vulgaris* from Jersey were more deeply divided, with conspicuously dentate lobes.

As regards the unidentified discoid accessions, progeny from L'Étacq and Ouaisné Common (B1, B2 and B7) were virtually indistinguishable from var. *vulgaris* from La Tête du Nièr Côte and interior sites in most characters, including leaf shape. The only exceptions were number of florets and number of achenes per capitulum, which were significantly higher in the former, although no differences were recorded for potential reproductive output. Conversely, progenies of both unidentified discoid parent plants (B3–B6) and putative hybrid individuals (C1 and C2) from Les Quennevais were generally closer in mean to each other and to subsp. *denticulatus*. In addition, all three groups had similar leaf shape characteristics, as shown in Fig. 4a,b, and were strikingly arachnoid. However, most developmental stages of the unidentified discoid plants from Les Quennevais were significantly shorter than those of subsp. *denticulatus*, though the differences were small.

Canonical variate analysis (C.V.A.) was conducted for the purpose of illustrating the interrelationships among accessions, and in particular to investigate the distinctiveness of both groups of unidentified discoid plants. Since the two groups were obtained a priori by visual impression during cultivation, there remains the possibility that differences between both groups

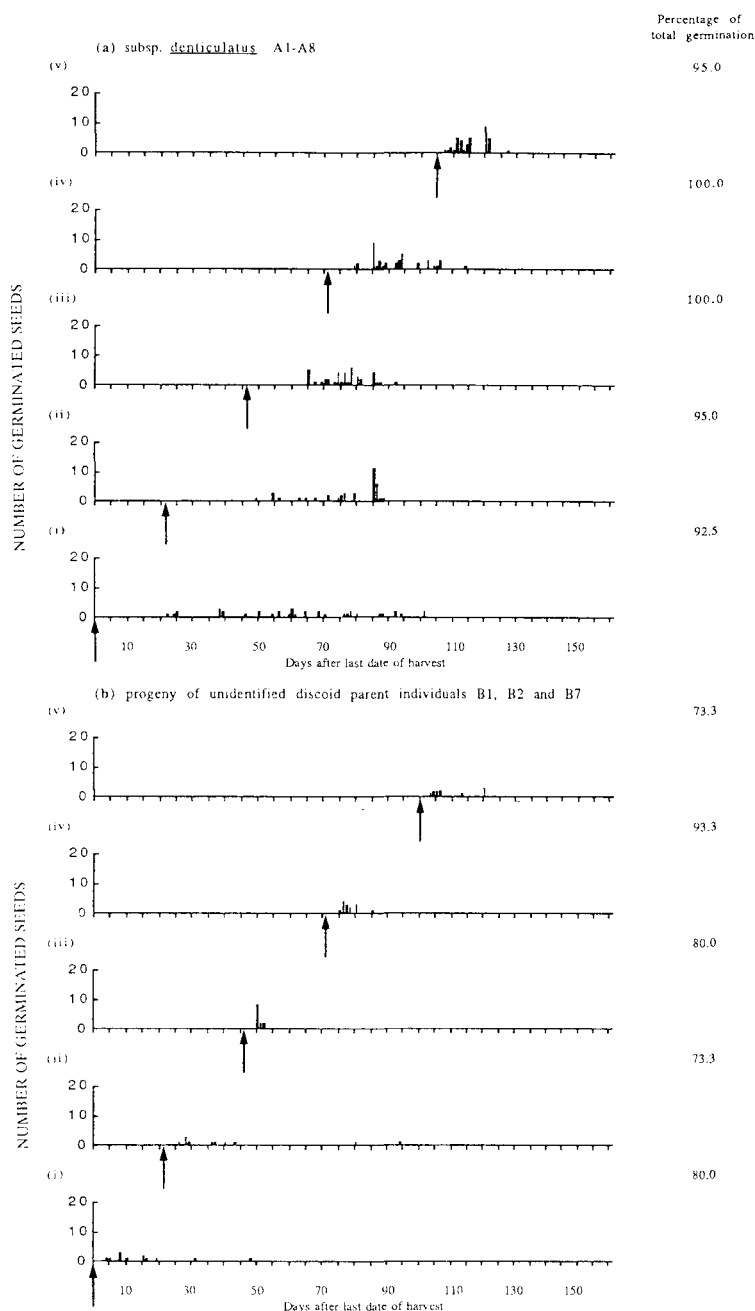


FIGURE 3. The germination behaviour of achenes of: (a) subsp. *denticulatus* (A1-A8); (b) unidentified discoid plants (B1, B2 and B7); (c) unidentified discoid plants (B3-B6); (d) putative hybrids (C1-C3); (e) var. *vulgaris*, Jersey (D1-D8); and (f) var. *vulgaris*, Germany (E1-E8). Achenes collected between 14 and 31 May 1992 were sown on five dates following the last date of harvest: i. 31 May, ii. 22 June, iii. 17 July, iv. 10 August, v. 8 September 1992. Arrows indicate the date of sowing. Also presented are percentages of total germination.

