

Cypripedium calceolus L.

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A perennial herb with horizontal rhizome (diameter about 6 mm) up to 10 cm underground. Roots long and fleshy, diameter up to 2 mm. Stem 20–60(70) cm, glandular-pubescent with brown basal sheaths; leaves 3–5, elliptical to ovate-oblong, acute to acuminate, sparsely pubescent (oval lanceolate, somewhat pleated, large), (7)11–17(22) cm long, (3)5.5–8(10) cm wide, veins obvious, bracts leaf-like, exceeding flowers; flowers 1–2(3) large; perianth segments purple-brown; dorsal outer tepal ('sepal') lanceolate, suberect, 3.5–6 cm long and 1.5–2.5 cm wide; lateral 'sepals' joined, hanging below labellum 3.5–5.5 cm, free tips up to 5 mm; inner tepals ('petals') 4–7 cm long and 0.5–1 cm wide, horizontal, twisted; labellum yellow, shoe-shaped (length 3–4 cm, width 2–3 cm, depth 1.5–2 cm), reflexed, covered with viscous hairs inside, not spurred; staminode petaloid shield-shaped, white with red spots, 1–1.2 cm long, 0.7–0.9 cm wide; ovary elongate, somewhat curved, pubescent (glandular hairs), not twisted, pedicellate. Two fertile anthers, one on each side of style; stigma and staminode forming a flat appendage on the front of the column. Capsule up to 3 cm long and about 0.9 cm in diameter, containing 6000–17 000 seeds; seeds oblong about 1 mm long with a mass of a few micrograms (seed volume 0.02 mm³).

From continental Europe, the all-yellow flowered var. *flavum* Rion has been recorded (Davies *et al.* 1984).

This exceedingly rare orchid was formerly more widespread in northern England in limestone woodland; it is more plentiful in wooded sites in northern Europe, but everywhere has suffered from collecting.

I. Geographical and altitudinal distribution

Cypripedium calceolus is mainly a boreal species. Formerly it grew in Britain in the three northern counties of Yorkshire, Durham and Westmorland (Summerhayes 1951), but nowadays is definitely native at only a single site on Carboniferous limestone in Yorkshire (Wood *et al.* 1984) (Fig. 1),

although other doubtfully native sites exist within the same counties and north Lancashire. The distribution of *C. calceolus* ranges from Great Britain and Scandinavia across northern and central Europe to north-east Spain and northern Italy, and from western Europe through southern Siberia to Rebus Island (Vergl. Chor.; Borodin *et al.* 1984; Hultén & Fries 1986; Cribb 1997) (Fig. 2). A similar decline to that in Britain has taken place in most of Europe (Wood *et al.* 1984; Ramsay & Stewart 1998).

The species is found close to sea level up to an altitude of 2700 m in Switzerland (Davies *et al.* 1984). In Britain the range of the altitude was 150–260 m (Alt. range Br. Pl.).

II. Habitat

(a) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Cypripedium calceolus occurs in shady deciduous and mixed woodland (rarely in full sunlight at higher altitudes) or, less frequently, on stone-strewn slopes, predominantly on calcareous soils (Füller 1981; Davies *et al.* 1984; Wood *et al.* 1984; Lid 1987; Delforge 1995). It can withstand cold winters and in northern parts of Eurasia it tends to grow in calcium-rich spring fens and on marshy grasslands (Ivanter & Kuznetsov 1995). The plant is favoured by suboceanic to subcontinental climates and is rare in regions with Atlantic and Mediterranean climate (Vergl. Chor.; Heinrich & Lorenz 1996; Terschuren 1998).

(b) SUBSTRATUM

Cypripedium calceolus is favoured by moderately moist nutrient-poor to moderately nutrient-rich, particularly nitrogen-poor base-rich neutral to moderately acid soils. In central Europe the pH in its habitats is higher than 7.1 (Procházka & Velisek 1983; Möller 1985, etc.). In habitats of eastern Europe, the soil pH (KCl) range is 5.4–7.7 (Moisejeva 1970; Varlygina & Matsenko 1986; Kull 1997). Closely related taxa from America are known to grow more vigorously at higher pH values (Stuckey 1967).

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*Abbreviated references are used for standard works, see *Journal of Ecology* (1975), 63, 335–344. Nomenclature of vascular plants follows *Flora Europaea*.

