Erica Tetralix L.

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BIOLOGICAL FLORA OF THE BRITISH ISLES

Erica tetralix L.

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Subgenus EUERICA Benth., section EREMOCALLIS Salisb. A low, much-branched, evergreen shrub up to about 0·6 m in height. Usually semi-prostrate, in wet habitats the lower branches are often buried in moss or litter layers and produce adventitious roots readily. In dry areas, in the absence of vigorous competition, it may form a hemispherical bush, but when in competition with *Calluna* the growth may be erect and straggling.

Leaves typically four in a whorl [populations in contact with *Erica ciliaris* may have only three leaves in a whorl (Gay 1957)], 3–4 mm, linear grey-pubescent and glandular-ciliate above with margins recurved almost to the midrib, hiding most of the under-surface. Leaves below the infloresecence shorter and more distant, often adpressed to stem and exposing the abaxial surface.

Flowers (four to twelve) in terminal, umbellate, clusters, pendant when flowering and more erect in fruit. Flower buds glandular and viscous. Pedicels 2–4 mm, pubescent, with three bracteoles immediately beneath the calyx. Flowers tetramerous, calyx lobes short (*c*. 2 mm) oblong-lanceolate, pubescent on surface, ciliate with interspersed glandular hairs on the edges. Corolla 6–7 mm ovoid, urceolate, rose-pink (not uncommonly paler beneath and occasionally completely white). Eight stamens with awned anthers, included in the corolla. Nectary in a ring around the base of the ovary. Capsule pubescent, 4-celled, loculicidal; many seeded, seeds *c*. 0·5 × 0·25 mm.

A variety (var. *martinésii* Benth.) in which the plant is thickly invested with white hairs has been described from Spain, but this may be a hybrid (Hegi *Fl.* 5, 3). In Britain both white and dark (rose) flowering forms are found. Polypetalous (Sigerson 1871); anandrous (with stamens either absent or replaced by petaloid structures), and pentamerous flowers (Hagerup 1928) may also occur.

An oceanic plant; native and widespread in Britain. Characteristic of wet heath and mire communities in oceanic West Europe, although a dominant of a dry lichen-heath (Ericetum tetralicis cladonietosum) in the Baltic area (Horst 1964). Normally a plant of acid to neutral waterlogged organic soils.

I. *Geographical and altitudinal distribution*. Throughout the British Isles (Fig. 1) but absent from the vice-counties of Cambridge, South Gloucester and North Wiltshire. Sparsely represented in the calcareous and well-cultivated areas of the English Midlands and South. In Europe from Central and North Portugal, North Spain (extending to the Sierra Morena and western and central Pyrenees, although only well represented in

oceanic areas), oceanic West and North France (extending eastwards to the Auvergnes), the Low Countries, Denmark, South Sweden and in Norway to 65° 36′ N. In the Baltic area through North Germany (less frequent in the east) to Poland with outposts in Latvia and possibly Estonia and even Finland. Introduced into South Germany with coniferous seedlings from the north (Hegi *Fl.* **5**, 3). Often mentioned as occurring in Iceland and the Faroes (Matthews 1955; Hegi *Fl.* **5**, 3; Hansen 1950) but the nineteenth-century records can be discounted (Gröntved 1942; Ostenfeld 1901). Recent extensive studies of the
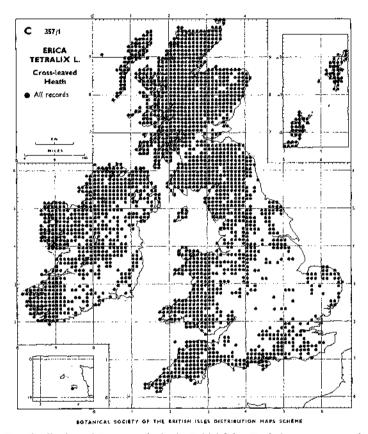

FIG. 1. The distribution of *Erica tetralix* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. (By permission of the Botanical Society of the British Isles and Thomas Nelson & Sons Ltd, taken from their *Atlas of the British Flora*).

Faroese flora (Hansen 1964a) failed to reveal the presence of *E. tetralix* (K. Hansen). In North America on Nantucket Island, probably introduced (Britton & Brown 1897).

In Britain ascends from sea level to *c.* 2500 ft (760 m). Upper limits (*Alt. Range Br. Pl.*) are 1820 ft (555 m) in West Lancashire, 2200 ft (670 m) in West Yorkshire, 2250 ft (685 m) in North Yorkshire (Lovely Seat); in Wales 1950 ft (595 m) on Tal-y-Fan, *c.* 2000 ft (610 m) in Mid-Wales [2020 ft (615 m) in the Carneddau (Ratcliffe 1959)]; in Scotland over 2000 ft (610 m) in West Ross, 2200 ft (670 m) on Rannoch Moor and 2400 ft (730 m) in the Eastern Highlands [2700 ft (820 m) on Cairn Toul (McVean & Ratcliffe 1962)]; in Ireland 1800 ft (550 m) in Donegal, 2050 ft (625 m) in Down and 2200 ft (670 m) in Dublin (Seefingan). The altitudinal limit of *E. tetralix* as a regular component

of any community would appear to be in *Trichophorum–Calluna* mires which ascend to *c.* 2500 ft (760 m) in the Cairngorms (McVean & Ratcliffe 1962).

On the Continent attains an altitude of 7150 ft (2200 m) in the Pyrenees (Hegi *Fl.* 5, 3); however, over most of the rest of its continental range, with the exception of central France and West Norway, *Erica tetralix* is confined to low-lying areas.
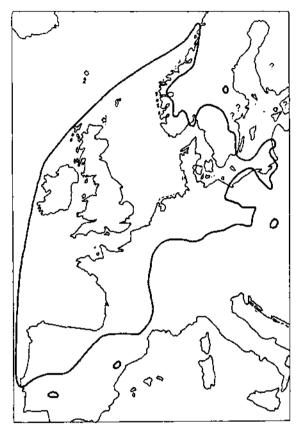

FIG. 2. The approximate limits of distribution of *Erica tetralix* in Europe.

II. *Habitat* (*a*) *Climatic and topographical limitations.* Widespread in oceanic West Europe. Somewhat more northern and continental in distribution than *E. cinerea.* Overwintering apices are capable of withstanding low temperatures (Till 1956—see V(*c*)). In British winters the water balance is intermediate between that of *E. cinerea* (small reductions in water content) and *Calluna* (large reductions), and it has been suggested (Bannister 1964c) that the ability of *Calluna* to tolerate large water deficits in winter might be a factor in determining its continental range. Such a consideration might apply, to a more limited degree, to *Erica tetralix.* Northern and western limits might be set by the effect of reduced summer temperatures on flowering and fruit maturation (Gay 1957), northern and eastern limits by the ability to withstand severe winters and southern and eastern limits by the ability to withstand summer drought (see V(*c*)).

Confined to the altitudinal zone of potential forest; probably more typical of lower altitudes but at present restricted to marginal and upland areas by cultivation and land

improvement. Most prevalent on areas of shallow slope, particularly when this leads to an accumulation of water. In Britain the transition from drier types of heath to wet heath with *E. tetralix* is often correlated with a change to a less steep slope (Bannister 1963; Gimingham 1964). In the more humid west of Britain *E. tetralix* may be found over a wider range of slopes. Although maximum development is in the open *E. tetralix* is capable of withstanding a reduction in light intensity as it is found in pinewoods with a daylight factor of 1/3–1/6 (McVean & Ratcliffe 1962).