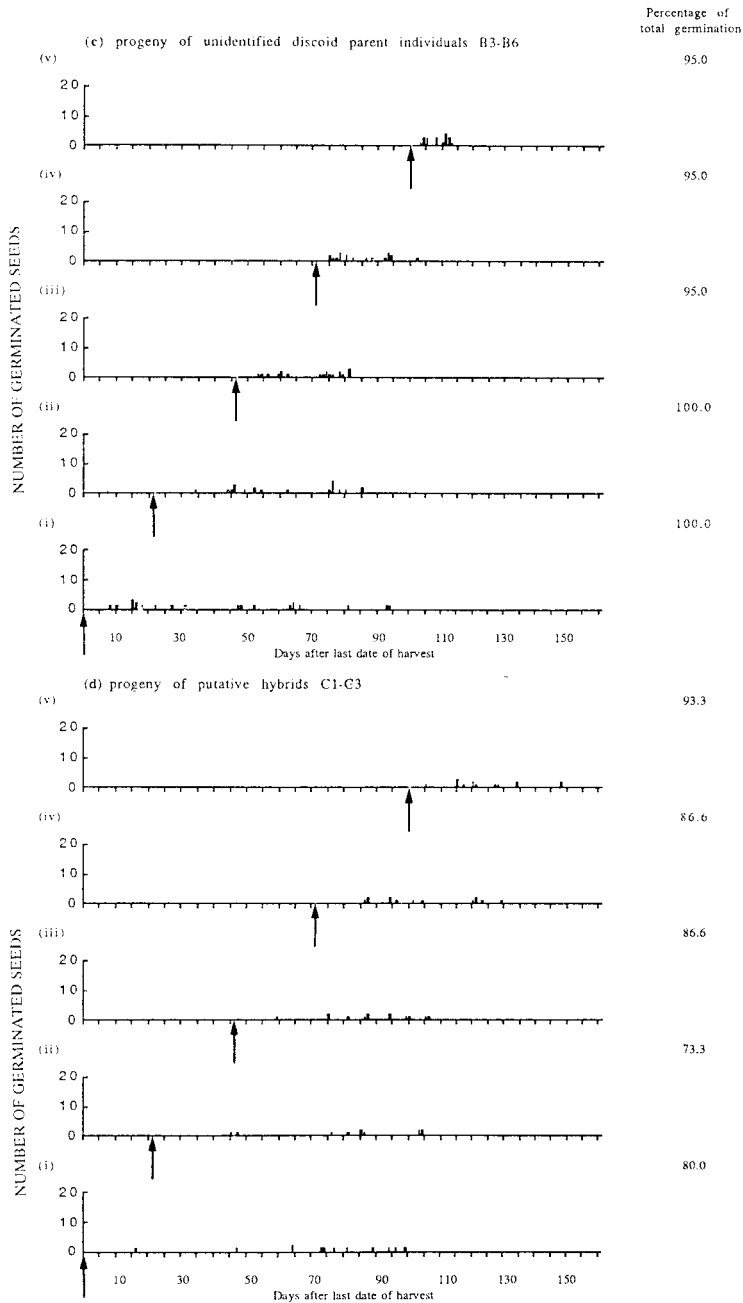


FIGURE 3. Continued.