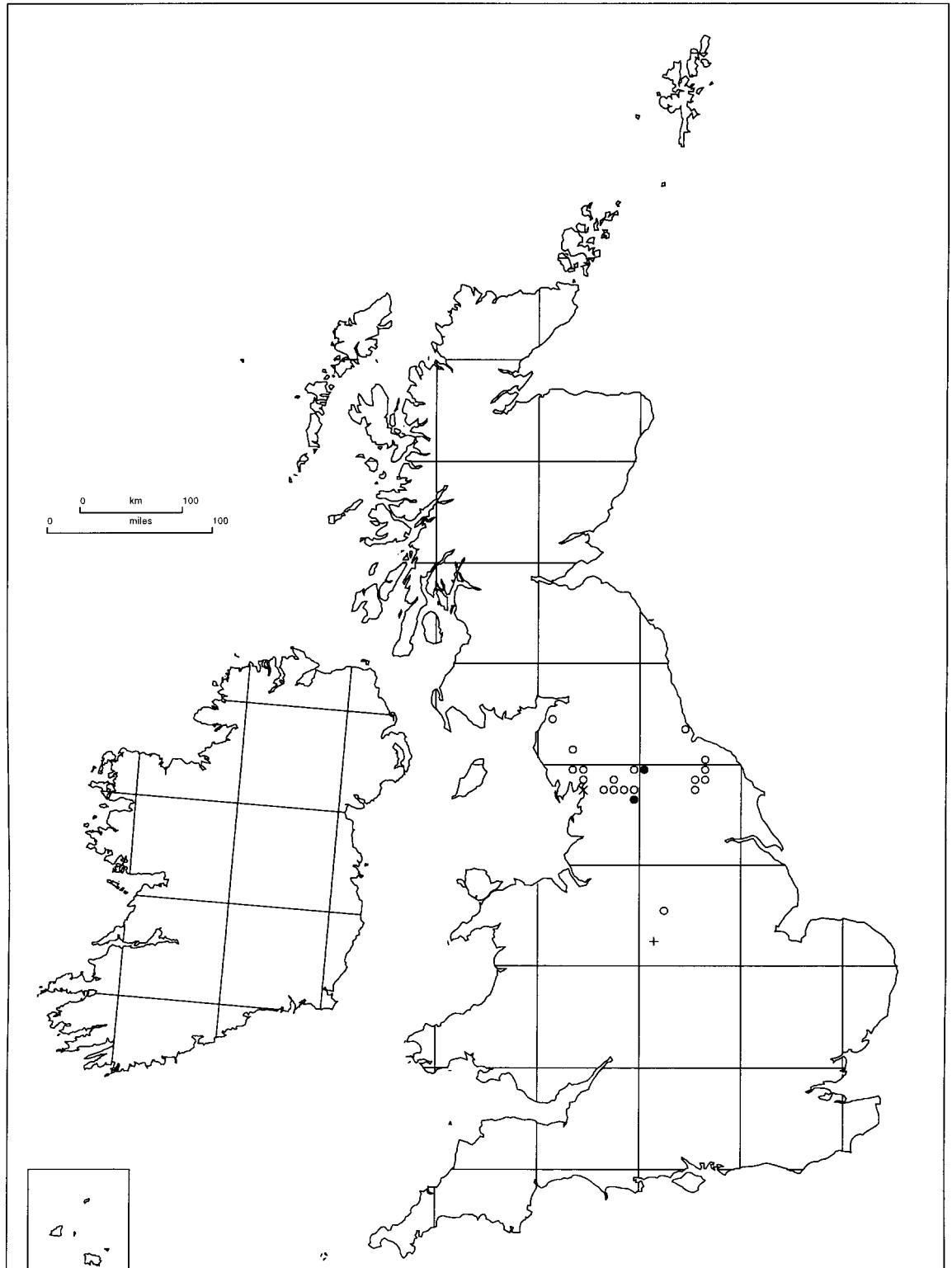


Fig. 1 The distribution of *Cypripedium calceolus* L. in the British Isles. (○) Pre-1950; (●) 1950 onwards; (+) introduced pre-1950; (x) introduced 1950 onwards. Mapped by Mrs J. M. Croft, Biological Records Centre, Institute of Terrestrial Ecology.

In a soil analysis (horticultural) carried out by the Agricultural Development and Advisory Service in 1994 (L. Farrell & P. Corkhill, personal communication) from the remaining site of the plant in

England, the pH was 7.9 and mean values (mg l^{-1}) of the major elements were: nitrate-N 4, P 6, K 89 and Mg 63; conductivity was $2050 \mu\text{S cm}^{-1}$. Calcium carbonate ranged up to 33% and particle size was

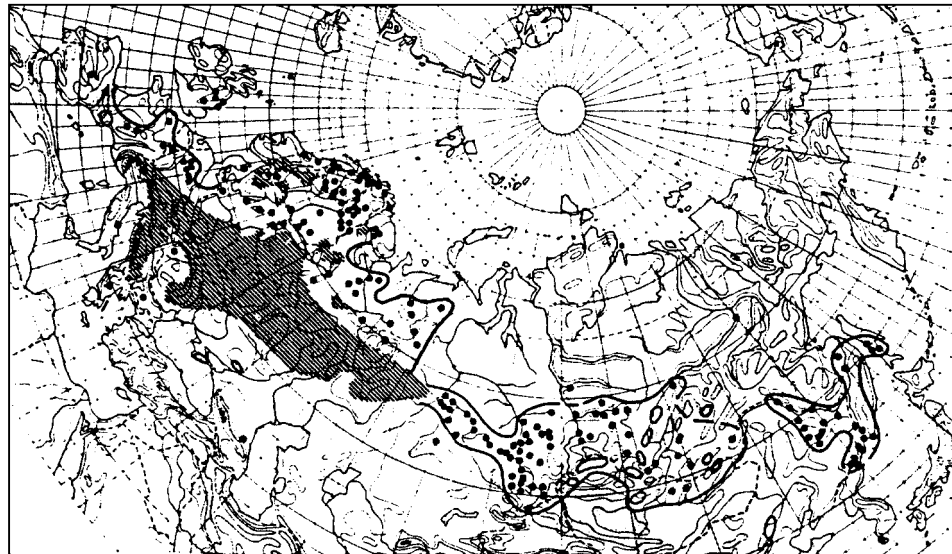


Fig. 2 The distribution of *Cyripedium calceolus* L. in Europe and Asia (Hultén & Fries 1986).

predominately 2000–200 µm. Data on comparative soil analysis from Germany (9–13) and Estonia (1–8) are given in Table 1.

III. Communities

In Britain, *C. calceolus* once formed part of the relatively open *Quercus*, *Fraxinus* and *Corylus* woodland or scrubland flora of limestone scree slopes in northern England (Summerhayes 1951; Wood *et al.* 1984). The only surviving native clump in the wild in Britain grows in a small shady clearing with scrubby tree growth at a woodland edge on freely draining black proto-rendzina soil derived from limestone with little organic material and abundant limestone fragments (P. Corkhill, personal communication). *Sesleria caerulea* is prominent in the sward, and the

wide range of associated species includes *Carex panicea*, *Epipactis atrorubens*, *Galium sternerii*, *Helianthemum nummularium*, *Leontodon hispidus*, *Linum catharticum*, *Polygala amarella*, *Primula farinosa*, *Sanguisorba minor* and *Succisa pratensis* (Farrell 1999). In the National Vegetation Classification, Rodwell (1992) describes this community as CG9c *Sesleria albicans*–*Galium verum* grassland, *Carex pulicaris*–*C. panicea* subcommunity.

