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Orchis ustulata L.

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Section *Orchis*. A native perennial herb with 1–2(–3) ovoid, subglobose or ellipsoid tubers positioned 3–6 cm underground; 5–10 unbranched fleshy roots of diameter 0.8–2 mm. Stem (5–)10–20(–50) cm, erect, usually slender, with basal sheaths. Leaves two to six, unspotted, oblong-acuminate to broadly lanceolate (rarely linear), 2–10(–15) cm × 0.5–2(–3) cm, forming a bluish-green rosette, sometimes with 1–2 bract-like leaves on the stem. Bracts small, membranous, reddish, slightly shorter than the ovary. Spike compact, ovoid, subcylindrical, dense, 1–10 cm long, elongating after anthesis. Flowers sessile, opening from the base upwards, dark purple when unopened. Spur cylindrical, directed downwards, 1/4–1/2 of the length of the ovary. ‘Sepals’ oval-lanceolate, purple, 3.5–4.5 × 1.5–2.5 mm, laterals asymmetric, 3–3.5 mm long. ‘Petals’ linear, subspathulate, keeled, 3–3.5 mm long. Labellum 4–8 mm, longer than wide, white or pale pink with papillose purple spots narrowing into 2 long ridges framing the spur entrance, deeply trilobed; the middle lobe dilated at the apex, itself normally bilobed, rarely entire; the lateral lobes oblong, obtuse. Stigma with strongly enlarged flaps on both sides of the rostellum, the column noticeably shortened. Retinacles are more or less reduced, with two pollinia. Gynostegium (ovary) short, resupinate. The flower scent varies between the early and late-flowering plants: strongly honey-like in the former and weak citron-like in the latter. No nectar is produced. Capsule is about 1 cm long, erect. Seeds are very numerous and tiny (*c.* 0.4 × 0.15 mm).

Variants

Most authors do not distinguish taxa below subspecies level within *Orchis ustulata* and *Flora Europaea* neither mentions forms nor varieties (Tutin *et al.* 1980). However, white-flowered plants are often found (Foley 1990; Reineke & Rietdorf 1991). According to Procházka (1980) various forms exist which differ in morphology

or size such as *f. ustulata*, *f. grandiflora* Gaud. 1825 (= *f. major* Weisb. 1891), *f. leopoliensis* Zapal. 1906, *f. emarginata* Zapal. 1906, *f. elongata* Zapal. 1906, *f. integriloba* Sabr. 1906), as well as others which differ in colour, such as *lusus albiflora* Thielens 1873, *lusus virescens* Caspary 1884, *lusus daphneolens* Beauv. 1905 and *lusus rubriflora* Vetter ex Keller et Soó 1931.

Kümpel & Mrkvicka (1990) have described the subspecies *aestivalis* that was previously considered to be an ecological form. This differs in its phenology, flowering about 1–2 months later than the nominal subspecies. Jenkinson (1995) claims that the British late-flowering form is not identical to *ssp. aestivalis* and should be regarded merely as a late-flowering variant. According to Reineke & Rietdorf (1991) there are two different forms of the late-flowering *O. ustulata* in Germany, one of them occurring together with early flowering plants in all the larger (more than 30 member) populations. Latest molecular research does not confirm existence of subspecies within Britain and Estonian material (K. Tali, M. Fay & R.M. Bateman, unpublished). In this paper, on the basis of their phenology, the early flowering populations are treated as *var. ustulata* and the late-flowering ones as *var. aestivalis*.

I. Geographical and altitudinal distribution

In the British Isles, *Orchis ustulata* (Burnt Orchid) was once locally frequent in suitable calcareous habitats throughout much of England as far north as Northumberland, but has subsequently declined drastically and is now extremely local. It is not recorded for Scotland or Ireland and only very locally from Wales.

Many of the best sites for *O. ustulata* are now protected as nature reserves or are on Ministry of Defence land, or at least have some conservation status. Unfortunately, others have none and, especially where these comprise small populations, they will come under considerable threat from man’s usage. Changing agriculture techniques, the increase in ploughing during World War II, the reduction in rabbit grazing following the onset of myxomatosis, and damage from man-made incursions seem to have been the main causes of loss.

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*Abbreviated references are used for standard works: see *Journal of Ecology* (1975) 63: 335–344. Nomenclature of vascular plants follows Stace (1997).