(b) *Substratum*. Typically waterlogged and poorly aerated with a concomitant high organic content. Rutter (1955) has shown that the change from a fluctuating to a constantly high water table is correlated with a decrease in the importance of *Calluna* and an increased proportion of *Erica tetralix*. Webster (1962) has shown that the percentage cover of *E. tetralix* increases with rising carbon dioxide and hydrogen sulphide concentrations in the ground water. Mesotrophic mires are often soligenous in nature and there may be an accretion of both mineral and organic matter whilst in eutrophic communities the substratum may be entirely mineral. A fluctuating water table (as in dune slacks) may lead to an efficient breakdown of organic matter in the drier seasons, with a resultant mineral soil. Transitions to drier soils are usually better aerated with a lower organic content. Various soil analyses are given in Table 1; samples are from the main rooting zone (0–10 cm). Surface pH values may range from *c.* pH 3·5 (drained peat) to *c.* pH 7·0 (eutrophic flushes), although communities characterized by the presence of *E. tetralix* show values of pH 4·0–5·0. Comparative data on base status is difficult to obtain as most measurements have been made on a dry weight rather than a volume basis; however, on organic substrata, exchangeable calcium values may vary from *c.* 80 mg/100 g in oligotrophic peats to *c.* 1000 mg/100 g in eutrophic peats (data: McVean & Ratcliffe 1962).

III. *Communities*. *E. tetralix* is found in a variety of communities, mostly within the forest zone, reaching its maximum expression on wet, usually organic, soils of a low nutritional status. It is typically associated with *Calluna vulgaris* but may be more frequent and more abundant than *Calluna* in wet mesotrophic–eutrophic vegetation. In Britain, soil moisture and nutritional status appear to be more important than plant geographical factors in determining the distribution and composition of communities containing *Erica tetralix*. Floristic lists are given in Table 2 and referred to in the text by number. Some indication of the relationships between communities is given in Fig. 3, which is a two-dimensional ordination (Bray & Curtis 1957) based on the relative presence of species in communities distinguished by McVean & Ratcliffe (1962) and Gimingham (1964).

(A) Oligotrophic communities

(i) Forest communities. *E. tetralix* is found (constancy *c.* 40%) in the two major British pinewood associations, the *Hylocomium splendens–Vaccinium myrtillus* (1) association and the *Vaccinium–Calluna vulgaris* (2) association (McVean & Ratcliffe 1962). Both associations are characterized by *Calluna*, *Vaccinium myrtillus* and *V. vitis-idaea*, the *Vaccinium* spp. being dominant in the first community and *Calluna* in the second. *Deschampsia flexuosa* and *Hylocomium splendens* are common in both communities but *Plagiothecium undulatum*, *Ptilium crista-castrensis* and *Sphagnum* spp. of the Acutifolia group with *Aulocomnium palustre* and assorted hepatics are more common in the second

community. The vegetation is most obviously related to *Calluna–Vaccinium* and *Calluna* moor but the more hygrophilous vegetation of the *Vaccinium–Calluna* community shows a resemblance to montane *Calluna–Eriophorum* bogs.

(ii) Dry heath communities. *Erica tetralix* is more common in heaths occurring at lower altitudes. (A comparison of the lists of McVean & Ratcliffe (1962) with those (more lowland) of Gimingham (1964) illustrates this point.) In *Calluna–Vaccinium* heaths (3 and 4) (Gimingham 1964) *Erica tetralix* shows a reduced constancy (*c.* 20%) as compared
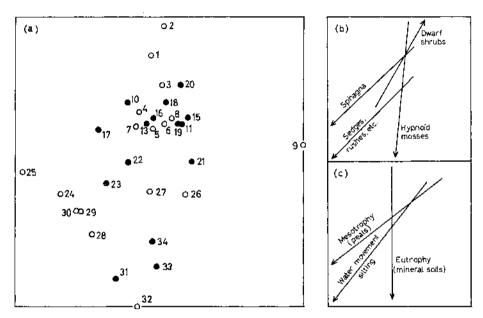

FIG. 3. An ordination of Scottish plant communities containing *Erica tetralix*.
(a) Ordination based on relative presence. [Community data from *The Vegetation of Scotland* (Ed. by J. H. Burnett).] 1, Pinewood *Vaccinium*-moss; 2, Pinewood *Vaccinium–Calluna*; 3, *Calluna–Vaccinium vitis-ideae*; 4, *Calluna–V. myrtillus*; 5, Oceanic *Calluna–Erica cinerea*; 6, *Calluna–Erica cinerea*; 7, *Calluna–Empetrum nigrum* (dry); 8, *Calluna–Arctostaphylos*; 9, Lichen-rich dwarf *Calluna*; 10, *Calluna vulgaris*; 11, Species-poor *Calluna–Arctostaphylos*; 13, *Calluna–Erica tetralix–Empetrum*; 15, *Calluna–E. tetralix–Trichophorum*; 16, *Calluna–E. tetralix–Molinia*; 17, *Calluna–E. tetralix*; 18, *Calluna–Eriophorum*; 19, Lowland *Calluna–Eriophorum* bog; 20, Upland *Calluna–Eriophorum* bog; 21, *Trichophorum–Eriophorum*; 22, *Molinia–Myrica*; 23, *Carex–Molinia*; 24, *Carex–Sphagnum*; 25, *Juncus–Sphagnum*; 26, *Narthecium–Sphagnum*; 27, Herb-rich *Calluna–Erica cinerea*; 28, Species-rich *Juncus squarrosus*; 29, *Juncus–Acrocladium*; 30, *Carex rostrata–Sphagnum*; 31, *Carex–Campylium*; 32 and 33, *Carex–Saxifraga azoides* (high and low level); 34, *Schoenus nigricans*.
(b) Dominance in various strata (arrows indicate direction of any trend).
(c) Habitat (arrows indicate direction of any trend).

with pinewood associations but may be entirely absent from the more montane examples (McVean & Ratcliffe 1962). In most other dry heath associations *E. tetralix* shows a constancy of <30% (5–9) although *Calluna*-dominated (10) and species-poor *Calluna–Arctostaphylos* (11) communities may exhibit *Erica tetralix* at >60% constancy (Gimingham 1964). More detailed descriptions of the floristics and distribution of such communities are given by Gimingham (1960, 1964) and Bannister (1965).

In south-west England *E. tetralix* is a constant component and co-dominant of a variant of the oceanic *Calluna–Ulex gallii* heath ('short heath' of Coombe & Frost 1956)

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(12) in which any of the three species mentioned, as well as *Agrostis setacea, Erica cinerea* and *Molinia caerulea*, may be dominant or co-dominant.