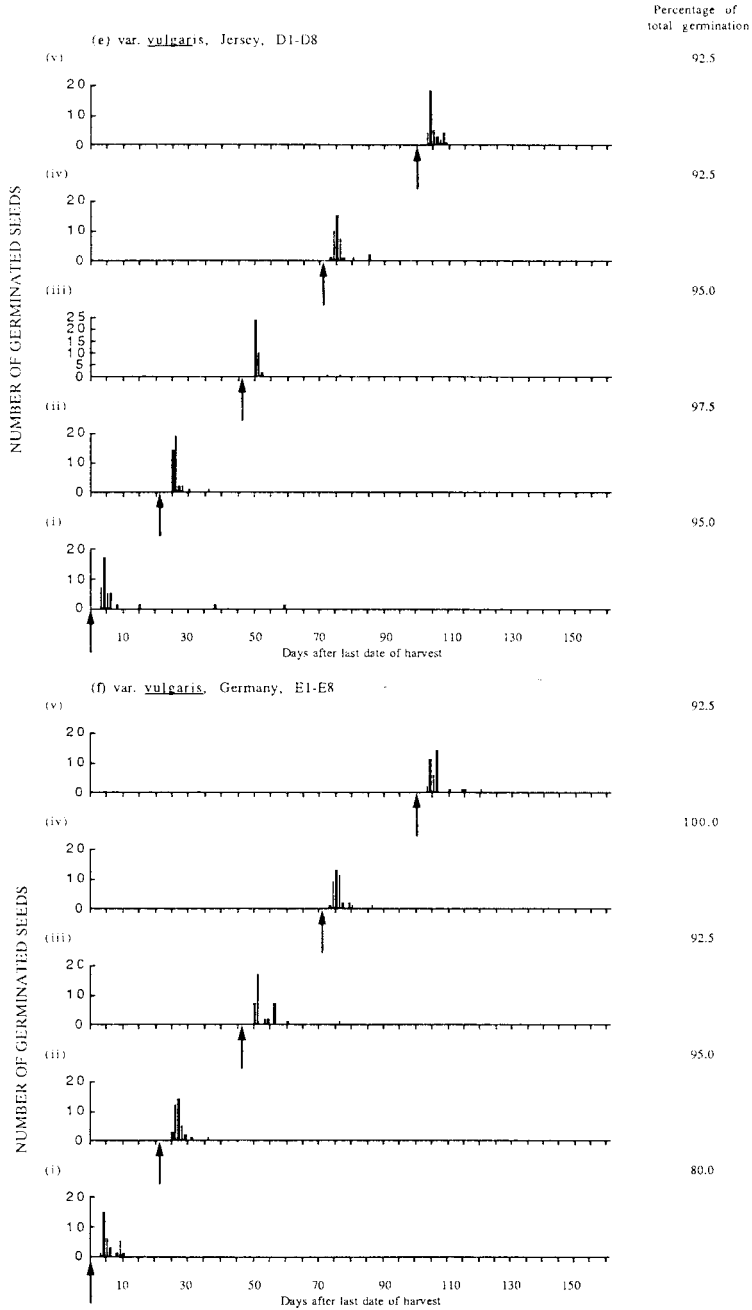


FIGURE 3. *Continued.*

TABLE 6. MEANS AND STANDARD ERRORS (S.E.) FOR CHARACTERS OF *SENECIO VULGARIS* RECORDED FROM PROGENY PLANTS CULTIVATED

The results of multiple comparisons of group means using Tukey's test (VMS Version of SAS Release 6.07) are given except for the hybrid progeny due to small sample size. Sample means for any character with the same superscript are not significantly different at the 1% level. Abbreviations of characters as in Table 2. N = sample size.

Character	1. Subsp. <i>denticulatus</i> (A1, A3, A4, A7)			2. Unidentified discoid plants (B1, B2, B7)			3. Unidentified discoid plants (B3-B6)			4. Putative hybrids (C1-C3)			5. Var. <i>vulgaris</i> Jersey (D1-D8)			6. Var. <i>vulgaris</i> Germany (E1-E8)		
	N	Mean	S.E.	N	Mean	S.E.	N	Mean	S.E.	N	Mean	S.E.	N	Mean	S.E.	N	Mean	S.E.
BUD	14	102.0 ^a	4.3	22	43.6 ^c	1.0	17	90.6 ^b	2.1	3	58.0	2.1	51	41.6 ^c	0.9	47	32.0 ^d	0.9
BA	14	48.1 ^a	3.4	21	13.0 ^c	0.8	16	37.6 ^b	3.3	3	40.3	14.7	51	12.8 ^c	0.4	44	12.1 ^c	0.4
ANTH	12	149.3 ^a	6.8	20	55.6 ^c	1.5	16	127.4 ^b	4.5	3	125.3	13.6	51	54.4 ^c	1.1	44	44.0 ^d	0.9
AF	12	20.2 ^a	1.3	20	9.6 ^b	0.3	14	23.6 ^a	2.6	2	21.0	6.0	50	10.9 ^b	0.6	44	10.4 ^b	0.5
FRUIT	12	169.4 ^a	6.6	21	65.1 ^{cd}	1.5	14	148.9 ^b	7.0	2	150.5	28.5	50	65.8 ^c	1.2	47	54.4 ^d	1.0
STH	13	32.2 ^a	1.1	22	29.1 ^a	1.0	15	29.0 ^a	1.0	2	37.4	5.4	50	27.9 ^a	0.7	47	15.8 ^b	0.5
NCAP	13	39.5 ^a	5.9	21	30.9 ^{ab}	3.7	15	46.7 ^a	9.1	2	44.0	34.0	50	29.6 ^{ab}	2.7	47	17.1 ^b	1.4
LRAY	14	2.77	0.17							3	1.97	0.17						
NACH	11	36.4 ^{ab}	7.1	22	53.8 ^a	2.5	15	27.9 ^b	7.3	3	29.7	13.4	49	36.7 ^b	2.1	46	38.5 ^b	1.7
NUNFO	11	41.6 ^a	7.3	22	8.7 ^b	2.0	15	46.5 ^a	7.2	3	41.3	16.3	49	12.6 ^b	1.5	46	6.7 ^b	1.3
NFLORET	11	78.0 ^d	4.1	22	62.5 ^b	1.6	15	74.3 ^a	1.8	3	71.0	3.8	49	49.2 ^c	1.1	46	45.2 ^c	1.1
REPRO	11	1119 ^{ab}	350	21	1763 ^a	264	15	647 ^b	155	2	450	60	49	1200 ^{ab}	172	46	675 ^b	60