In Europe and Asia, it is found in a variety of habitats including both deciduous and coniferous woodland, open scrub and alpine meadows. However, the majority of its habitats are woodland, described according to the Council of Europe Palearctic typology as neutrophile (Terschuren 1998), limestone and southern beech forests, oak–hornbeam forests, ravine and riverine forests, ther-

Table 1 Soil chemical analyses for selected localities in Estonia (localities 1–8) and Germany (localities 9–13) (at a depth of 0–10 cm) (German data calculated from Möller 1985)

| Locality | mg kg ⁻¹ dry soil | | | | | | | | | |
|-----------|------------------------------|-----------|-----|------|--------|-----|--------|-----|-------|-------|
| | pH | Nitrate-N | P | K | Ca | Mg | Fe | B | Cu | Mn |
| Tooma | 5.4 | 55.3 | 5.3 | 71.0 | 10 000 | 574 | 750 | 3.7 | Trace | 34.2 |
| Õisu | 6.2 | 11.3 | 4.8 | 36.8 | 6500 | 400 | 17 800 | 8.2 | Trace | 224.2 |
| Muhu I | 7.1 | 14.8 | 4.6 | 100 | 31 500 | 730 | 1060 | 2.1 | 2.8 | 95.4 |
| Muhu II | 7.0 | 20.8 | 5.2 | 60.4 | 23 500 | 990 | 1100 | 2.7 | 4.2 | 75.0 |
| Ussisoo | 7.0 | 13.8 | 4.6 | 50 | 3500 | 90 | 1060 | 1.1 | Trace | 132.4 |
| Hiiumaa | 7.4 | 5.9 | 4.9 | 50 | 14 600 | 60 | 1289 | 1.3 | 1.0 | 88.2 |
| Puhtu | 7.2 | 9 | 10 | 30 | 8500 | 780 | 1260 | 3.2 | 6 | 9.5 |
| Laelatu | 7.1 | 6 | 10 | 60 | 5000 | 970 | 2400 | 3.1 | 4 | 130 |
| Thüringen | 7.1 | | 65 | 233 | 4850 | 100 | 300 | 26 | 143 | 130 |
| Solling | 7.3 | | 39 | 75 | 9800 | 60 | 490 | 9.5 | 59 | 160 |
| Diemeltal | 7.4 | | 271 | 150 | 3000 | 120 | 460 | 8.5 | 14 | 60 |
| Alfeld | 7.1 | | 35 | 242 | 3350 | 110 | 490 | 28 | 45 | 320 |
| Jena | 7.1 | | 35 | 200 | 3500 | 90 | 190 | 5 | 18 | 48 |

mophilous forests, mesophile birch and alder woods, fir forests, spruce, larch and arolla, mountain pine forests, mire conifer woods, mountain dwarf juniper scrub, calciphile thickets and thermophile forest fringes. Besides woodland, tall herb and herb-rich taiga, subatlantic *Sesleria* semi-dry calcareous grassland and terrestrialization zones of rich fens are also mentioned (Terschuren 1998). In Sweden and Estonia, wooded meadows are often rich in *C. calceolus*.

In France, it occurs in communities of Gymnocarpio–Seslerietum, *Viola rupestris*–Seslerietum, *Geranium sanguineum*–*Gentiana–Daphnetum laserpitiosum*, *Carici umbrosae*–*Brachypodietum*, *Berberidion*, *Sorbo–Franguletum*, *Carici albae–Fagetum*, *Carici montanae–Quercetum*, *Dentario–Fagetum* and *Aceri–Fraxinetum* (Didier & Royer 1994; Heinrich & Lorenz 1996).

In Poland, the species occurs in *Galio–Carpinetum lathyretosum verni*, *Tilio–Carpinetum melittetosum*, *Carici–Fagetum*, *Mercuriali–Fagetum*, and *Cephalanthero rubrae–Fagetum* communities (Wika & Bernacki 1984). In southern taiga, associations with *Juniperus–Cypripedium–Fragaria*, *Betula–Cypripedium–Convallaria*, *Betula–Pinus–Convallaria*, *Betula–Pteridium–Convallaria* and *Betula–Centaurea jacea–Trifolium montanum* are referred to as habitats of *C. calceolus*. In Estonia, the species occurs in alvar (habitat with thin soil layer on limestone) forests and shrublands, in mesic boreal forests (*Oxalis* site type), in fresh boreo-nemoral forests (*Hepatica* site type), in drained peatland forests (*Oxalis* site type) and in wooded meadows (Kull 1991, 1995). Vascular plant species growing often with *C. calceolus* are *Aegopodium podagraria*, *Anemone nemorosa*, *Convallaria majalis*, *Fragaria vesca*, *Hepatica nobilis*, *Paris quadrifolia* and *Rubus saxatilis*.

In northern conditions in Karelia, sometimes the species may occur in communities with *Pinus sylvestris*, *Phragmites australis* and *Sphagnum warnstorffii* (Dyachkova *et al.* 1997).

IV. Response to biotic factors

Cypripedium calceolus suffers severely from competition with tall plants (herbs, grasses) favoured by increased light conditions, e.g. after clear-cutting, the result of which is population decline (Sjöberg & Ericson 1992).