(iii) Wet heath communities. *Erica tetralix* is a constant component of such communities and may achieve dominance or co-dominance. Most wet heaths have an intermediate

Table 1. *Analytical data for soils from communities containing* Erica tetralix

Site	pH	Ignition loss (%)	Coefficient of humidity	Total exchangeable Hydrogen	Bases	Base saturation (%)	Vegetation type (see text)
(a) DRY HEATHS							
1	3·7	50	5·1*	16·8 (4·3)	2·9 (0·7)	15	(5)
2	4·6	27	1·8	11·6 (4·4)	1·8 (0·7)	13	(3)
3	(C) 4·9	13	–	– –	– –	–	(12)
(b) WET HEATHS							
4	3·8	93	4·3*	32·4 (4·6)	5·1 (0·6)	14	(14)
5	4·2	91	7·0	15·6 (2·1)	10·3 (1·4)	40	(18)
6	(N) 4·2	30	7·4*	– –	– –	29	(16)
7	(M) 4·4	96	–	– –	6·5 –	–	(15)
8	4·6	95	4·5	18·6 (2·2)	7·1 (0·9)	28	(16)
(c) BOGS							
9	4·0	94	17·8*	48·6 (3·5)	12·6 (0·8)	21	(19)
10	4·1	96	9·1	20·4 (1·9)	11·6 (1·1)	36	(20)
11	4·3	96	6·4	15·0 (1·8)	11·6 (1·4)	44	(21)
12	(N) 5·0	86	17·3*	– –	– –	48	Valley bog
(d) OLIGOTROPHIC FLUSHES							
13	4·5	88	17·1*	32·4 (2·5)	16·8 (1·2)	34	(25)
14	4·9	95	10·9	21·6 (1·3)	6·6 (0·4)	23	(22)
(e) MESOTROPHIC–EUTROPHIC COMMUNITIES							
15	5·0	6	3·6	1·0 (0·7)	3·6 (2·6)	78	(13) dune heath
16	(N) 5·3	65	22·0*	– –	– –	56	*Schoenus* mire
17	(N) 5·8	72	17·7*	– –	– –	58	(22)
18	(M) 6·0	16	–	– –	18·9 –	–	(31)
19	(C) 6·1	11	–	– –	– –	–	(35)

(C) Data from Coombe & Frost (1956). (M) Data from McVean & Ratcliffe (1962). (Exchangeable bases calculated from values for exchangeable Na, K and Ca). (N) Data from Newbould (1960). (Mean values for each vegetation type calculated from graphs.)
* Determinations in wet season.
pH by glass electrode, *c.* 1 : 2 fresh soil–water.
Organic content estimated by ignition loss (% of dry soil) at 800° C.
Water content (% of dry soil) by oven-drying at 105° C.
Exchangeable bases and hydrogen by the method of Brown (1943)—expressed as m-equiv/100 g dry soil and /100 ml fresh soil (in parentheses). In samples 1, 4, 9, 13 the determination was carried out on fresh soil; samples 2, 5, 8, 10, 11, 14, 15 on oven-dry soils.
Sites. 1, 13, Aberfoyle, Perthshire; 2, Kindrogan, Perthshire; 3, 19, Lizard, Cornwall; 5, Milngavie, Dunbartonshire; 6, 12, 16, 17, Cranesmoor, Hampshire; 7, Beinn Eighe, West Ross; 8, 14, Benderloch, Argyll; 9, West Flanders Moss, Stirlingshire; 10, 11, Mainland, Orkney; 15, Balmedie, Aberdeenshire; 18, Killiecrankie, Perthshire.

status between drier heaths and bogs in terms of floristic composition and spatial relationships. However, the ecological and phytosociological relationships are insufficiently known at the present.

Calluna–Empetrum (13) and *Calluna–Vaccinium* (14) wet heaths show a strong interrelationship and both have affinities to pinewood associations (1, 2) on the one hand and montane blanket bog (20) on the other. Certain northern examples of *Calluna–Empetrum* heath may show a reduction in importance or a complete absence of *Calluna* with *Erica*

tetralix achieving co-dominance with *Empetrum nigrum. Sphagnum* spp. may dominate the ground layers in both communities and species of wet habitats are common associates (e.g. *Eriophorum vaginatum* (often replaced by *Trichophorum cespitosum*), *Eriophorum angustifolium, Juncus squarrosus, Narthecium ossifragum, Aulocomnium palustre* and *Polytrichum commune*). *Empetrum* spp. and *Vaccinium myrtillus* are characteristic of both Scottish (McVean & Ratcliffe 1962) and Irish (Moore 1962a) montane blanket bogs as well as those of North England. These wet heaths are found in northern and montane areas of Britain, wet heaths with *Vaccinium* tending to be slightly more western in their distribution whilst those with *Empetrum* are slightly more northern.

Other *Calluna–Erica tetralix* wet heaths represent a complex of related and intergrading communities. Two major types are *Calluna–Trichophorum* (15) and *Calluna–Molinia* (16) communities whilst other examples may show decreased importance of *Trichophorum* and *Molinia* with increased dominance of either dwarf shrub species (17). *Calluna–Trichophorum* communities are floristically poor and additional constant species include *Eriophorum vaginatum, Narthecium ossifragum* and *Molinia. Calluna–Molinia* communities are more species-rich and probably less oligotrophic, *Trichophorum* is a frequent associate and *Potentilla erecta, Hypnum cupressiforme, Hylocomium splendens* and *Pleurozium schreberi* are species of high constancy. This type of community is widespread and occurs commonly in transitions to blanket bog (Ratcliffe & Walker 1958), to valley bog (Rutter 1955; Newbould 1960) and even to mesotrophic fen (Poore 1956). Both types are common in the British Isles; *Trichophorum* communities are more characteristic of upland areas whilst the *Molinia* communities are common from sea level and extensive in South England from south-west England to East Anglia. Although common on peats *Molinia* communities may develop on gleyed mineral soils, particularly in the south, and even in northern areas are often found on less peaty soils than the *Trichophorum* communities. Dry, strongly oceanic, communities (*Calluna–Erica cinerea* heaths) relate to *Calluna–Molinia* heaths. Oceanic heath plants such as *Erica ciliaris* and, to a lesser extent, *E. vagans* are found in *Calluna–Molinia* wet heath in England, whilst *E. mackaiana* and *E. mediterranea* may occur in similar communities in Ireland.

A further community, *Calluna–Eriophorum vaginatum* wet heath (18) may relate to either upland or lowland *Calluna–Eriophorum* bog communities and often may be formed after such bogs have become drier. Ground layers may be dominated by *Polytrichum commune. Erica tetralix* is a constant associate.

(iv) *Bog communities. E. tetralix* is a constant member of all but the most montane bogs. Species found in most bog types include *Calluna vulgaris, Erica tetralix, Eriophorum vaginatum, E. angustifolium, Drosera rotundifolia, Narthecium ossifragum; Sphagnum rubellum* is often the main hummock former whilst *S. cuspidatum* is found in hollows (*S. recurvum* seems to indicate lateral water movement). Lowland bogs, particularly in the west, may include *Sphagnum fuscum* and *S. imbricatum* as hummock formers with *S. magellanicum* forming carpets (these species are typical of raised bogs in Ireland (Moore 1962a) but all occur in blanket bog); additional species are *Drosera anglica* and *Rhynchospora alba* in the wetter portions of the bog. *Vaccinium oxycoccus* and *Andromeda polifolia* are almost exclusive to raised bogs [lowland *Calluna–Eriophorum* bog (19)] and serve as good differential species. Upland *Calluna–Eriophorum* bogs (20) are somewhat different in character; *Rubus chamaemorus* is a characteristic species (except in Ireland) and dwarf shrubs are common (particularly *Empetrum* and *Vaccinium* spp. and locally in Scotland *Arctous alpinus, Betula nana, Arctostaphylos uva-ursi*). *Hylocomium splendens, Rhytidiadelphus loreus* and *Pleurozium schreberi* are associated with *Sphagnum* spp. in the moss