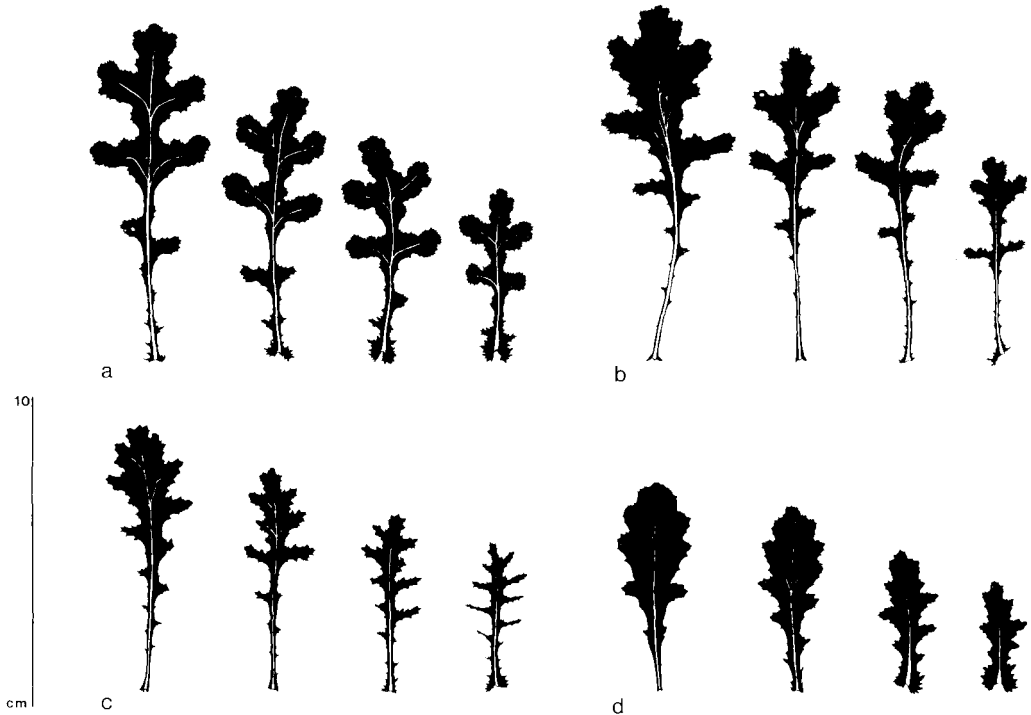


FIGURE 4. Silhouettes of representative middle and upper cauline leaves of cultivated progeny of: a. subsp. *denticulatus*, Les Quennevais (A4); b. putative hybrid, Les Quennevais (C1); c. var. *vulgaris*, Jersey (D1); and d. var. *vulgaris*, Germany (E2). Note that leaves of cultivated progeny of unidentified discoid plants B1, B2 and B7, and B3–B6 were similar to (c) and (a), respectively.

that may have been slight at the outset were 'strengthened' by the C.V.A., because this analysis seeks to maximize the separation between groups (Reyment 1991). It should be emphasized that the results of the C.V.A. were not used to investigate which characters contributed most to the separation between groups.

Fig. 5 shows a plot of the canonical variate scores for 137 out of 154 individuals projected on to the plane of the first two canonical axes. 17 individuals raised had missing values for some of the characters scored, and thus were not included in the analysis, which requires equal sample sizes for all characters (S.A.S. Institute Inc. 1988). The first two canonical variables were statistically significant (at $p < 0.0001$), and accounted for 86% and 9% of the total variation, respectively.

The plot of the canonical variates illustrates that all plants derived from unidentified discoid parent individuals fall into two broad clusters. Progeny raised from individuals collected at L'Etacq (B1 and B2) and Ouaisné Common (B7) are nearly completely intermixed with var. *vulgaris* from La Tête du Nièr Côte and inland sites, and to a lesser extent associated with var. *vulgaris* from Germany. In contrast, offspring of four unidentified discoid plants from Les Quennevais (B3–B6) form a distinct cluster both with subsp. *denticulatus* from Les Quennevais (A1, A3 and A4) and from La Tête du Nièr Côte (A7), as well as with progeny of putative hybrids from Les Quennevais (C1 and C2). Rather interestingly, the C.V.A. shows at least moderate separation between both populations of var. *vulgaris* from Jersey and Germany.

Except for progeny of putative hybrids and unidentified discoid plants from Les Quennevais, canonical means of all six groups were significantly different according to Hotelling's multivariate T^2 -test ($p < 0.0001$). However, the picture outlined in Fig. 5 is clearly reflected by the Mahalanobis' distances (Table 7).