(a) LIGHT

As fires in low forest layers are known to be favourable for *C. calceolus*, it means that the species is sensitive to the presence of a dense bush layer. Increasing shade is a limiting factor for *C. calceolus*. Dementjeva (1985) considers 1/14–1/20 of full light optimal in the southern taiga zone and demonstrates that the lighter the locality the shorter the ramets and leaves are. The same has been shown in Poland, and also that the proportion of generative ramets is larger in light conditions (Wika & Bernacki 1984; Brzosko & Werpachowski 1991). However, in Estonian populations (Table 2) height of flowering ramets is correlated with the light conditions but not the percentage of flowering ramets. In shady localities small clones dominate and it is more probable that some of them do not have above-ground shoots in some years, the buds staying in dormant phase underground (clone dormancy exists) (Kull 1995).

V. Response to environment

(a) GREGARIOUSNESS

Being a rhizomatous plant, *C. calceolus* grows in smaller or larger patches that may belong to one or several clones. Clones identified by isoenzyme analysis are seldom larger than 70 cm in diameter. Clones that have reached a diameter of 20–40 cm virtually cease to increase in diameter, which can be explained by an increase in the death rate of rhizome branches in bigger (denser) clones (Kull 1997).

Table 2 Effect of light conditions on ramet height and type

| Population | Light penetration coefficient* | Height of flowering ramets (cm ± SD) | Percentage of flowering ramets among adult ramets (% ± SD) | Percentage of juveniles (% ± SD) |
|------------|--------------------------------|--------------------------------------|--|----------------------------------|
| Hiiumaa | 0.46 | 26.7 ± 5.0 | 34.7 ± 7.1 | 49.7 ± 8.7 |
| Laelatu | 0.41 | 24.3 ± 1.0 | 34.2 ± 18.6 | 8.7 ± 3.9 |
| Õisu | 0.30 | 39.8 ± 3.3 | 52.0 ± 10.2 | 43.1 ± 11.5 |
| Muhu II | 0.24 | 39.1 ± 1.8 | 78.7 ± 3.6 | 7.6 ± 3.5 |
| Ussisoo | 0.21 | 35.2 ± 3.7 | 62.2 ± 10.6 | 2.4 ± 1.4 |
| Muhu I | 0.18 | 37.9 ± 3.2 | 49.4 ± 13.2 | 8.4 ± 4.4 |
| Tooma | 0.15† | 39.1 ± 4.0 | 40.7 ± 14.6 | 2.2 ± 1.9 |
| Puhtu | 0.13† | 41.3 ± 5.6 | 32.8 ± 12.9 | 4.6 ± 3.8 |

*The quantity of light reaching the herb layer relative to the fully open site.

†Estimation

Most populations consist of a few plants; only in a few localities can thousands of specimens be found.

(b) PERFORMANCE IN VARIOUS HABITATS

Counts have been carried out on several populations over different time periods. Counts over a few years have often indicated stability (Salmia 1988; Korczynski & Spiewakowski 1991; Blinowa 1993).

Plants at a single station and at all stations within a limited geographical area behaved similarly in any one year (Curtis 1954). Long-term counts made in Denmark (Høst 1989; Wind & Ballegaard 1996) and Germany (Drüke 1980) showed a drastic population decrease, whereas 15-year monitoring of eight populations in Estonia showed a certain increase (Kull 1997) (Fig. 3). Since being protected, the surviving English plant has spread and more flowers have