Table 2. *Community data*

Reference No. (text)	2	10	13	14	15	16	18	19	20	21	22	23	25	29	31	33	34
Altitude (ft)	150	300	650	600	1500	50	300	60	400	200	50	1000	600	1150	1300	1400	450
Slope (degrees)	5	5	5	5	15	5	5	10	10	0	0	0	10	4	25	25	2
Aspect	SE	SW	NW	NW	W	SW	W	W	SE	–	N	–	NE	SE	S	W	NW
Plot area (m²)	16	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Calluna vulgaris	7	9	5	3	7	7	7	3	6	3	1	2	4	.	.	1	.
Empetrum nigrum	3	.	5	.	.	.	.	.	3	3	.	.	1	.	.	.	.
Erica tetralix	3	1	5	5	4	3	4	5	2	4	3	6	4	2	4	3	3
Myrica gale	.	.	.	.	.	.	3	5	.	.	4	.	.	.	.	.	2
Vaccinium myrtillus	5	1	1	5	.	.	.	.	1	1	.	.	.	.	.	.	.
V. oxycoccus	.	.	.	.	.	.	.	+	.	.	.	.	.	.	2	.	.
V. vitis-idaea	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Selaginella selaginoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	2
Agrostis canina	.	.	.	.	.	1	.	.	.	.	.	.	4	2	.	.	.
Anthoxanthum odoratum	.	.	3	4	.	4	.	.	.	.	.	2	2	.	.	.	.
Deschampsia flexuosa	1	.	.	4	.	1	.	.	.	.	.	.	1	3(r)	4	4	4
Festuca ovina/rubra (r)	.	1	4	4	2	4	1	.	.	.	7	3	.	2	4	3	.
Molinia caerulea	.	.	4	4	.	.	6	6	6	8	.	3	.	4	4	3	4
Nardus stricta	.	.	3	3	.	.	1	.	1	.	.	3	2	.	.	.	2
Carex echinata	.	.	.	.	.	.	.	.	.	.	1	2	.	1	4	.	.
C. hostiana	.	.	.	1	3	2	.	.	.	.	.	4	.	1	4	6	.
C. nigra	.	.	.	1	2	1	.	.	.	.	2	.	2	1	4	4	.
C. panicea	.	.	.	.	.	.	.	.	.	.	.	.	1	2	4	4	.
Eriophorum angustifolium	.	.	3	.	.	.	3	4	4	1	.	4	.	.	3	3	2
E. latifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	3	.
E. vaginatum	.	1	.	.	8	4	6	6	6	8	2	.	6	5	.	.	4
Juncus acutiflorus	.	.	.	.	.	.	.	.	.	.	.	.	6	.	2	2	.
J. articulatus	.	.	.	.	.	.	.	.	.	.	1	2	.	3	3	3	.
J. effusus	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
J. squarrosus	.	1	3	5	3	2	.	3	.	5	3	4	3	1	2	2	2
Narthecium ossifragum	.	.	2	.	2	2	.	.	+	.	3	4	.	.	.	1	8
Schoenus nigricans	.	.	7	4	.	4	.	1	.	.	3	2	.	.	3	4	4
Trichophorum cespitosum	.	.	.	.	8	.	6	.	6	8	3	.	.	.	2	.	.
Drosera rotundifolia	.	.	.	.	.	.	.	.	.	3	3	2	.	5	.	1	2
Euphrasia officinalis (agg.)	.	.	.	.	.	2	.	+	.	.	.	.	4	1	3	1	.
Galium saxatile	.	.	3	3	.	3	.	.	.	.	.	1	3	1	.	1	.
Potentilla erecta	.	.	.	.	.	.	.	.	+ +	1	2	1	.	1	3	2	1
Pinguicula vulgaris	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	1	1
Saxifraga aizoides	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	4	.
Succisa pratensis	.	.	.	.	.	3	.	.	1	2	1	3	.	.	2	1	.
Acrocladium cuspidatum	.	.	.	.	.	.	.	.	.	.	.	.	.	4	3	.	.
Aulocomnium palustre	.	.	4	3	.	.	.	.	.	2	2	3	.	2	.	.	.
Campylium stellatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3	5

Reference No. (text)	2	10	13	14	15	16	18	19	20	21	22	23	25	29	31	33	34
Clenidium molluscum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dicranum scoparium	.	1	2	3	.	3	2	.	2	.	.	.	.	.	5	1	.
Drepanocladus revolvens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	.
Hylocomium splendens	5	.	.	.	.	1	1	.	1	4	.	1	5	.	3	3	1
Hypnum cupressiforme	.	2	3	2	3	7	1	.	2	4	1	.	.	.	.	.	.
Plagiothecium undulatum	2	2	2	1	.	2	5	.	3	1	1	1	1	.	.	.	.
Pleurozium schreberi	2	2	2	6	.	2	4	3	3	2	1	1	6	8	.	.	.
Polytrichum commune	.	.	.	4	4	.	.	.	.	.	.	.	.	.	.	.	.
Pseudoscleropodium purum	.	2	2	.	.	.	.	.	.	.	1	.	.	.	2	.	.
Rhacomitrium lanuginosum	1	.	.	.	.	1	.	.	1	1	.	.	.	.	.	.	2
Rhytidiadelphus loreus	.	.	.	.	4	.	.	1	.	.	3	.	.	.	.	.	.
R. squarrosus	.	.	.	.	.	.	.	.	.	.	.	.	3	2	2	.	3
Scorpidium scorpioides	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	8	3
Sphagnum capillaceum	8	6	6	5	4	.	6	7	.	6	4	.	1	8	.	.	.
S. cuspidatum	.	.	.	.	.	.	.	.	.	.	.	4	1	.	.	.	.
S. palustre	.	.	3	.	.	.	.	3	.	3	5	8	.	7	.	.	.
S. papillosum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
S. recurvum	.	.	.	.	.	.	.	.	.	6	4	5	.	.	2	.	.
S. rubellum	.	.	5	.	.	.	4	4	6	.	.	.	.	.	.	.	.
Aneura pinguis	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	2	2
Cephalozia sp.	.	3	3	2	.	.	1	.	.	.	3	1	.	.	.	.	.
Calypogeia muelleriana	.	.	3	3	.	.	.	.	.	2	3	.	.	.	2	.	.
Lophocolea bidentata	.	.	3	.	.	.	3	3	1	.	3	.	.	.	.	.	.
Odontoschisma sphagni	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.
Cladonia impexa	.	.	.	.	4	3	.	.	4	.	.	.	.	.	.	.	.

Species not included in the table. (2) *Sorbus aucuparia* 1, *Pteridium aquilinum* 2, *Melampyrum pratense* 1, *Dicranum majus* 3, *Ptilium crista-castrensis* 2; (10) *Leucobryum glaucum* 2; (14) *Polytrichum juniperinum* 2; (15) *Diplophyllum albicans* 1, *Leptoscyphus taylori* 1, *Scapania gracilis* 1, *Cladonia uncialis* 2; (16) *Erica cinerea* 5, *Pedicularis sylvatica* 2, *Thuidium tamariscinum* 1, *Pellipera* sp. 1; (19) *Rhyncospora alba* 3, *Campylopus flexuosus* 2, *Sphagnum magellanicum* 4, (21) *Listera cordata* 1, *Mnium hornum* 2, *Cladonia sylvatica* 2; (22) *Dactylorchis maculata* ssp. *ericetorum* 1, *Polygala serpyllifolia* 1, *Lophozia ventricosa* 3; (23) *Carex pauciflora* 4, *Pellia epiphylla* 1; (29) *Equisetum fluvatile* 1, *Holcus lanatus* 3, *Carex dioica* 2, *C. demissa* 1, *Luzula multiflora* 3, *Achillea ptarmica* 1, *Ajuga reptans* 2, *Cirsium palustre* 1, *Polygonum viviparum* 3, *Epilobium palustre* +, *Rumex acetosella* 2, *Ranunculus acris* 1, *Trifolium repens* 1, *Mnium punctatum* 1, *Philonotis fontana* 2; (31) *Carex pulicaris* 3, *Thalictrum alpinum* 3, *Dicranum bonjeanii* 3, *Fissidens adianthoides* 2, *Chiloscyphus polyanthus* 1; (33) *Eleocharis pauciflora* 3, *Juncus kochii* 3, *Tofieldia pusilla* 2, *Taraxacum* sp. 1, *Blindia acuta* 1, *Bryum pseudotriquetrum* 2, *Cratoneuron commutatum* 4, *Ditrichum flexicaule* 1; (34) *Carex rostrata* 2, *Potamogeton polygonifolius* 4, *Menyanthes trifoliata* 2, *Utricularia intermedia* 3, *Campylopus atrovirens* 1, *Sphagnum inundatum* 3, *Pleurozia purpurea* 1.