DISCUSSION

DISTRIBUTION, HABITAT AND ECOLOGY OF SUBSP. *DENTICULATUS* AND VAR. *VULGARIS* ON JERSEY

On Jersey, subsp. *denticulatus* is only known from the dune systems of the coastal plains on Ouaisné Common and St Ouen's Bay, where it is particularly common on Les Quennevais. The Quennevais area in the south of St Ouen's Bay was deliberately chosen for more detailed studies because it has long been known to harbour extensive populations of subsp. *denticulatus* (Babington 1839; Trimen 1871; Lester-Garland 1903; Le Sueur 1984), and because it has suffered relatively little from soil disturbance due to human activities in the past (Mrs F. Le Sueur, pers. comm., 1992). Thus, it can safely be taken as representing the specific ecological requirements of subsp. *denticulatus* in its natural maritime habitat. This dune system, which is obviously susceptible to various destructive and catastrophic agencies, e.g. salt-laden winds and severe winter storms, sand mobility, water shortage and grazing by rabbits, has mild temperatures in winter, high levels of insolation and even rainfall throughout the year (Ranwell 1976). Here, subsp. *denticulatus* most characteristically grows on mobile sand dunes or fixed calcareous dune grassland, where it is commonly associated with other winter-annuals and species of Mediterranean affinity (Table 4). It seems likely that subsp. *denticulatus* has gone unnoticed in the past as a member of the association *Tortuleto-Phleum arenarii* of the calcareous dune communities, investigated in detail by Tüxen (1937) and Westhoff (1947). According to the latter author the main occurrence of this association is in S.W. Europe with its main period of growth in the winter. The obviously close phytosociological relationship of subsp. *denticulatus* to this association on Jersey is all the more interesting, as subsp. *denticulatus* has been postulated to have migrated from the Mediterranean northward along the coasts of W. Europe at the end of the latest glacial period (Kadereit 1984b). Similar to other community associates, it thus would seem to have colonized in the north of Europe one of the regions mildest in winter.

The results obtained from soil analyses (Table 3) do not provide any meaningful clue to the

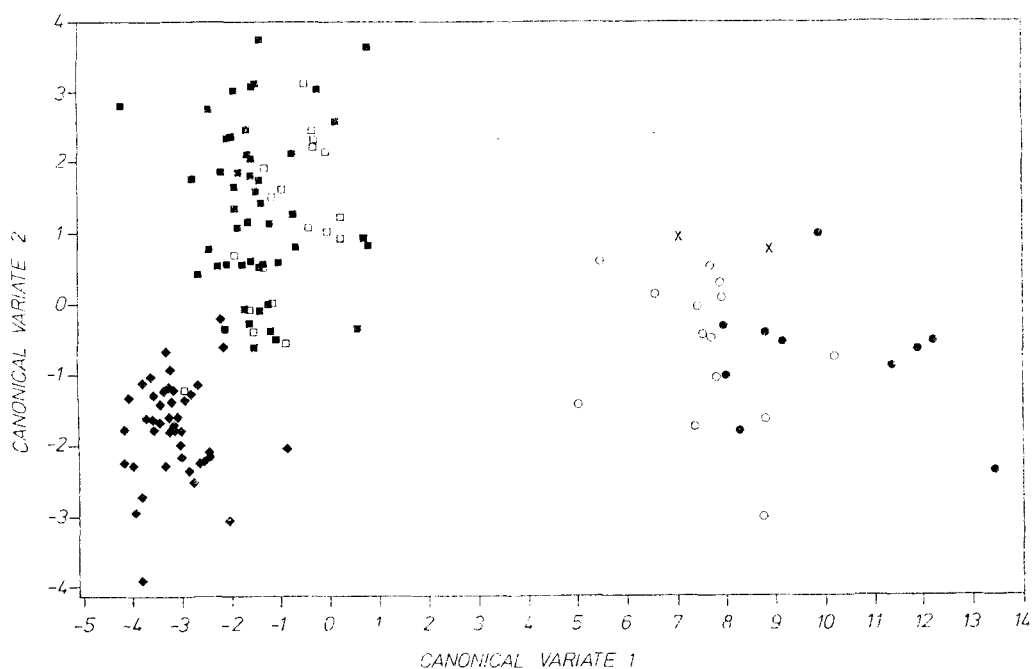


FIGURE 5. Canonical variate analysis for individual progeny plants of *Senecio vulgaris*. ● = subsp. *denticulatus* (A1, A3, A4, and A7), □ = unidentified discoid plants (B1, B2 and B7), ○ = unidentified discoid plants (B3–B6), × = putative hybrids (C1, C2), ■ = var. *vulgaris*, Jersey (D1–D8), ◆ = var. *vulgaris*, Germany (E1–E8). Analysis includes characters listed in Table 2 except L.RAY (length of ray floret).