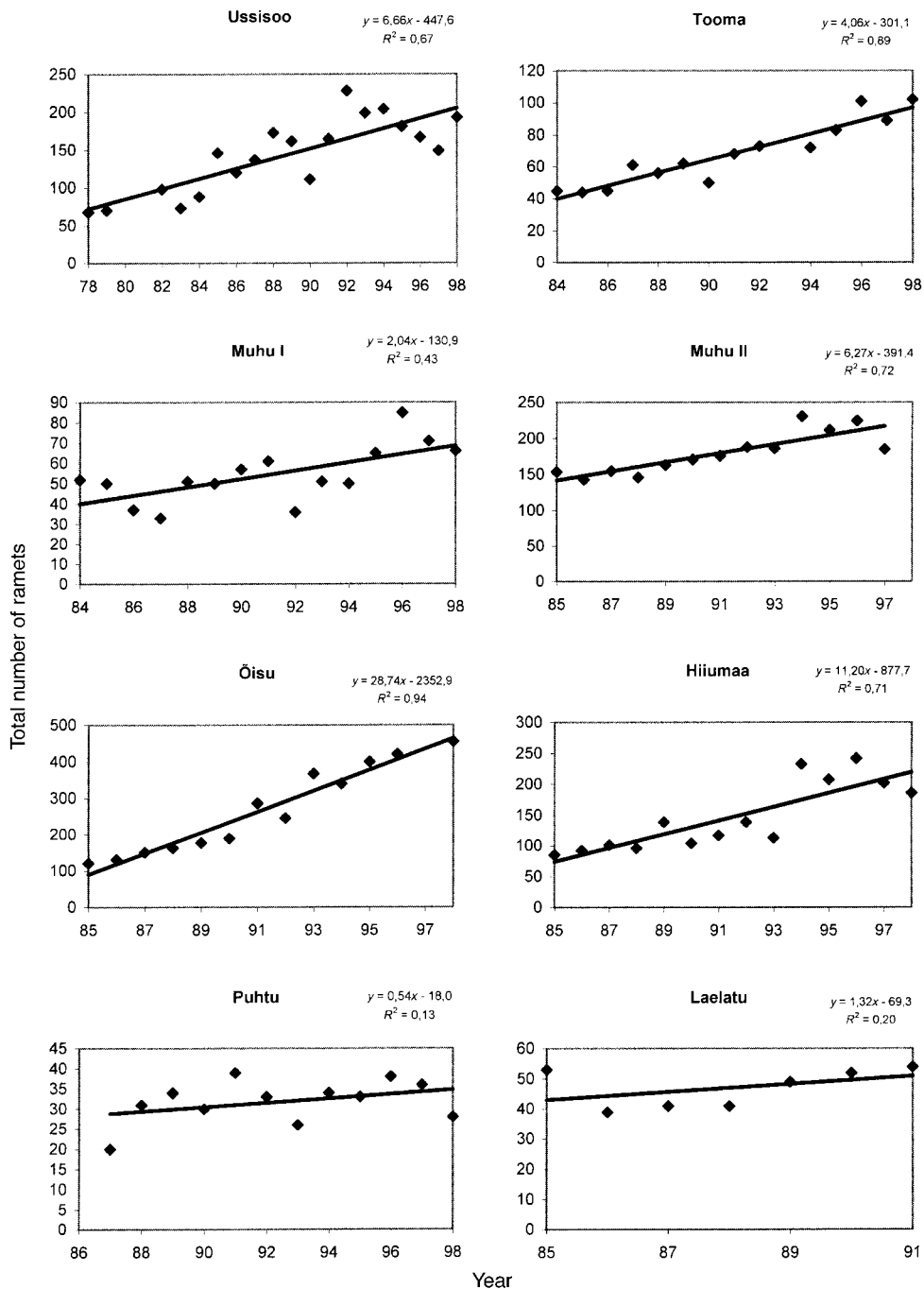


Fig. 3 Dynamics of the total number of ramets of *C. calceolus* in permanent plots of eight populations in Estonia. The horizontal axis shows the years and the vertical axis the total number of ramets. The permanent plot sizes were: Ussisoo, 126 m²; Tooma, 600 m²; Muhu I, 30 m²; Muhu II, 72 m²; Õisu, 60 m²; Hiumaa, 2 m²; Puhtu, 65 m²; Laelatu, 3 m².

been produced, with new plants arising nearby (L. Farrell, personal communication).

(c) EFFECT OF FROST, DROUGHT, ETC

Late frosts may affect flowers, leaving brown spots on the labellum (Eberle 1973). Severe frosts in June reduce shoot survival and flowering in clear-cut areas at high latitudes (Sjöberg & Ericson 1992), but no frost damage has been observed in Britain. *Cypripedium calceolus* is sensitive to drought. In particular, young seedlings require constant moderate moisture (Corkhill 1996).

VI. Structure and physiology

(a) MORPHOLOGY

The creeping horizontal rhizome, with a diameter of 0.4–0.9 cm, is situated at a depth of up to 10 cm. Every year, the rhizome usually produces two apical buds. From the larger bud the following year's shoot develops, forming the new increment (average length 1 cm) of the sympodial rhizome. The position of the larger bud (left or right) alternates each year, resulting in the characteristic zigzag growth pattern

of the rhizome (Kull & Kull 1991). The smaller, or dormant, bud may start growing in the year of formation or in the following year (Fig. 4). However, in some cases the smaller bud may start growing in the first year and in other cases several years later, but usually it will stay dormant until it dies (e.g. after 15–20 years). The angle between subsequent annual increments formed from the bigger buds is about 130°. In the far north the development can be slower and it may take more than 1 year for a bud to form a new shoot above ground (Blinowa 1998). Roots with a diameter of 1–2 mm grow without branching for several years and achieve a length of 50 cm (Kull 1987a). Root hairs are usually present but seldom abundant (Rosso 1966). On the lower surface of a leaf the mean number of stomata is 29 mm⁻²; on the upper surface they are mostly absent.

(b) MYCORRHIZA

Type: Orchidaceous. During the first growing season, seedlings appear to be wholly dependent on the symbiotic fungus. The extent of mycotrophy decreases as plants produce more and larger leaves.