Figures represent abundance on the Domin scale.

Sites. (2) Loch Maree, Ross-shire (NH 006645); (10) Milngavie, Dunbartonshire (NS 522758); (13) Cruach Muasdale, Kintyre (NR 688389); (14) Queen's View, Stirlingshire (NS 511808); (15) Beinn Dearg, W. Ross (NH 215828); (16) Benderloch, Argyll (NM 878402); (18) Milngavie, Dunbartonshire (NS 551758); (19) W. Flanders Moss, Stirlingshire (NS 536957); (20) (21) Orkney, Mainland (HY 393102) (HY398112); (23) Glen Banchor, Inverness (NH 690000); (25) Duke's Pass, Perthshire (NN 517024); (29) Loch Mharaich, Perthshire (NO 117569); (31) Kinlochlaggan, Inverness (NN 560908); (33) Glen Clova, Angus (NO 289776); (34) Loch Buine More, Ross (NC 092151).

(2) (15) (23) (31) (33) (34) from McVean & Ratcliffe (1962).

layer. *Erica tetralix* may be absent from some Scottish bogs of this type but it has a high constancy in other British and Irish examples. Lowland blanket bog (*Trichophorum–Eriophorum* bog) (21) shows similarities to raised bog (19) but *Trichophorum cespitosum* is perhaps more common; species such as *Molinia caerulea*, *Campylopus atrovirens*, *Pleurozia purpurea* and *Schoenus nigricans* emphasize the more western character of this type. The valley bogs of the New Forest contain vegetation comparable to that of raised bog, but the movement of water contributes to the formation of other communities (e.g. 22 below). *Calluna–Eriophorum* raised bogs are found throughout the British Isles, mainly away from the West coast. Many have been much reduced in extent through agriculture. Upland *Calluna–Eriophorum* bog is common in mountainous regions of Scotland, North England and East Ireland. Blanket bogs are common in all the western, upland, regions of the British Isles.

(v) Flushed oligotrophic mires. *Erica tetralix* is common in a variety of communities with a higher base-status than those mentioned above. The least base-rich of these are those in which an acid habitat is permeated by moving water which results in better aeration and the replenishment of minerals. A typical community formed under such conditions is the *Molinia–Myrica* (22) community which may be found in flushed sites in all types of bog and wet heath, but are perhaps most common in the blanket bog of the west and the *Calluna–Molinia* wet heaths of the west and south of the British Isles. *Potentilla erecta* is a constant associate of this community and *Erica tetralix* is frequent (constancy >60%). *E. tetralix* plays a more prominent, and sometimes dominant, role in a related flushed community, *Carex–Molinia* (23) mire, which occurs within blanket bog or *Calluna–Molinia* wet heath. *Carex panicea* and *C. echinata* are the most common sedges; other species of high constancy are also typical of blanket bog. *Sphagnum* species are more common than in the previous community. Species such as *Selaginella selaginoides*, *Nardus stricta* and *Succisa pratensis* are indicative of the mineral enrichment and water movement. Some related flushed communities contain *Erica tetralix* less frequently (<40%); these include sub-alpine *Carex–Sphagnum* mires (24) and *Juncus–Sphagnum* mires (25), which are widespread in acidic upland areas of Britain and Ireland. In these *Sphagnum* spp. (notably *S. recurvum*, *S. palustre* and *S. papillosum*) may share dominance of the moss layer with *Polytrichum commune*. *Carex nigra* and *Potentilla erecta* have a high constancy in both communities; *Eriophorum angustifolium* and *Viola palustris* are more characteristic of *Carex–Sphagnum* mires whilst *Galium saxatile* is more common in *Juncus–Sphagnum* communities. *Carex echinata* and *C. nigra* are physiognomic dominants of the first community whilst *Juncus effusus* is characteristic of the second but may be placed by *J. acutiflorus* in the west of Britain.

A more montane *Narthecium–Sphagnum* (26) acid flushed community is local in Scotland and parts of North England where *Narthecium*, *Trichophorum* and *Nardus* may occur with *Sphagnum* spp. (*S. tenellum*).

(B) Mesotrophic–eutrophic communities

(i) Herb-rich examples of oligotrophic communities. *Erica tetralix* occurs with low constancy (*c*. 25%) in herb-rich examples of *Calluna–Erica cinerea* heaths (27) (Gimingham 1964) and is occasional in other herb-rich heaths. It also occurs with low constancy in herb-rich examples of sub-alpine *Juncus squarrosus* mires (28) (McVean & Ratcliffe 1962).

(ii) Flushed mesotrophic mires. *J. acutiflorus–Acrocladium cuspidatum* (29) mires are the mesotrophic equivalents of the oligotrophic *Juncus–Sphagnum* mires (25) and *Erica*

tetralix has approximately the same degree of constancy. *Epilobium palustre, Potentilla erecta* and *Rhytiadelphus squarrosus* are constant associates, whilst *Holcus lanatus, Carex panicea, Prunella vulgaris* and *Ranunculus acris* indicate the more mesotrophic conditions. Somewhat more prevalent in southern and eastern parts of upland Scotland and quite common in North England and Wales.

A more local and montane type of vegetation, *Carex rostrata–Sphagnum warnstorfianum* mire (30) (McVean & Ratcliffe 1962) relates to the oligotrophic *Carex–Sphagnum* mires (24). The vegetation is more basiphilous with a variety of sedges and herbs. Constant associates include *Selaginella selaginoides, Festuca ovina, Viola palustris, Hylocomium splendens, Aulocomnium palustre, Mnium pseudopunctatum, Sphagnum teres.* Local in Central Highlands, South Scotland and North England.

Erica tetralix also occurs in lowland equivalents of the above communities where species such as *Carex rostrata* and *Phragmites communis* may be dominant (Spence 1964). The constant association of *Myrica gale* and *Molinia caerulea* and *Carex* spp. relate these communities to flushed mires mentioned above (22, 23).

(iii) Flushed mesotrophic–eutrophic mires. *Erica tetralix* may have a constancy of 50–100% in the communities mentioned below. *Carex panicea–Campylium stellatum* mires (31) are found in calcareous flushes in Scotland and North England. They are herb-rich and sedge-rich, most of the species associated with *Carex rostrata–Sphagnum* mires are present, but Sphagnum spp. are typically absent, being replaced by hypnoid mosses. *Selaginella selaginoides, Juncus articulatus* and *Drepanocladus revolvens* are additional constant species whilst *Carex demissa, C. dioica, C. echinata, C. flacca* and *C. nigra* may be all or severally present and either share dominance or be individually dominant. *Carex–Saxifraga aizoides* flushes (32, 33) relate to the former community but vegetation cover is less complete, although much the same species may be present. *Erica tetralix* is common in low-level facies but virtually absent from the more montane examples. The low level examples may contain much *Molinia caerulea* and *Schoenus nigricans* and relate to the next communities. *Carex–Saxifraga* flushes are frequent in the Scottish Highlands and the appropriate parts of North England and Ireland. Other upland areas in the British Isles may support a similar vegetation lacking *Saxifraga aizoides*.