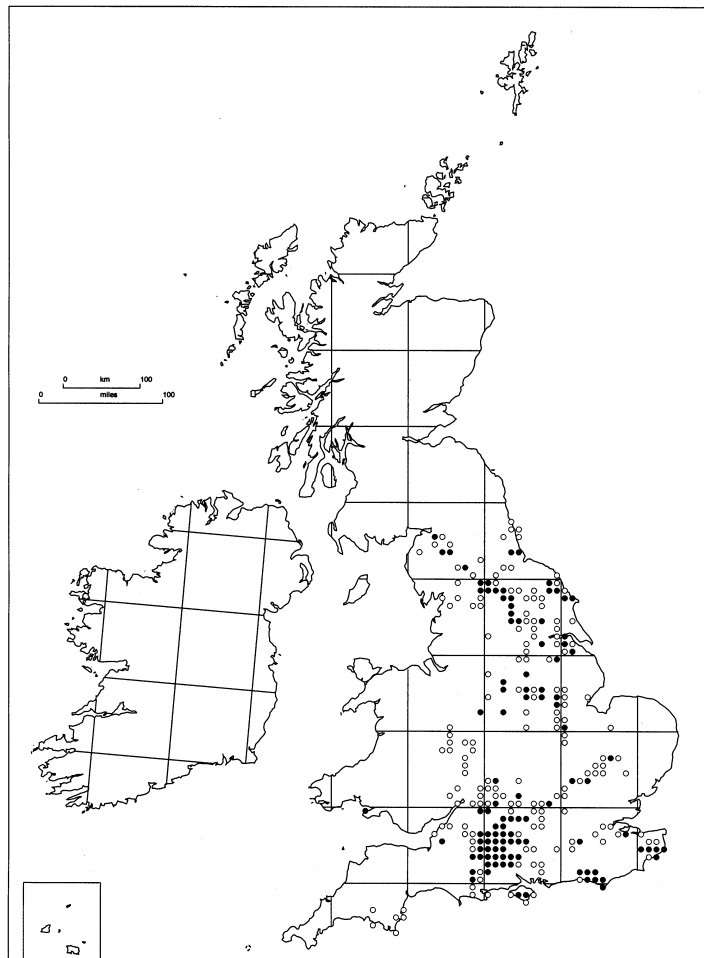


Fig. 1 The distribution of *Orchis ustulata* L. in the British Isles. Each symbol represents at least one record in a 10-km square of the National Grid. (○) Pre-1950, (●) 1950 onwards. Mapped by H. R. Arnold, Biological Records Centre, Centre for Ecology and Hydrology, mainly from records collected by members of the Botanical Society of the British Isles.

Of the formerly recorded 435 separate British populations only 75 have definitely survived (Fig. 1). Most of these are small, only 10 populations regularly comprising more than 200 flowering plants (Foley 1987, 1990). Nevertheless, a few populations are very large, for example that at Parsonage Down, Wiltshire, is estimated to contain 30 000 plants.

As well as in England, *O. ustulata* occurs throughout much of Europe, reaching its northern geographical limit in the Faroes, Gotland and Estonia, the southern shore of Lake Ladoga and the rivers of Vjatka and Kama. The species has been found also in the Urals and on the West-Siberian plains (Baumann & Künkele 1982; Vakhrameeva *et al.* 1991) whilst its southern distributional limit passes through Spain and the Mediterranean coast of France. It also occurs in Italy north of Rome, on almost the whole of the Balkan Peninsula and probably in the southern Ukraine up to the Volga River (Füller 1983) as well as in the Caucasus (Vakhrameeva *et al.* 1991) (Fig. 2). This species is in general decline and is protected throughout its range; it is sometimes abundant in mountains, but rare elsewhere and very rare in the Mediterranean region (Delforge 1995).

In the mountains and in subalpine meadows of Europe, *O. ustulata* populations have been found up to 2400 m altitude (Delforge 1995) but in Britain this is essentially a lowland plant occurring from almost sea level up to nearly 300 m in Derbyshire (Alt. Range Br. Pl.).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Orchis ustulata is classified as a European temperate species (Preston & Hill 1997). It appears to be favoured by regions where the summers are humid and warm. It can withstand quite cold conditions but probably not repeated freezing and melting, as its rosettes are wintergreen. Very dry conditions appreciably restrict flowering. In some localities plants are also found in damper transition zones.

Orchis ustulata is favoured by sunny, open habitats in short, lightly grazed calcareous grassland with only moderate competition, but in continental Europe it can also inhabit light, open woodland. The largest populations

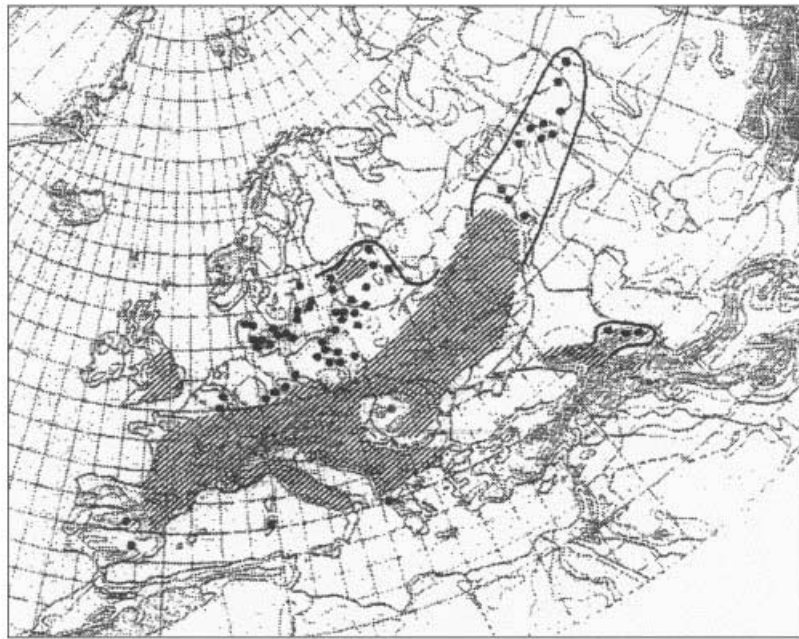


Fig. 2 The distribution of *Orchis ustulata* in the world (Hultén & Fries 1986).