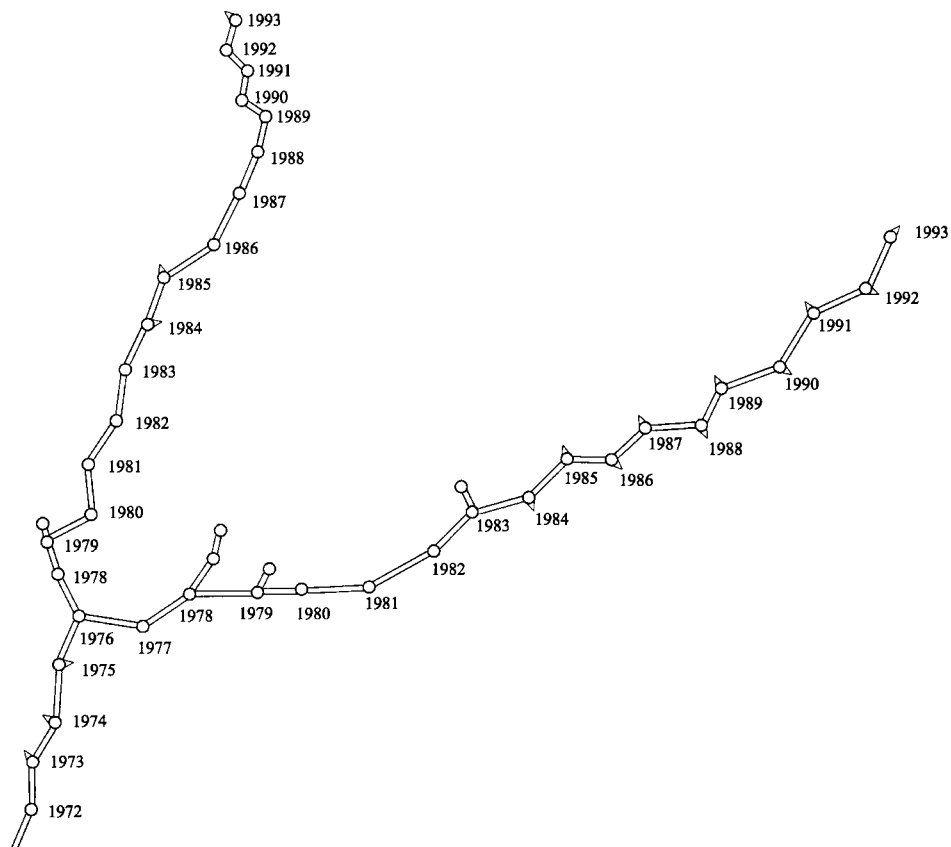


Fig. 4 A schematic view of the *C. calceolus* rhizome. Circles indicate shoot scars, triangles denote dormant buds and numbers show years.

The rhizome is uninfected but roots become re-infected from the soil. Therefore isolates from mature plants could differ entirely from those of the seedling fungus (Rasmussen 1995). The percentage of cells infected by hyphae increased from 12.4% to 24.4% when soil pH decreased from 6.0 to 5.1 (Sizova & Vahramejeva 1983). As in other orchids, the surface area of *Cypripedium* roots, which is in contact with the soil, appears to be smaller than in many other herbs. It is not clear how the orchid compensates for this, unless fungal connections are more persistent and prevalent than they appear to be (Stoutamire 1990).

(c) PERENNATION: REPRODUCTION

Cypripedium calceolus is a geophyte. The rhizome with buds perennates through the winter. Vegetative reproduction occurs by rhizome ramification. Mean temporal distance between two branchings (on a rhizome branch) is 4.9 years. Webster (1886) suggested that the species reproduces vegetatively because its pollination system is too complicated. Indeed, in many populations vegetative reproduction plays the main role. The ratio of sexual reproduction to clonal growth in recruitment in such populations is 1 : 200. However, in populations with vigorous sexual reproduction, where juveniles make up nearly half of the total ramet number, vegetative reproduction is less important.

Cypripedium calceolus is a long-lived species. Many plants are more than 30 years old, and some are more than 100 years old (Kull 1988). The vegetative period before flowering lasts at least 6–10 years (Fast 1985; Rasmussen 1995). A life cycle scheme is depicted in Fig. 5.

(d) CHROMOSOMES

$2n = 20, 22$ (Delforge 1995; Cribb 1997).

(e) PHYSIOLOGICAL DATA

No information.

(f) BIOCHEMICAL DATA

Glandular hairs of the American relatives of *C. calceolus* have been noted to cause skin irritation attributed to the action of the allergen cypripedin. The irritant action of the plant on the skin increased with the development of the plant, and a maximum effect was reached during seed capsule formation (MacDougal 1895).

Cypripedin (2,8-dimethoxy-7-hydroxy-1,4-phenanthrene quinone), possibly derived from the phytoalexin orchinol, and obtained from the leaves of *C.*

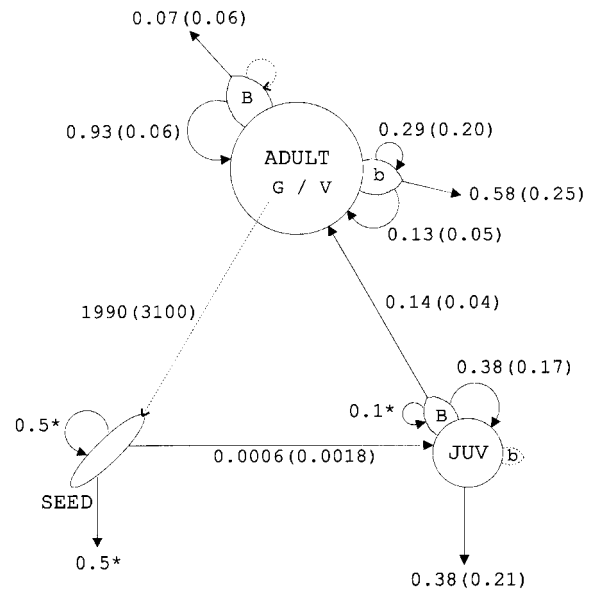


Fig. 5 Life cycle scheme of *C. calceolus*, based on ramet changes. Numerical values reveal the proportion of changes occurring per ramet per year (with SD in parentheses). Open-ended arrows denote death. ADULT ramet produces annually a larger bud (B) that may die before the following year, or produce another ramet (exceptionally, may stay dormant), and a smaller bud (b) that may die, produce a ramet or remain a bud. Juveniles (JUV, defined as ramets with one or two small leaves and a thin stalk) may also produce a smaller bud (b), but this does not develop further. Larger buds (B) in juveniles may produce a juvenile or an adult ramet the following year. They may also remain dormant, but without exact data we can only estimate this parameter. A SEED may germinate, die or remain as a seed (values of the two last parameters are also estimations). In adult ramets no distinction has been made between vegetative (V) and generative (G) ramets; the number of seeds is calculated per generative ramet.

calceolus, does not appear to have anti-fungal activity (Schmalle & Hausen 1979; Arditti 1992).

The flowers contain the anthocyanin pigment chrysanthemine, cyanidin-3-monoglucoside (Arditti 1992).

(g) GENETICAL DATA

Estonian populations of *C. calceolus* are characterized by high levels of heterozygosity (0.40–0.53) in three loci of aspartate aminotransferase. Geographically closer populations do not show a higher genetic similarity than more distant populations. Equally high levels of genetic variability in isolated populations of a species of restricted distribution can be explained by wider occurrence in previous times (Kull 1988; Kull & Paaver 1997).