Schoenus nigricans communities (34) are local in West Scotland (McVean & Ratcliffe 1962); they may be poor in species with *Molinia caerulea, Eriophorum angustifolium* and *Campylium stellatum* as the most constant species. *Erica tetralix* may occur in association with *Schoenus* in other communities throughout the British Isles. These vary from blanket bog communities in West Ireland and West Scotland to more mesotrophic examples (New Forest valley bogs and East Anglican fens) to the 'tall heath' communities of the Cornish Serpentine (35) with basiphilous vegetation and the most eutrophic variants showing strong affinities with the Scottish communities mentioned above (Coombe & Frost 1956). Typical tall heath may be dominated by *Erica vagans, Molinia* and *Schoenus. Erica tetralix* may attain co-dominance whilst constant associates include *Genista anglica, Potentilla erecta, Sanguisorba officinalis, Succisa pratensis* and *Ulex gallii* in addition to various *Carex* spp.

IV. *Response to biotic factors.* May become dominant after fire, largely through regeneration from shoot bases. Fritsch & Salisbury (1915) considered that regeneration from buried stools was better in *Erica tetralix* than in either *E. cinerea* or *Calluna*, on account of the protection to the crown afforded by the accumulation of humus around the upright stems. In moist burnt areas, seedling regeneration may be relatively frequent

(cf. Hansen 1964b). In *Calluna–Molinia* communities repeated burning may lead to the extermination of *Erica tetralix* and a conversion to *Molinia* grassland, whilst a similar situation in montane bog leads to the exclusion of dwarf shrubs and dominance by *Eriophorum vaginatum* (Tansley, *Br. Isl.*; Ratcliffe 1959).

Erica tetralix is generally considered to be less palatable to grazing animals than *Calluna*; however the ability to regenerate from shoot bases gives the plant a reasonable resistance to grazing pressures. Under heavy grazing all dwarf shrubs may be exterminated and replaced by hemicryptophytes (Tansley, *Br. Isl.*; Fenton 1949; Ratcliffe 1959).

Erica tetralix is not particularly common in woodland communities; however, its spread has probably been favoured by the felling of wet pinewood and its conversion into wet heath or bog. On the other hand, draining and improvement of bogland, although it may lead to a temporary increase in the importance of *E. tetralix*, ultimately leads to the elimination of suitable habitats and a resulting decline in the representation of characteristic species (cf. Moore 1962b).

V. (*a*) *Gregariousness*. In wet habitats the growth is creeping, groups of vertical shoots arising at intervals from a mass of plagiotropic shoots ramifying through the uppermost horizons of the substratum. In such situations many apparent 'seedlings' are found to be attached to this rhizome system. In drier habitats, or where competition from *Calluna* is not marked (e.g. after burning), growth may be tussocky and occasionally the tussocks may be found to be discrete and not attached to any extensive underground system. In moister Calluneta, attentuated plants of *Erica tetralix* frequently form a discontinuous understorey.

(*b*) *Performance in various habitats*. Although a plant of wet habitats in the field, under experimental conditions seedlings show a much better growth on well-drained mineral soils than on waterlogged peats (A. C. Brynard; Bannister 1964b). After one season's growth, seedlings grown on a moist mineral soil were on average three times as tall and seven times as heavy (dry weight) as those from wet peats (Bannister 1963). More mature plants grown in wet heath show a greater annual increase (2·3 : 1) in the logarithm of shoot weight than those from valley bog (K. Loach). In most drier heath communities the competition from *Calluna* suppresses *Erica tetralix* although its maximum development is in the relatively dry Ericetum tetralicis cladinetosum of Scandinavia and North Germany (Böcher 1943; Horst 1964; Hegi *Fl.* **5**, 3) where *E. tetralix* is strongly dominant. In Britain *E. tetralix* may show a robust development on drier sites in the absence of *Calluna*, but becomes weak and attenuated when growing in competition with it. Maximum development is found in wet heaths and oligotrophic flushes, especially where *Calluna* is reduced in importance. Growth is weaker and straggling in most bogs.

(*c*) *Effects of frost, drought, etc*. Frost resistance varies through the year. In North Germany overwintering plants are capable of resisting temperatures of $-19.5°$ C (buds) to $-20°$ C (leaves), whilst young expanding shoots may have a resistance of $-3.5°$ C, although, in contrast to many species, frost resistance increases during the period of shoot expansion (Till 1956). In consequence it seems that winter frost damage is unlikely and the rapid hardening of young shoots would minimize the risk of damage by late spring frosts. Winter drought damage is also unlikely; plants in their natural habitat show no great increases in water deficits during the winter and plants under a snow cover appear to be capable of making up any water deficit (Bannister 1964c). Shoots show a maximum heat resistance (*c*. 51° C) in summer and winter, with minima (*c*. 44° C) in

spring and autumn (Lange 1961). Young leaves are generally less frost and heat resistant than older ones.

Plants show little reduction of transpiration in drying soils. Those on the driest soils show a sudden increase in water deficits followed by the shedding of leaves and death. Death appears to occur after a smaller increase in shoot water deficits and soil moisture tension than in *Calluna* and *Erica cinerea*. However, a protracted period of waterlogging can be endured with no damage to the plant and its water balance, in marked contrast to the effect of such conditions on *Calluna* and *Erica cinerea* (Bannister 1964c).

VI. (*a*) *Morphology*. Seedlings and young plants may have a taproot which may persist for several years. The prostrate rootstock is short and branched and the production of adventitious roots from stem bases makes a compact tussock. In wet conditions prostrate stems produce abundant adventitious roots. Older roots are black, much branched, often spreading laterally and strongly suberized and lignified. Younger roots are white and support a mycorrhiza in their cortical cells. There are no root hairs. A well-developed surface mat of fine roots is produced after 4 years (Heath & Luckwill 1938). Maximum rooting depths are from *c.* 16·5 cm (Fritsch & Salisbury 1915: 18 cm, Heath & Luckwill 1938) to *c.* 30 cm (Rutter 1955—including 17 cm of *Molinia* tussock). Absorption is virtually confined to the superficial layers (Boggie, Knight & Hunter 1958). Growth is monopodial in the young seedling; on moist, well-drained, soils branching may occur in the first season (Bannister 1964b). Branches arise from the base of the seedling and may overtop the original. Subsequent growth is sympodial. Lateral shoots are usually produced from near the base of each season's growth although branching may be more general on flowering shoots and lateral buds from beneath the terminal umbel may continue growth in the subsequent season. The termination of each season's growth is marked by the presence of crowded whorls of leaves of decreasing size out of the centre of which the new growth, with longer internodes, extends. Shoots also arise from the base of the plant and may either grow erect or become prostrate and root adventitiously.

The leaf anatomy has been described by Smith (1930), Glanville (1957) and Lambert (1955). Stomata are confined to the under surface and the pore is *c.* 3 μ long (Stocker 1923).

(*b*) *Mycorrhiza*. Ternetz (1907) isolated *Phoma radicis tetralicis* from roots of *Erica tetralix*. Freiseleben (1936) showed that a different, sterile, isolate from *Vaccinium myrtillus* (*Mycelium radicis myrtilli*) was capable of forming a synthetic mycorrhiza with many species, including *Erica tetralix*. However, Rayner (1927) considered that infection, both in *E. tetralix* and other ericaceous plants, was systemic and cyclic, reinfection from the seed being essential to the successful establishment of the plant. These observations are open to doubt and the situation has been critically reviewed by Harley (1959). The nitrogen fixation claimed by Ternetz (1907) has not been substantiated in *Calluna* plants (Bond & Scott 1955) and it is possible that the status of the mycorrhizal association might be similar to that in trees, the mycorrhiza being more important in the poorer soils (cf. Morrison 1957).