Table 1 Soil chemical analyses for five localities in Estonia

Locality	pH	N (%)	P (mg kg ⁻¹)	K (mg kg ⁻¹)	Ca (mg kg ⁻¹)	Mg (mg kg ⁻¹)	Organic matter (%)
Aljava	4.9	0.369	14.81	75.9	1636	282.0	7.84
Lõetsa	7	0.405	23.54	263.2	4014	368.2	8.66
Kapi	7.3	0.516	16.64	128.2	4418	360.3	10.76
Sillukse	7.3	0.261	18.40	106.9	3391	330.0	5.40
Jäneda	7.6	0.359	19.59	25.1	6001	69.7	6.70

in Britain are usually on old moderately rabbit- or sheep-grazed pastures, which have never been treated with artificial fertilizers, herbicides or pesticides.

(B) SUBSTRATUM

In Britain, *Orchis ustulata* usually grows best on well-aerated humus-rich soils, and is mainly a plant of calcareous substrates (chalk, and oolitic, Carboniferous, and Magnesian limestones). In Sweden, Estonia and elsewhere it can also be found on stony alvar where the soil is sparse as well as in limestone cracks which also have a very shallow soil (e.g. locality Kapi in Table 1). The plant has also been found on sand and gravels (Davies *et al.* 1983). The pH of sites it occupies range from 5.2 to 7.3 (Arditti 1992) and 6.0 to 8.5 (Procházka & Velíšek 1983). Soil analyses from sites of five different populations in Estonia are shown in Table 1.

III. Communities

In Britain, fairly constant associates of *Orchis ustulata* include *Anthyllis vulneraria*, *Centaurea nigra*, *Conopodium majus*, *Gentianella* spp., *Hippocrepis comosa*, *Lotus corniculatus*, *Polygala* spp., *Primula veris*, *Rhinanthus minor* and *Sanguisorba officinalis*. Orchids such as *Dactylorhiza*

fuchsii, *Gymnadenia conopsea*, *O. mascula*, *O. morio* and *Platanthera bifolia*, are frequent associates (Foley 1990). *Orchis ustulata* is also associated with *Juniperus communis* on the southern Downs (Lang 1980). The majority of populations occur in short-grazed pasture, usually with a southerly or westerly aspect, and often on a moderate slope. This is the *Festuca ovina*–*Avenula pratensis* (*Helictotrichon pratense*) community (CG2 of the NVC classification; Rodwell 1992). Some of the largest British populations occur where there is a well-documented history of traditional grazing and farming over past centuries. Having remained undisturbed for long periods, the banks of ancient prehistoric earth-works are also favoured. Whilst ploughing and agricultural improvement are usually anathema to the plant, there are instances where it has recolonized disturbed ground relatively quickly. One such instance is a Hampshire population at Martin Down where it reappeared about 30 years after the cessation of ploughing, presumably from a nearby seed source rather than from dormant vegetative stock. One small population on a golf course in northern England is apparently ungrazed but the habitat is kept open by the passage of golfers. Another atypical habitat is in lush meadowland near Eastoft, Lincolnshire, where grazing is absent; plants here are perhaps more robust and so compete adequately

with the taller surrounding vegetation. *Orchis morio* is also present in good numbers at this site. Abnormally tall plants are also known at one of the Wiltshire populations.

The late-flowering British populations are nearly always well separated from those of the early flowering variety and no precise localities are known where both occur; also the associated species are basically the same for both varieties. In one part of Wiltshire, there are several early flowering populations in close proximity to each other whilst in seemingly identical habitats nearby there are none. However, somewhat later in the year the late-flowering form is found at several of these 'uninhabited' sites; this is a phenomenon that is difficult to explain, although it is possible that this form originally occurred as an ecotype and has evolved into its present variety through different land management over a considerable period of time. The late-flowering variety also appears to occupy multi-aspect sites, and not necessarily those facing only south or west. The plants are also taller but this is probably a response to the higher competing vegetation present at this time of year. However in Britain, the subtle morphological differences between the two forms (i.e. labellum shape and markings, and degree of opening of the flowers) are not as consistent or marked as found in some German populations. Indeed some British populations are known in which flowers on the same plant exhibit both morphologies (D. C. Lang, personal communication). More than 20 late-flowering British populations are known, the majority of these being in East Sussex, with a few also in Wiltshire and Hampshire. This form is unknown anywhere north of the Thames valley.

In continental Europe, *Orchis ustulata* grows on limestone pastures or poor meadows, in light scrub on rather dry base-rich (also lime-free) mildly to moderately acid humus. There the majority of populations occur in the Mesobromion alliance, rarely also in Cirsio-Brachypodium or poor Arrhenatherion (Oberdorfer 1994). The accompanying species according to Oberdorfer (1992) include *Brachypodium pinnatum*, *Briza media*, *Carex caryophylla*, *Centaurea jacea*, *C. scabiosa*, *Dactylis glomerata*, *Euphorbia cyparissias*, *Galium verum*, *Salvia pratensis* and *Scabiosa columbaria*.