TABLE 7. MAHALANOBIS' SQUARED DISTANCES AMONG GROUPS ANALYSED IN THE CANONICAL VARIATE ANALYSIS OF PLANTS OF *SENECIO VULGARIS*

	Groups					
	1	2	3	4	5	6
1	—					
2	133.46***	—				
3	22.29***	83.23***	—			
4	16.71*	84.24***	10.11 N.S.	—		
5	144.42***	4.15***	90.81***	92.55***	—	
6	185.13***	15.12***	123.65***	134.27***	13.00***	—

Notes: See Table 6 for explanation of group numbers. F value significance: * $p \leq 0.05$, *** $p < 0.001$, N.S. = not significant.

unusual and disjunct distribution of subsp. *denticulatus* and several community associates (*Honkenya peploides*, *Phleum arenarium*, *Saxifraga tridactylites* and *Viola kitaibeliana*) within the Quennevais area, as detected in the present study (Fig. 2; Table 4). Böcher (1954) has recorded a pH value of 5.8 farther inland, thereby noting the disappearance of *Phleum arenarium*, *Koeleria macrantha* and *Tortula ruraliformis* (Besch.) Ingham, and Ranwell (1975) encountered both a low pH of 4.8, and a minimum value of carbonate content at a dune plain site c. 550 m inland from the shore. The present results, however, show neither a drop in carbonate nor in pH value at the landward dune plain (3), and the plateau scarp site (4). Taking account of both the close proximity of Ranwell's 550 m site to site 3, and the fact that the vegetation around these sites is characterized by *Cladonia rangiformis* Hoffm. (Table 4), a well-known acidophilous species (Böcher 1954), it seems reasonable to assume a rather patchy variation in edaphic composition in the region. Quite clearly, more fine-grained estimates of edaphic factors, especially pH, as well as availability of water and mineral nutrients, will be necessary to settle the problem of disjunct species distribution on Les Quennevais. Nevertheless, soil analysis does indicate that *Senecio vulgaris* subsp. *denticulatus* occurs on soils which have large amounts of carbonate, undoubtedly resulting from crushed mollusc shells, and low amounts of mineral nutrients, out of which nitrogen and phosphorus are considered to be of major significance (Grime 1988).

On Jersey, var. *vulgaris* can be found in man-disturbed inland and coastal localities throughout the island, such as on waste ground or along roadsides. Since subsp. *denticulatus* is virtually absent from ruderal interior sites, this might provide a first clue to the possibility that both taxa are also ecologically distinct in utilizing ephemeral resources to different degrees. It seems likely that due to human disturbance (e.g. roads and sand pits at St Ouen's Bay; building work at Ouaisné Common) the ruderal var. *vulgaris* has been recurrently introduced into the coastal habitat of subsp. *denticulatus*. Sympatry of the two taxa at St Ouen's Bay and Ouaisné Common thus might indicate that their ranges of ecological tolerance are not mutually exclusive. At St Ouen's Bay, however, it appears that preference for fertile and highly disturbed soils is a factor limiting the distribution of var. *vulgaris* to areas outside Les Quennevais, as larger numbers of var. *vulgaris* plants were only found growing in disturbed localities with soils characterized by relatively high amounts of organic matter and nitrogen, e.g. at Ville des Quennevais, St Brelade and L'Etacq (sites 8, 9 and 11; Table 3). Furthermore, during another visit made to Jersey in August 1992, some tall growing plants of var. *vulgaris* were also found on shingle in front of the seawall near L'Etacq, associated with the drift-laden portion of the beach, an extremely unstable habitat which undoubtedly is very rich in nitrogen from decaying organic matter (e.g. Chapman 1978).

POLLINATION STRATEGY OF SUBSP. *DENTICULATUS* AND VAR. *VULGARIS*

Although both taxa are self-compatible, there is a difference in pollination strategy between subsp. *denticulatus* and var. *vulgaris*. Visits of insects (flies and syrphid flies) to var. *vulgaris* have been reported (Abbott & Irwin 1988; Comes & Kadereit 1990), but this taxon normally appears to be an obligatory selfer with outcrossing rates seldom exceeding 1% under field conditions (Marshall & Abbott 1982, 1984). From the field observations presented above it seems that subsp. *denticulatus* is much more attractive to insects (mostly flies in this case) than either the discoid variant or the short

ligulate hybrid. Thus, in direct analogy to the self-compatible and radiate var. *hibernicus* that shows outcrossing frequencies between 3 and 35% (Marshall & Abbott 1982, 1984), it is probable that subsp. *denticulatus* has a higher potential for outbreeding than var. *vulgaris* due to the possession of female ray florets which may outcross at a higher frequency than the hermaphrodite disc florets and convey a greater attractiveness of the radiate capitula to pollinators. The difference in pollination strategy between both taxa probably accounts for the fact that subsp. *denticulatus* consistently exhibits a greater amount of variation in the characters contained in Table 6 than var. *vulgaris*.

GREENHOUSE EXPERIMENTS

The present study has confirmed that, when grown under standard conditions in the greenhouse, subsp. *denticulatus* and var. *vulgaris* differ consistently in a number of morphological and life history characters, including leaf shape, degree of hairiness, germination behaviour and speed of development. Moreover, formal genetic (Trow 1912, 1916; Kadereit 1984a) and quantitative genetic studies (Comes 1994) involving subsp. *denticulatus* from Jersey have shown that the differences between both taxa are genetically based, and in general under multigenic control, except the presence/absence of both seed dormancy and ray florets (and probably also speed of development). However, at all loci assayed by standard protein electrophoretic techniques, Jersey subsp. *denticulatus* has an identical phenotype to British and German var. *vulgaris* (Ashton & Abbott 1992; Comes, unpublished results), whereas subsp. *denticulatus* from Ainsdale has unique alleles at the β EST-2 and β EST-3 loci (Ashton 1990; Ashton & Abbott 1992).