(*c*) *Perennation; reproduction*. Nanophanerophyte or woody chamaephyte; no bud scales. Stems of 19 years of age have been recorded (Rutter 1955; Hegi *Fl.* 5, 3). Robust plants may produce flowers in second or third season and thereafter annually; seed is set annually.

(*d*) *Chromosome number*. 2n = 24 (Hagerup 1928—Danish material).

(*e*) *Physiological data*. A comparatively small increase in shoot water deficit leads to stomatal closure (Bannister 1964a) but transpiration does not appear to be effectively

reduced in drying soils and the resultant reductions in water content may prove lethal (Bannister 1964d). Transpiration rates in the spring and autumn are of the order of 80 mg/g fresh weight/h. Transpiration may be relatively higher in the morning and evening than in the middle of the day whilst plant water deficits may increase rapidly after dawn and be partially made up later in the day. Water deficits in the field are potentially greatest in winter and spring but are never great on wet sites (Bannister 1964c). Stocker (1923) found that transpiration bore approximately the same relationship to evaporation throughout the year; maximum transpiration rates were of the order of 3·6 g/dm^2 of leaf surface and winter rates about 10% of this. Transpiration was high in relation to root development and leaf 'succulence' (water content/unit transpiring surface) was higher than that of *Calluna* (1·5 : 1). However, shoot 'succulence' (turgid water content/dry weight) is lower than that of *Calluna* (Bannister 1964c).

Bonnier (1910–34) gives the following analysis of plant ash: oxides of Si 48·4%; Ca 16·3%; K 16·7%; Na 3·2%; Fe 2·7%; Mg 4·9%/sulphates 3·5%; chlorates 2·0%. Tissue concentrations of nutrients (mg/g, dry weight) in plants from valley bog and wet heath (K. Loach) are: N 9·6–13·1; P 0·45–0·57; K 7·1–8·7; Ca 3·31–3·76; Mg 0·87–0·88.

VII. *Phenology.* Terminal shoots expand in April and May; lateral buds may develop concurrently or later in the season. Flowering commences in June and reaches a peak in July and August, somewhat before *Erica cinerea* and *Calluna*, and is largely completed by the end of September. Mature seed can be collected from September to October but is largely shed by December. Leaves usually shed during their second growing season, rarely persisting longer. Germination may take place in autumn shortly after the seed is shed and thereafter through the following growing season. Seedlings are not common in the field.

VIII. (a) *Floral biology.* Reproduction amphimictic; probably both self- and cross-pollination occur. Feebly protandrous? Abundant nectar; visited principally by Hymenoptera less frequently by Lepidoptera and Diptera [lists in Willis & Burkill (1895, 1903); Knuth, *Poll.* 3]. The efficacy of insect pollination has been questioned by Hagerup & Hagerup (1953), who considered that the awns on the anthers press against the corolla in such a way that the release of pressure when the flower opens causes pollen to be shed onto the stigma. They consider that thrips [*Taenothrips ericae* (Hal.) and *Frankliniella intonsa* (Tryb.)] act as pollinators in the absence of self-pollination. They also note that most bees have probosci which are too short to reach the nectar and certain bumblebees merely pierce the corolla in the vicinity of the nectaries and extract the nectar directly, thus avoiding any contact with the reproductive parts.

The following insect visitors have been noted in Britain (O. W. Richards). Hymenoptera. Apidae. *Halictus rubicundus* (Christ.), *Anthophora furcata* (Pz.), *Nomada flavopicta* (Kby.), *Bombus terrestris* (L.), *B. ruderarius* (Müll.), *B. lucorum* (L.), *B. jonellus* (Kby.), *B. hortorum* (L.), *B. sylvarum* (L.), *Psithyrus campestris* (Pz.). Diptera. Syrphidae. *Vollucella bombylans* (L.)

(b) *Hybrids.* The following have been reported: *E. ciliaris* × *tetralix* = *E.* × *watsonii* Benth., *E. mackaiana* × *tetralix* = *E.* × *praegeri* Ostenf., and *E. tetralix* × *vagans* = *E.* × *williamsii* Druce. A further hybrid *E.* × *stuartii* E. F. Linton has been found only once and is allegedly *E. mackaiana* × *mediterranea*, but on the basis of mophological characters and the absence of any overlap in flowering time of the putative parents, it has

been variously considered to be a mutant form of *E. mackaiana* (Smith 1930; Webb 1954), *E. praegeri* (Glanville 1957) or *E. tetralix* (Lambert 1965).

E. watsonii is intermediate in many respects between its parents and shows a range of forms. The most obvious characters of the hybrid are the combination of the less robust growth form of *E. tetralix* with the flowers and inflorescence of *E. ciliaris* (i.e. gibbous flowers and racemose inflorescence). Leaves are intermediate in shape, folding, ciliation and pubescence. Occurs with its parents from Dorset to south-west England. Hybrids have reduced pollen viability and seed set. Some hybrids appear to have colonized drier habitats (Gay 1957).

E. praegeri (Webb 1955; Glanville 1957; Lambert 1965) is intermediate in most characters between *E. mackaiana* and *E. tetralix*, but can be distinguished from *E. mackaiana* by the slight pubescence of ovary and sepals and the less robust appearance of the whole plant. The presence of half cells in the leaf epidermis would seem to be a useful anatomical feature which serves to distinguish *E. praegeri* from *E. tetralix* (Smith 1930; Glanville 1957; Lambert 1965). Glanville (1957) has demonstrated the fertilization of ovules of *E. tetralix* with pollen from *E. mackaiana*. Common with parents in the Irish stations of *E. mackaiana*. Pollen viability very low, seed set not observed.

E. williamsii has been observed in one Cornish locality and was first described as *E. vagans* × *cinerea* (Davey 1910). Druce (1911) suggested that *E. tetralix* was the more likely parent on account of the glandular hairs on the leaves of the hybrid. The plant has been further described by Turrill & Boodle (1911). Superficially the plant has the habit of *E. vagans* and the corolla and inflorescence of *E. tetralix*, flowers being produced in lateral (sometimes terminal) umbellate racemes. In leaf and ovary pubescence resembles *E. tetralix*. Anthers resemble those of *E. vagans* but are included in the corolla. A proportion of non-viable pollen is produced (Turrill & Boodle 1911).

Various authors (e.g. Hansen 1950; Gay 1957) have considered *E. mackaiana* to be a hybrid between *E. tetralix* and *E. ciliaris*, although their primary hybrid is *E. watsonii*. The arguments against species status for *E. mackaiana* are the reduced pollen viability, the absence of seed in Irish stations (a very few seeds found by Glanville (1957)), the paucity of correlated taxonomic characters (Gay 1957) and the difficulties of distinguishing *E. praegeri* from *E. tetralix* in biometric analyses of mixed populations (Gay 1957). *E. ciliaris* has been rediscovered in one Irish locality (Co. Galway) near to *E. mackaiana* (D. A. Webb).

On the other hand, Spanish material is fertile and seedlings are produced (Webb 1955), and reciprocal cross-pollination with Irish material is feasible (Glanville 1957). In Spanish localities with *E. mackaiana*, *E. ciliaris* and *E. tetralix* are separated altitudinally (Webb 1955) and opportunities for hybridization are correspondingly reduced. *E. mackaiana* is readily distinguished from *E. tetralix* and *E. praegeri* by biometric techniques (Gay 1957) and on a summation of characters *E. praegeri* is found to be intermediate between its putative parents (Glanville 1957; Lambert 1965). There are no irregularities in the formation of bivalents at meiosis, whereas these do occur in *E. praegeri* and *E. watsonii* (Glanville 1957). It has been suggested that the Irish populations may have been reduced to a self-sterile biotype (Webb 1965).