In Estonia, as in Sweden, the early flowering plants grow on former limestone alvar (with a shallow soil layer) pastures and meadows, some of which are now overgrown with thick juniper and/or young pines. Late-flowering plants often inhabit localities with deeper soil. In these countries, associated species of *O. ustulata* are similar to those in Britain, the most frequent being *Antennaria dioica*, *Anthyllis vulneraria*, *Briza media*, *Campanula rotundifolia*, *Carex flacca*, *C. tomentosa* (*C. filiformis*), *Festuca rubra*, *Filipendula vulgaris*, *Helictotrichon pratense*, *Plantago media*, *Sesleria caerulea*, *Stellaria graminea* and *Trifolium aureum*. Apart from these, *Cirsium acaule*, *Fragaria vesca*, *Potentilla reptans* and *Veronica verna* are characteristic of communities including the early flowering populations.

IV. Response to biotic factors

In Britain plants occur only in open, unshaded habitats, invariably with a sunny aspect, but in continental Europe (Estonia) plants have been found under the direct shade of trees. In some cases these plants have flowered for six consecutive years. There also, young plants of *O. ustulata* are established in the lighter, open places near to path sides or in forest clearings, and young seedlings can often be found in ground disturbed by wild boar, such conditions aiding their establishment. Compared to the tubers of other orchids, those of *O. ustulata* are small and so less attractive to mammals; nevertheless some of the continental populations have sometimes suffered major damage from uprooting and grazing. In Britain this is unlikely to be a problem although the inevitable presence of rabbits in the closely grazed pastures where *O. ustulata* often occurs may occasionally result in plants becoming dislodged. Flower or leaf damage by slugs or insects has been observed, but this appears to have no adverse effect, the plants developing normally the following year.

V. Response to environment

(A) GREGARIOUSNESS

In England individual flowering plants usually grow in fairly close proximity to each other forming discrete, local populations; but in a few clearly favourable British localities the populations can be very extensive. Also in Estonia, the situation where several groups of plants or subpopulations are sparsely scattered over a suitable area of several square kilometres is common.

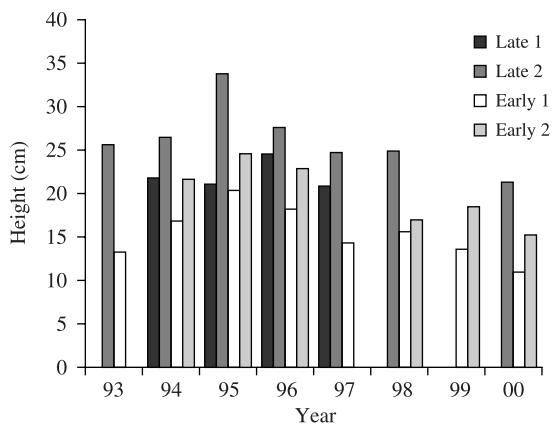
Occasionally, plants that appear to be vegetatively propagated form groups of 2–5. Usually only 1–2 spikes in such a group flower at the same time, but 4–6 flowering spikes are not rare. In one population in northern England, there were 10 plants, probably a clone, flowering within a radius of a few cm but no other plants could be seen within 100 m. Fruit set for plants in such groups in continental Europe was not found to be higher than for singly growing plants (Tali 1996).

(B) PERFORMANCE IN VARIOUS HABITATS

Evidence is available where individual plants have been marked and monitored in Estonia. The figures given in Table 2 reflect the situation in permanent plots (ten 1 m² squares at each locality). As new plants are usually not established in the same plots the actual decline is not so great in populations. A severe decline was caused by quarrying, which destroyed over half of the Sillukse population. The noticeable height difference between late-flowering and early flowering plants appeared to be due to the differing height of the surrounding vegetation at their respective flowering seasons. Variation in the average height of any population depends on the conditions applicable that year and is fairly similar for

Table 2 Number of flowering *Orchis ustulata* plants for permanent plots in five different Estonian populations. H = average height (cm) of flowering plants; Average = average height (cm) of flowering plants in a population during the study; SD = standard deviation

		1993		1994		1995		1996		1997		1998		1999		2000		Average
		No.	H	No.	H	No.	H	No.	H	No.	H	No.	H	No.	H	No.	H	H
Late	Sillukse	40	25.5	31	26.3	20	33.9	13	27.7	14	24.7	7	25.0	0	3	21.3	26.4	
	SD		5.5			6.7	7.9		8.7		5.5		6.4			6.8		
	Jäneda			46	21.7	5	21.0	2	24.5	16	20.8	0	0		2	26.0	22.8	
Early	Lõetsa	24	13.2	77	16.8	47	20.3	54	18.1	16	14.2	29	15.6	14	13.6	2	11.0	15.3
	SD		4.6		4.6		6.8		4.7		6.4		5.2		4.0		1.4	
	Kapi			100	21.6	47	24.6	42	22.9	0		41	16.9	21	18.5	7	15.3	20.0
Aljava	SD		4.0		6.5		4.0		4.4		4.4		4.7		6.6			
	SD		3.5		5.7		4.5		4.8		5.0		3.6					18.6

**Fig. 3** Comparison of the height of flowering plants in two late-flowering and two early-flowering populations in Estonia.

each population (Fig. 3). The inflorescence varies greatly in length and comprises 10–60 flowers, with approximately 6 flowers per cm of inflorescence.