As regards the germination behaviour of the cultivated material investigated here, the amount of difference between both taxa does not conform entirely to experimental results obtained previously. Kadereit (1984a) found that subsp. *denticulatus* from Les Quennevais required a minimum time of 111 days after harvest for germination. Contrastingly, no pronounced seed dormancy of subsp. *denticulatus* derived from the same locality and two other sites (La Tête du Nièr Côte and Ouaisné Common) was found in this study (Fig. 3). Apart from different experimental conditions after sowing, these different findings may, in part, be attributable to different conditions experienced by achenes during formation and ripening on the mother plant, as Kadereit (1984a) used greenhouse-produced seeds in his experiment. These arguments do not rule out the possibility that phenotypic variability of germination behaviour in subsp. *denticulatus* could also be due to multiple allelism at the seed dormancy locus. However, the findings of the present study still indicate that subsp. *denticulatus* shows a markedly slower and less synchronized rate of germination than var. *vulgaris* (Fig. 3).

Also, in contrast to what was previously reported by Kadereit (1984a) from a study of Les Quennevais material of subsp. *denticulatus* and British var. *vulgaris*, no differences between both taxa were recorded for potential reproductive output in the cultivated material (Table 6). Kadereit's findings largely resulted from a significantly smaller average number of capitula and buds present at the time of maturity of the first capitulum in subsp. *denticulatus*. As plants were grown under different conditions and there was significant variation among families for this character (Kadereit 1984a), there is the possibility of both a great amount of genotypic variability and a considerable genotype \times environment interaction for this feature.

Perhaps one of the most intriguing results of the progeny tests is that the pattern of germination behaviour (Fig. 3), the leaf shape characteristics (Fig. 4) and the canonical variate analysis (Fig. 5) clearly show that all discoid progenies that were raised from the unidentified discoid plants (B3–B6) from Les Quennevais were very similar to subsp. *denticulatus*. Although – with the exception of character AF (time from anthesis to first fruiting) – these variants are consistently associated with slightly lower values of all phenological characters (Table 6), the phenological differences are slight compared to those between discoid and radiate subsp. *denticulatus* on the one hand and Jersey var. *vulgaris* on the other. Thus, the present study has demonstrated that the presence of ray florets alone might be insufficient to identify subsp. *denticulatus* on Jersey. Evidently, when growing in drought-prone coastal sites, Jersey var. *vulgaris* may approach the discoid *denticulatus*-like variant in phenotype, and thus may impede identification in the field. Such a possibility has been demonstrated by the fact that, when collected, discoid seed parents from the fertile site at L'Étaq (B1 and B2) and the dune grassland on Ouaisné Common (B7) could not be assigned to either taxon using morphological criteria, but progeny analyses proved this material to be typical Jersey var. *vulgaris*. It is worth noting that two earlier records exist concerning the occurrence of discoid

variants of subsp. *denticulatus* in coastal habitats, namely in the British Isles at Pevensey, Sussex (Wilmott 1925, 1949), and on Bornholm, Denmark (Lange 1851), but there is no evidence that these variants are of similar, i.e. hybridogenous, origin as those described here. This will be discussed in more detail below.

HYBRIDIZATION AT ST OUEN'S BAY

For the following discussion of hybridization at St Ouen's Bay it is irrelevant whether subsp. *denticulatus* represents a local ecotype or a population of a widely distributed monophyletic taxon. Evidence for the latter comes from the observation of pronounced seed dormancy and strongly elongated generation time in short ligulate material of *S. vulgaris* from S. Spain and Sicily (J. W. Kadereit, pers. comm., 1993).

All plants scored and collected as putative hybrids at St Ouen's Bay have been interpreted as such because of their intermediate ray floret length. However, direct evidence of their hybrid status is lacking because offspring individuals derived from two different short ligulate seed parents collected on Les Quennevais did not produce the expected intermediate phenotype but resembled subsp. *denticulatus* closely (Fig. 5). The fact that both individuals failed to segregate for capitulum type is not a strong argument against their hybrid status since lack of segregation could have reflected sampling error due to the very small number of progeny grown ($N=3$). Nevertheless, it appears reasonable to assume that the short ligulate plants, together with the discoid *denticulatus*-like variants described above, are the products of hybridization between subsp. *denticulatus* and var. *vulgaris*. Alternatively, they could reflect a polymorphism for capitulum type in populations of subsp. *denticulatus*, or even represent intermediate stages in the evolution of subsp. *vulgaris*. The hypothesis of their hybrid status is preferred, however, because: (i) subsp. *denticulatus* and var. *vulgaris* grow sympatrically at St Ouen's Bay; (ii) both taxa are visited by a similar set of putative pollinators; and (iii) fertile crosses can easily be obtained in the greenhouse (e.g. Gilmer & Kadereit 1989).