It would seem that controlled breeding experiments are needed to confirm that status of *E. mackaiana* and the putative parentage of the known hybrids of *E. tetralix*.

(c) *Seed production and dispersal.* Numerous (60–100) seeds are produced in each capsule, of which a large proportion (c. 60%) may fail to set. Capsules are retained on the plant after the seed is shed and seedlings are not usually found at any great distance

from the plants. Seedlings are most common in disturbed sites and are rare in closed vegetation.

(*d*) *Viability of seeds: germination.* In moist conditions seeds germinate readily with little pretreatment. However, seeds kept in dry storage since autumn 1961 showed substantial germination (61% in 7 weeks) in spring 1966.

Optimum germination at constant temperature is at 25° C but equally good germination is obtained when temperatures fluctuate from 2° C to 30° C (A. C. Brynard). Germination is much better in the light (A. C. Brynard, Hegi *Fl.* 5, 3); cold pre-treatment does not substitute the light requirement (A. C. Brynard) which may, however, be less marked in older seed (P. Bannister). 70–80% germination may be obtained in 3 months
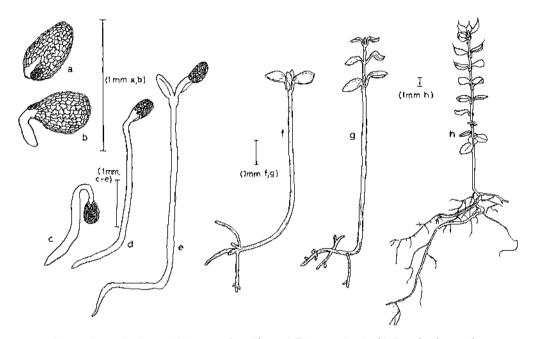

Fig. 4. Stages in the establishment of seedlings of *Erica tetralix.* (a, b) Germinating seeds, (c–e) 1–2 weeks after germination, (f) 4–8 weeks, (g) 8–12 weeks, (h) established seedling taken from the field in September.

on filter paper without any pretreatment, but small increases in hydrostatic tension may decrease germination (Bannister 1963). On natural soils in pots (in an unheated glasshouse) germination varied between 50–60% on humus and mineral soils and 80% on peats (Bannister 1964b). Germination may be poor on very acid peats and calcareous soils (A. C. Brynard). Seeds germinate successfully when covered with water (A. C. Brynard; Bannister 1963) and can survive periods of at least 3 months' waterlogging with no diminution of germination (Bannister 1963).

Seedling establishment (in terms of both height and dry matter) is much better on well-drained soils than on waterlogged soils, and on mineral soils rather than peats (Bannister 1964b). Dry matter production increases with increasing height above the water table on both mineral soils and peats (A. C. Brynard).

(*e*) *Seedling morphology* (Fig. 4). Germination epigeal, the radicle emerging from the narrow (attachment) part of the seed some 2 weeks after sowing. Cotyledonary expansion

takes place within the next week, the testa often remaining attached to one of the cotyledons. Seedlings with three cotyledons are not uncommon. Subsequent leaf expansion depends on environmental conditions and is much more rapid on well-drained mineral soils than on waterlogged peats. In favourable conditions the seedling is branched by the end of the first year (see VI (*a*)).

(*f*) *Effective reproduction.* In wet habitats vegetative spread by the adventitious rooting of prostrate branches is the most common mode of reproduction. Reproduction by seed is common only in disturbed habitats.

IX. (*a*) *Animal feeders and parasites.* Provides some food for sheep, cattle and grouse but generally considered to be inferior to *Calluna*. Insects particularly associated with *Erica tetralix* include the thrips *Frankliniella intonsa* (Tryb.) which breeds in the flowers: the snowy fly, *Tetralicia ericae* Harr. (mostly in north-east England); the scale insect *Eriococcus devoniensis* (Green) causing a gall with a characteristic twist to the stems (widespread in Britain) and *Myriocomyia mediterranea* (F. Loew) which caused a small gall oppressing the terminal leaves (O. W. Richards). The other insects listed below may be associated with other *Erica* spp. and *Calluna* as well as *Erica tetralix* (O. W. Richards).

THYSANOPTERA
Thripidae: *Taenothrips ericae* (Hal.), *Thrips debilis* Bagn.

HETEROPTERA
Lygaeidae: *Kleidocerys truncatalus* (Walk.) ssp. *ericae* (Horv.), *Macroderma micropterum* (Curtis), *Ischnocoris angustulus* (Boh.), *Scolopostethus decoratus* (Hahn), (last three feeding on seeds, often on the ground).

HOMOPTERA
Ulopidae: *Ulopa reticulata* (Fab.).
Psyllidae: *Strophingia ericae* (Curt.).
Coccidae: *Diaspidiotus bavaricus* Lindinger.

LEPIDOPTERA
Noctuidae: *Graphiphora agathina* (Dup.), *Lycophotia porphyrea* (Schiff.), *Anarta myrtilli* (L.).
Geometridae: *Eupithecia goosensiata* Mabille, *E. nanata* (Hb.), *Emeturga atomaria* (L.), *Pachycnemia hippocastanaia* (Hb) (South England), *Dyscia fagaria* (Thunb.) (local).
Phyciditae: *Salebria fusca* (Haw.).
Tortricidae: *Acleris hyemana* (Haw.) [*A. mixtana* (Hb.)], *Ancylis unguicella* (L.), *A. uncana* (Hb.) (also on *Betula*).
Gelechiidae: *Gelichia betulae* (Haw.), *Xenolechia aethiops* (Westw.).
Oecophoridae: *Pleurota bicostella* (Clerck).
Scythridae: *Scythris variella* (Steph.).
Coleophoridae: *Coleophora pyrrhulipennella* Zell., *C. juncicolella* Staint.

COLEOPTERA
Curculionidae: *Strophosomus lateralis* (Payk.), *Micrelus ericae* (Gyll.).

DIPTERA
Cecidomyiidae: *Wachtiella ericina* (F. Loew) (terminal leaves forming a gall).

(*b*) *Plant parasites. Cuscuta epithymum* (Fritsch & Salisbury 1915). Fungal parasites mentioned under (IX (*c*)) below.

(*c*) *Diseases.* Most diseases have been recorded from cultivated species and there are few specific references to *Erica tetralix. Marasmius androsaceus* Fr. may attack *E.*

tetralix in the field (MacDonald 1949). In cultivation foot-rots due to *Corticium solani* (Prill. & Delacr) Bourd & Galz. (Foister 1961) and *Phytophthora cactorum* (Leb. & Cohn) Schroet with *P. cinnamomi* (Moore 1959) have been reported. Moore (1959) also lists *Dematium pullulans* de Bary (sooty mould on *Erica lusitanica*), *Oidium ericinum* Erikss. (powdery mildew) and *Phyllosticta* sp. (leaf browning).

X. *History*. Found in late-glacial (zones I and III) and post-glacial (V–VII) deposits (Godw., *Hist*.). Presumably increased in extent in the British Isles both as a result of forest clearance by man and the climatic deterioration associated with the Sub-Atlantic period when bog replaced forest, especially in the west. Suitable habitats, too wet for tree growth, have probably existed since late-glacial times. More recently the improvement of peatlands, particularly in lowland areas, must have lead to a decrease in the representation of *Erica tetralix*.

Historical uses of the plant have been in the production of charcoal, as a substitute for hops in beer and for oak in tanning and in the manufacture of brooms (Bonnier 1910–34). The first written record in Britain (1570) is by Lobel '*Vulgatior Ericae folio Myricae* . . . ad Bristoiam' (Druce, *Comit. Fl.*).

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