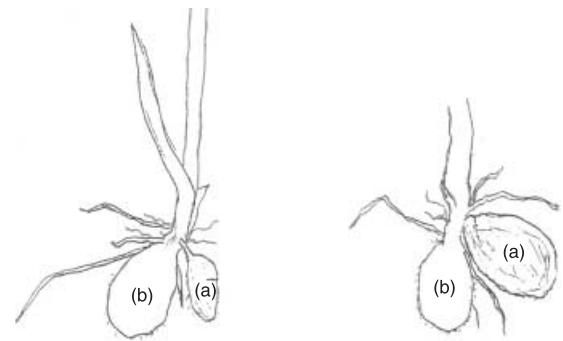
(C) EFFECT OF FROST, DROUGHT, ETC.

This plant is favoured by a warm, humid climate and is more affected by moisture than by temperature. The rosettes withstand frosts well, the leaves showing only minor damage in spring (monthly mean temperatures of -11° to -12°C are not uncommon in Estonia). In extremely dry years, plants seem to flower less with the rosettes perishing before flowering time.

VI. Structure and physiology

(A) MORPHOLOGY

At flowering time each plant has two underground tubers, one of which has produced the current year's growth and subsequently become wrinkled and brown, the other ready to produce the following season's

**Fig. 4** Tubers of *Orchis ustulata* during the flowering season: (a) old tuber; (b) new tuber.

growth from its tip; this tuber is new, white and fleshy (Fig. 4). Stomata occur only on the lower (abaxial) surface of the leaf at a density of $80\text{--}90\text{ mm}^{-2}$. According to Mrkvicka (1994) seed size of the early flowering variety is $0.29\text{--}0.44 \times 0.13\text{--}0.17\text{ mm}$ whilst that of the late-flowering variety is $0.35\text{--}0.50 \times 0.12\text{--}0.15\text{ mm}$. The seed morphology of the two is also different, the early flowering variety having smaller seeds with thicker walls and a bigger embryo (Mrkvicka 1994). The seeds of the late flowering plants from Estonia seen by scanning electron microscopy showed appreciable variation in size and shape (Fig. 5).

(B) MYCORRHIZA

Orchis ustulata forms mycorrhiza with fungi of the genus *Rhizoctonia*. The degree of mycorrhizal infection for *O. ustulata* is high, i.e. 6 on a 6-point scale as given by Sadovsky (1965); however, according to Rasmussen (1995) the extent of mycorrhizal colonization is only 1 on a 3-point scale. This needs further clarification.

A mycorrhizal fungus isolated from pelotons in a mature root of *O. ustulata* from East Sussex, England, and subsequently grown in axenic culture, was identified using molecular methods as being a *Ceratobasidium*

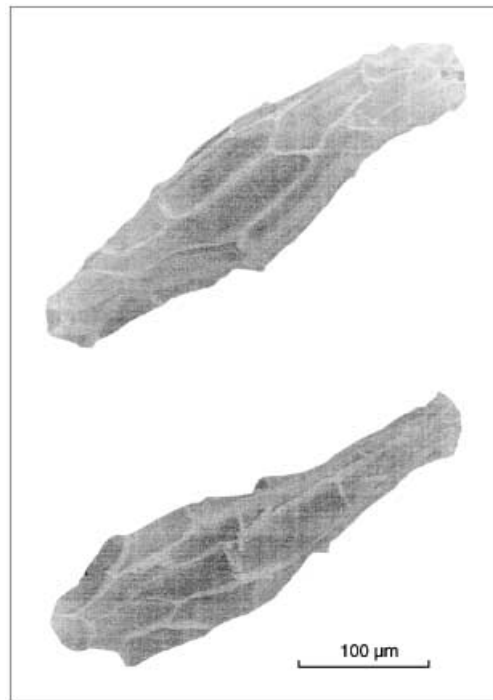


Fig. 5 Scanning electron micrograph of the seeds of *O. ustulata* (taken with Tesla BS 301 at 17 kV, sputter coated with gold). Scale bar = 100 μ m.

species (M. Bidartondo & D. J. Read, personal communication). Fungi of this genus have been shown to be capable of inducing germination in several other *Orchis* species (Muir 1989).