One morphological marker, absence of ray florets, that is fixed in var. *vulgaris* but – in general – absent from subsp. *denticulatus*, is regulated by an allele of a single gene that is only weakly linked to the gene(s) controlling speed of development (Comes 1994). If both taxa interact along an extensive hybrid zone (sensu Harrison & Rand 1989) at St Ouen's Bay, particularly in the man-disturbed area north of Les Quennevais, Mendelian segregation of this morphological marker in the resultant population is to be expected. The observation that the discoid variants tended to complete their life cycle somewhat earlier than typical subsp. *denticulatus* (see above) might be attributed to the weak linkage between the ray floret gene and the gene(s) controlling speed of development. Under the polymorphism hypothesis, however, this association remains unclear (excluding the highly unlikely possibility of pleiotropic or developmental effects of the ray floret gene on this phenological character), and under the intermediate hypothesis it is unclear why no truly intermediate or *vulgaris*-like individuals were found on Les Quennevais (Fig. 5).

Although the discoid and short ligulate *denticulatus*-like phenotypes thus might be considered as products of hybridization between subsp. *denticulatus* and var. *vulgaris*, their mode of origin remains obscure. It is possible that these phenotypes too are the products of many generations of introgression with the subsp. *denticulatus* population on Les Quennevais as the likely recipient population. Alternatively, they may be early recombinant segregants having arisen following self-fertilization of an F_1 hybrid. Evidence in favour of the latter possibility is offered by hybridization experiments between both taxa (Comes 1994). In these experiments, following spontaneous selfing of the F_1 hybrid (57% self seed set), several recombinant individuals occurred in the F_2 that were discoid (or short ligulate) but had phenological and morphometric features characteristic of subsp. *denticulatus*.

Irrespective of their mode of origin, it remains to be established why all discoid and short ligulate plants that were found on Les Quennevais showed characteristics typical of subsp. *denticulatus*. One likely explanation is that the hybridization boundary around this area is less permeable for genes regulating germination, phenological and morphological characters typical of var. *vulgaris* that are more likely to have ecological and adaptive significance, than for those determining capitulum type that is more likely to be influenced by random drift, especially in the presence of efficient self-fertilization and in the absence of tight linkage with other life history characters. Moreover, different mechanisms of mineral uptake and utilization could select for the *denticulatus* genotype in

the Quennevais area. It seems likely that subsp. *denticulatus* is adapted to harvest and retain scarce resources under the poor nutrient-supplying power of this area in a similar way to well-known stress tolerators on calcareous soils, e.g. the associated *Saxifraga tridactylites* and *Myosotis ramosissima* (Grime *et al.* 1988). Under these circumstances, both a prolonged phase of vegetative growth and a delayed onset of reproduction in *Senecio vulgaris* subsp. *denticulatus* (Table 6) may be indicative of rather low rates of mineral nutrient capture and utilization (Grime 1988). If this is so, the need for early, rapid, and heavy resource allocation to reproduction in the ruderal var. *vulgaris* genotype will be incompatible with its survival or competitive ability on Les Quennevais. The potential of nutrient deprivation as a selective factor that might influence the establishment or spread of var. *vulgaris* has been demonstrated by Aarssen & Burton (1990). These authors reported evidence that maternal plants of var. *vulgaris* grown in nutrient-poor soils produced seeds with lower individual mass, seeds that germinated later, and seedling offspring that had significantly lower biomass and height than those individuals with high maternal soil nutrient level (but, unexpectedly, also seedling offspring that survived longer in the absence of external nutrients). Although it is tempting to attribute differential survival or competitive ability in the Quennevais area to different metabolic mechanisms, other edaphic or biotic factors on Les Quennevais could also select for the *denticulatus* genotype. For example, rabbit grazing and poor water supply might well be expected there, but not (or to a lesser extent) in the man-disturbed localities around this area, and this would also be likely to influence life history characters like speed of development.

Whatever its selective advantage on Les Quennevais, provided there is in situ selection, and given both an efficient self-pollination strategy and low levels of hybridization, subsp. *denticulatus* will be able to maintain its integrity there.

EPILOGUE

There is documentary evidence to suggest that subsp. *denticulatus* was once more widely distributed on Jersey. Populations of subsp. *denticulatus* may have existed on the coastal plains of St Aubin's Bay at least until the first half of the 19th century (Babington 1839), but since this locality was not referred to any more by Lester-Garland's account in 1903 (Lester-Garland 1903) it seems plausible that they were extinguished by the stabilizing of the dunes or the building of the sea walls towards the end of the 19th century. Equally, since Lester-Garland (1903) reported this taxon at St Brelade's Bay (including Ouaisné Common), the current population on Ouaisné Common appears to be a mere remnant of those populations that existed along St Brelade's Bay at the beginning of this century. Thus, even if it is not threatened by hybridization with or introgression from var. *vulgaris*, subsp. *denticulatus* might be seriously endangered from progressive destruction of its habitat by man.

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