VII. Phenology

Dependent on the latitude and altitude, growth in spring begins in March or April, and in plants close

to the northern limit, as late as June (Vorobjeva & Moskvitcheva 1987). Flower-producing shoots appear earlier than vegetative shoots. Flowering begins in May or June, and in some places in the far north even in July (Eberle 1973; Vorobjeva & Moskvitcheva 1987). Duration of flowering is 2–3 weeks (Eberle 1973). A single flower may persist 11–17 days, but withers on the sixth day after the pollen has reached the stigma (Savina 1964). The sum of positive (above +5°C) daily temperatures needed for flowering in north-east Europe (latitude 58°26'; longitude 26°43') is 178 day-degrees as a mean of 4 years (Kull 1987b). Shoots start to turn yellow at the end of August. Fruits ripen in September. By this time non-fruiting shoots have withered but others remain in a dried state until the following summer. Capsules split open and liberate seeds in September–October.

A new rhizome segment starts to grow at the end of flowering. Above-ground parts of juveniles persist for considerably shorter periods than adult ramets. They appear shortly before flowering of adult ramets and wither before others.

VIII. Floral and seed characters

(a) FLORAL BIOLOGY

Trap flowers of *C. calceolus* lack nectar, and pollinators are deceived as no reward is available. Crimson spotted floral structures are false nectar guides that are important for attracting and trapping bees. Floral fragrance is dominated by acetates. Chemical correspondence with pollinators' pheromone secretions suggests that fragrance might interfere with pheromone-controlled alighting reactions (Nilsson 1979). The pollen grains are in sulcate monads, more or less smooth-surfaced, and covered by a layer not resistant to acetolysis (Burns-Balogh & Hesse 1988). The mean size of a pollen grain is $17 \times 28 \mu\text{m}$.

Pollinating bees enter the opening in front of the labellum and are prevented from leaving through the same opening by the downward projecting rim of the entrance. The escape route through the narrow base of the labellum forces the insect to crawl below and touch the stigma. Escape is possible through openings on either side of the column, and to pass one of these the insect has to force its way under one of the anthers carrying along with it some pollen mass. Dimensions of the labellum entrance, the escape route under the stigma, and the final opening under the anther are selective as to visitor size (Stoutamire 1967). Medium-sized female solitary bees of the genera *Andrena*, *Lasioglossum* and *Halictus* are the most frequent pollinators as far as Sweden is concerned (Nilsson 1979). In Czechoslovakia mainly large *Andrena* spp., e.g. *A. tibialis* (Kirby) and *A. nigroaenea* (Kirby), pollinate

C. calceolus (Daumann 1968). In England *A. scotica* Perkins and *A. haemorrhoea* Fabricius have been recorded as pollinators (P. Corkhill, personal communication). *Apis mellifera* L. too can act as a pollinator.

The flower age at pollination has an effect on seed characteristics; the proportion of seeds with full embryos increases with increasing flower age at pollination (Light & MacConaill 1998). Fertilization occurs about 20 days after pollination and embryogenesis lasts up to 50 days (Wagner & Hansel 1994).

Seeds of *C. calceolus* are some of the biggest among temperate orchids (about $1.2 \times 0.3 \text{ mm}$) (Fig. 6a). The seed has a firm brown fusiform testa, the outer surface of which is not easily wettable. The cells of a spherical embryo, length of 0.2 mm (Eberle 1973), are isodiametric and little differentiated (Cribb 1997). The shape, size and relatively large air volume in the testa of seeds provide an explanation for their buoyancy in the atmosphere, which is an adaptation for dispersal by wind (Arditti *et al.* 1979).

(b) HYBRIDS

Cypripedium × *ventricosum* Sw., a natural hybrid of *C. calceolus* and *C. macranthos*, was first described from cultivated conditions in Switzerland in 1908. Later it was reported from Siberia, Manchuria and

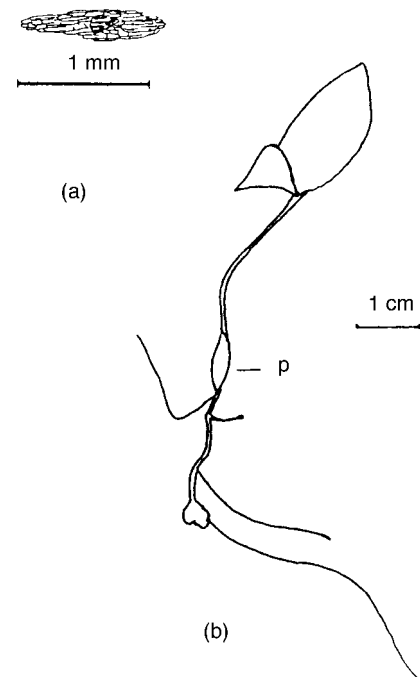


Fig. 6 Seed and seedling morphology of *Cypripedium calceolus*. (a) Seed; (b) two-leaf seedling; p, bud for the next year's shoot.

Table 3 Measurements of flowers of *C. calceolus*, *C. macranthos* and their hybrid (Mandl 1924)

| Character | <i>C. calceolus</i> | <i>C. calceolus</i> × <i>macranthos</i> | <i>C. macranthos</i> |
|---|---------------------|---|----------------------|
| Length to width ratio of lateral 'petals' | 1:10 | 1:5 | 1:2.5 |
| Length to width ratio of median 'sepal' | 1:2.5 | 1:1.8 | 1:1.7 |
| Length to width ratio of lower 'sepals' | 1:2.5 | 1:2 | 1:1.5 |
| Labellum length (cm) | 3 | 4 | 5.5 |
| Labellum width (cm) | 2 | 3 | 4 |
| Labellum depth (cm) | 1.8 | 2 | 3 |

Sakhalin and the Japanese island of Rebun (Perner 1996). Measurements of flowers of *C. calceolus*, *C. macranthos* and their hybrid are given in Table 3.