(C) PERENNATION: REPRODUCTION

The plant is a geophyte, perennating by the tuber formed during the previous spring. Dormancy is very common and a plant is able to survive without forming any above-ground parts for 1–3(–4) years (Fig. 6). Owing to dormancy, calculation of depletion curves is complicated and inaccurate. The species is relatively short-lived (Tali 2002). Among 464 plants, individually monitored over a 6–8 years period in five different populations in continental Europe, only four flowered for seven consecutive years; most plants flowered for 1–4 years and then either died or remained in a vegetative or dormant state for several years. Patterns of transition between the flowering, dormant and vegetative stages show that the transition to dormancy both from vegetative and generative stages is frequent and occurs more often in the late-flowering variety (Tali & Kull 2001). The early flowering variety shows a greater tendency for vegetative–vegetative and generative–generative transitions (Fig. 7).

Sexual reproduction dominates. Some studies have indicated that vegetative reproduction is possible by a secondary rhizome (Foley 1994) or that tubers may

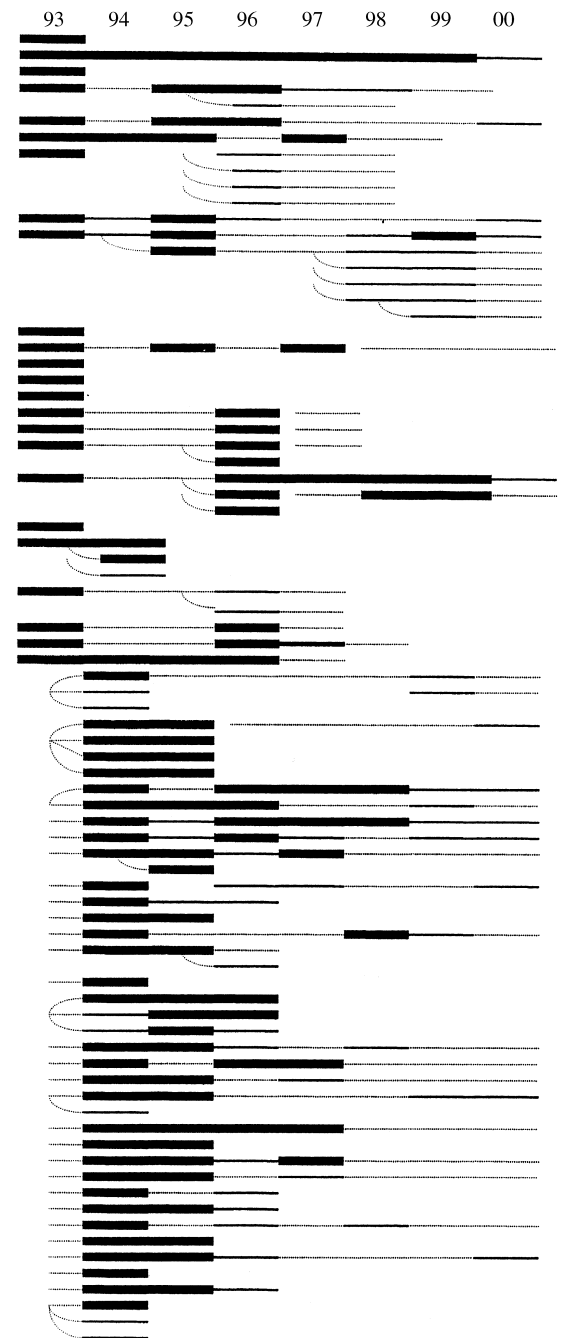


Fig. 6 Behaviour of plants in the early flowering Lõetsa population (Estonia) 1993–2000. Solid line – plant is flowering; normal line – plant is vegetative; dotted line – plant is dormant.

be produced from more than one of the basal buds, both in culture and under good conditions in nature (Rasmussen 1995). In four populations in Estonia, 5%–28% of the plants formed clusters of 2–6 specimens whereas one inland locality (Jäneda) lacked such clones altogether.

(D) CHROMOSOMES

$2n = 42$ (Tutin *et al.* 1980), $2n = 20, 40$ (Procházka 1980).

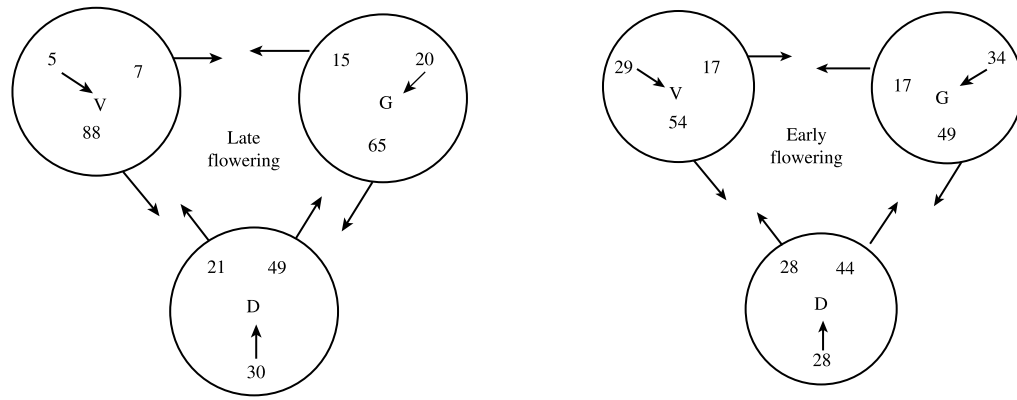


Fig. 7 Transitions (%) between three stages (V – vegetative, G – generative, and D – dormant) calculated from five populations in Estonia.