(c) SEED PRODUCTION AND DISPERSAL

The size of a pollen load was not significantly correlated with seed numbers of capsules in an American relative of *C. calceolus* (Proctor & Harder 1994).

The overall mean percentage of fruiting observed in eight Estonian populations over 11 years was 10.5% (Kull 1998). The number of seeds in five capsules varied between 5940 and 16 700 (Kull 1997). Fruit set in the other parts of the range is: Moscow district 4–14% (Varlygina & Matsenko 1986), Byelorussia 33–57% (Stavrovskaja 1984) and Sweden up to 25% (Nilsson 1979). Fruit set is pollinator limited. However, fruit set per flower is not higher in large populations of *C. calceolus* (Kull 1998). The dust-like seeds are wind-dispersed. However, the valves of the capsule are reported to separate in wet weather and release the seeds in rain-drops (Böckel 1972).

Cypripedium species often retain some quantity of seeds during the dormant period and release them slowly (Stoutamire 1974).

(d) VIABILITY OF SEEDS: GERMINATION

Cypripedium calceolus germinates presumably in spring (Fuchs & Ziegenspeck 1926; Rasmussen 1995). Delayed germination would not be expected in nature, even though it has been observed in laboratory conditions (Stoutamire 1974; Ramsay & Stewart 1998). High phosphorus content of the media suppresses seed germination (Sheviak 1983). With advancing seed maturity, germination in *in vitro* conditions decreases. Seeds collected 40 days after pollination germinate most successfully (Wagner & Hansel 1994).

(e) SEEDLING MORPHOLOGY

The protocorm develops during the first growing season. During the second growing season it produces two roots and a scale leaf enclosing the stem

tip. During the third summer, the elongating stem produces a large apical bud, while on the lower internodes one or more additional roots begins to develop in the third autumn. An aerial leaf with a very long sheath emerges in the fourth spring (Fuchs & Ziegenspeck 1926; Curtis 1943). Irmisch (1853) and Böckel (1972) have registered the first green leaf by 1 year after germination. In the following years the elongating and enlarging rhizome produces increasingly larger leaves annually. The rhizome is orthotropic in the first years, and plagiotropic later. A seedling 5 or 6 years old from a natural population is depicted in Fig. 6b.

The average time from seed germination to flowering is 12 years in *C. parviflorum* in America (Curtis 1943) and the time could be similar in *C. calceolus*.

IX. Herbivory and disease

(a) ANIMAL FEEDERS OR PARASITES

No strictly species-specific associations are known to exist between *C. calceolus* and other organisms. However, a number of species have been recorded being in contact with *C. calceolus*. The trap flower serves as a prison for many other insects besides pollinators. They can be classified as follows: (i) obligatory pollinators (bees); (ii) facultative pollinators (small Coleoptera); (iii) Diptera species that may accidentally fly in and get trapped (mainly species from the families Culicidae, Empididae, Syrphidae); (iv) bigger beetles and bumblebees that destroy flowers while visiting them; (v) caterpillars that destroy the perianth. At the end of flowering, 10–30% of flowers contain dead insects (Masing 1980). High concentrations of insects are taken advantage of by crab spiders [*Misumena vatia* (Cl.)] and sometimes by other spiders which make nets across the main labellum entrance.

Voies may bite through shoots at ground level, which may be a serious destruction in small populations of *C. calceolus*, for example in the single British locality in 1991. Sheep have also eaten off shoots and flowers of the English plant (Lindop 1992).

(b) PLANT PARASITES

No information.

(c) PLANT DISEASES

Unassigned potyvirus has been reported in *C. calceolus* from Germany (Brunt *et al.* 1997).

X. History

Fossil records are lacking.

Linnaeus described the species in *Species Plantarum* in 1753, but his first records of this species date back to 1737. However, the plant was certainly known before, as pieces of art depicting this plant originate from the 16th century (Heinrich & Lorenz 1996; Cribb 1997). The first British record was made in 1640 by Parkinson (1640) in his *Theatrum Botanicum*, from the Ingleton area near the Lancashire–Yorkshire border (Summerhayes 1951). Excessive and rapacious collection of the plant from the mid-18th to the end of the 19th century reduced it so much that it was believed extinct in Britain from the late 1910s to 1930. Since then it has had a precarious existence but is now actively conserved (see Section XI).

XI. Conservation

Cypripedium calceolus belongs to the group of flagship species of nature protection and is legally protected in all European countries and Russia. The species is also protected at the supranational level by the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), European Union Directive CE/92/43 on the Conservation of Natural Habitats and of Wild Fauna and Flora, and the Convention on International Trade in Endangered Species (Washington Convention) (Terschuren 1998). Nowadays the largest local populations in Europe seem to be preserved in the West-Estonian Archipelago Biosphere Reserve and in some parts of Poland.

In Britain the species has been a rare plant for at least the last 100 years and the main reason for decline has been the rapacity of collectors, who have dug the plants up and transplanted them to gardens (Summerhayes 1951). Besides the cutting of flowers and digging up of rhizomes, habitat destruction with logging and habitat alteration with overgrowing grassland by dense brush or closing up of the tree canopy are mentioned as main threats through the distribution range of *C. calceolus* (Terschuren 1998). In Britain the species has been saved from near extinction through the combined efforts of *in situ* conservation and propagation from seed in the laboratory (Ramsay & Stewart 1998). Besides the

permanent guarding of the surviving plant, the *Cypripedium* Committee has aimed to re-introduce the plant to some of its former sites, from plantlet production at Kew. This work is now co-ordinated by English Nature's Species Recovery Programme (L. Farrell & P. Corkhill, personal communication).

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