(E) PHYSIOLOGICAL DATA

No data.

(F) BIOCHEMICAL DATA

Tubers yield salep (containing starch and mucilage) and were once used as an aphrodisiac in ethnomedicine in a way similar to the tubers of other species of *Orchis*. A study of floral pigments showed that the plant differs clearly from other *Orchis* species in containing mecocyanin, but lacks cyanin and orchicyanins (Pridgeon *et al.* 1997).

(G) GENETIC DATA

Work has been conducted on this aspect in continental Europe. Enzyme systems phosphoglucomutase, malate dehydrogenase, leucine dehydrogenase, superoxide dismutase (SOD) and phosphoglucoisomerase (PGI) were analysed in six Estonian populations and one Gotland (Sweden) population to detect differences in allele frequencies between var. *ustulata* and var. *aestivalis*. No unique alleles were found; all alleles were detected in both varieties. The first three systems were monomorphic. No significant differences occurred in PGI diversity; the frequencies of the more rapid allele of SOD were higher in the late-flowering Sillukse and Pilguse populations and in the early flowering Gotland populations than in three geographically closer, early flowering populations from Muhu Island, Estonia (K. Tali & T. Paaver, unpublished).

From dendrograms based on the degree of heterozygosity for 10 enzyme loci, Schlegel *et al.* (1989) concluded that *O. ustulata* as well as *O. morio* are more distantly related to the other *Orchis* species and should therefore be considered to be members of another genus. Based on the nuclear ribosomal DNA internally transcribed spacers ITS1 and ITS2, it is evident that *O. ustulata* forms a well distinguished clade with *O. tridentata*, *O. lactea* and *Neotinea maculata* (Pridgeon *et al.* 1997), and in 1997 the species was described as *Neotinea ustulata* (L.) R. M. Bateman, Pridgeon, & M.W. Chase, based on ITS trees (Bateman *et al.* 1997).

VII. Phenology

Kümpel & Mrkvicka (1990) studied the phenology of the two varieties of *O. ustulata* in several plots in Austria at altitudes from 300 m to 1070 m a.s.l. (see Table 3). Rosettes of both varieties are produced in the autumn. In Britain, flowering occurs from about the second or third week of May until mid-June for var. *ustulata* and from early July to August for var. *aestivalis*. Plants without inflorescence primordia (i.e. vegetative plants) largely disappear by flowering time, when the leaves of flowering plants also start to decay. Capsules ripen in late June to July (var. *ustulata*) and August onwards (var. *aestivalis*). Stems bearing capsules can be encountered the following year.

Based on observations in continental populations, Kümpel & Mrkvicka (1990) claim that plants of the late-flowering variety begin to emerge in March to April whilst early flowering plants are wintergreen.

Table 3 Phenology of two varieties of *O. ustulata* in plots in Austria (from Kümpel & Mrkvicka 1990)

	var. <i>ustulata</i> (early)	var. <i>aestivalis</i> (late)
First leaves	September–November	October–December
Rosette formation	November–February	March–April
Beginning of flowering	April	End of May–June
Full flowering	May (June)	July–August
Fruiting	Middle/end of July	End of August–September
Withering	Middle/end of July	End of August–September

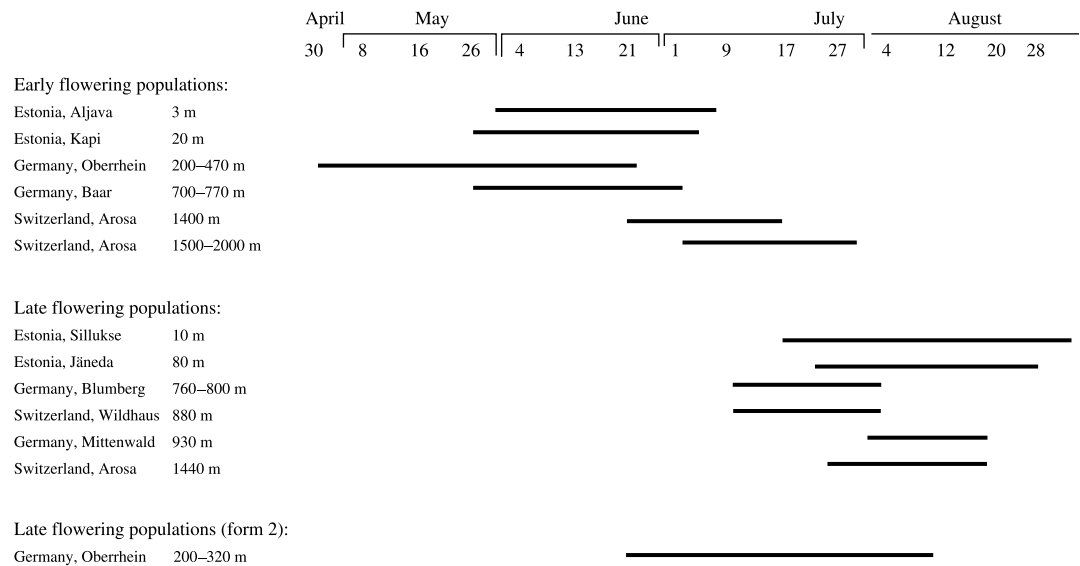


Fig. 8 Flowering times of different populations of *Orchis ustulata* (data for German and Swiss populations from Reineke & Rietdorf 1991).

Reineke & Rietdorf (1987, 1991) are of the opinion that in all *O. ustulata* populations new rosettes emerge continuously during autumn and winter, even under snow cover.

In 1993, in Estonia, measurements were made on one late-flowering and one early flowering population during anthesis. The early flowering var. *ustulata* started flowering on 20 May, continuing for about 30 days; the average length of the inflorescence at the start was 3.6 cm whilst at the end it was 4.2 cm. The late-flowering var. *aestivalis* started flowering at the beginning of July and flowered for about 50 days; the average length of the inflorescence increased from 2.1 cm at the start to 6.8 cm at the end.

Another form of late-flowering *O. ustulata* was described from Germany by Reineke & Rietdorf (1991). These plants grew together with early flowering ones and emerged in the period September to November; their flower buds developed at the same time as those of the early flowering plants. When the early flowering plants withered at the end of the flowering period, the plants of this late-flowering form remained green, like vegetative plants. The flower spike started to grow in mid-June and developed more rapidly than the spike of the early flowering variety. These lengthened, flowered and set fruit quickly. For this form, intermediate flowering has also been recorded. Differences in flowering times can also be related to the altitude of the various populations (Fig. 8).

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

In *Orchis ustulata* nectar is not produced. Differences in scent (sweet for var. *ustulata* and rather unpleasant for var. *aestivalis*) suggest the existence of different

pollinators for the early flowering and late-flowering plants. The uppermost buds usually fail to open.

The stigma of *Orchis ustulata* has strongly enlarged flaps on both sides of the rostellum and a noticeably shortened column, through which the bursicles and viscidia approach the labellum; also the spur entrance is narrowed (van der Cingel 1995). Data on pollen vectors for this species are scarce. Vöth (1984) and Mrkvicka (1991) have recorded a tachinid fly (*Echinomyia magnicornis* Zett.) for var. *aestivalis*. The number of *E. magnicornis* individuals counted by Vöth is appreciable: 9 approaches and 49 visits per small population of 11 plants during a 4-h period on a single day. Seven individuals out of 13 carried 26 pollinia. Jürgen Böhm has observed the same insect visiting *O. ustulata* several times in a German population (personal communication). The beetle *Leptura livida* Fabricius (Cerambycidae) has been recorded as a pollinator of var. *ustulata* (van der Cingel 1995). Although *O. ustulata* has been referred to as a butterfly flower (e.g. Pfl. Exk.; Baumann & Künkele 1982) conclusive evidence for this appears to be lacking.

(B) HYBRIDS

Rothmaler (1976) stated that *O. ustulata* produces hybrids with *O. simia* and *O. tridentata* but van der Pijl & Dodson (1969) argued that *O. ustulata* can form hybrids only with *Anacamptis pyramidalis*. According to Baumann & Künkele (1982) they can also occur with *O. morio* and *O. militaris*, whilst Davies *et al.* (1983) recorded hybridization with *O. coriophora* and R. M. Bateman with *Neotinea lactea* (personal communication). British populations, where *O. ustulata* and *O. morio* grow in close proximity, have frequently been examined for the presence of hybrids but none has so far been recorded.

Table 4 Flowering and fruiting data for five populations in Estonia, 1993–2000

	Early Aljava	Early Kapi	Early Lõetsa	Late Sillukse	Late Jäneda	Total or mean
Total number of flowering plants	266	323	274	141	69	1073
Number of fruiting plants	21	78	51	60	14	224
Number of capsules	62	306	173	176	49	766
Fruiting percentage	7.89	24.1	18.6	42.6	20.3	20.9
Mean number of capsules per flowering plant	2.95	3.92	3.39	2.93	3.5	3.4

(C) SEED PRODUCTION AND DISPERSAL

The overall average percentage of fruiting, calculated over an 8-year period for all flowering plants in five Estonian populations, was 20.9% (Table 4). Seed set is relatively infrequent in Great Britain and is not likely to exceed this figure. The number of seeds estimated in three capsules varied between 2000 and 4000 per capsule. The seed is very tiny and so can be dispersed hundreds of kilometres by the wind.

(D) VIABILITY OF SEEDS: GERMINATION

According to Sadovsky (1965) the germination of *Orchis ustulata* seed in cultivation is almost impossible. Vermeulen in the 1940s and Eiberg in the 1960s failed to germinate fresh seeds of *O. ustulata* in water (+0.05% Tween 80 detergent) (Rasmussen 1995). However, some gardeners (<http://gardenbed.com>) claim that ripe seed may germinate if surface-sown in the glasshouse.

(E) SEEDLING MORPHOLOGY

Orchis ustulata is characterized by normal embryo sac development and by the presence of T-tetrads. The embryos have a suspensor. Embryo size is 88–120 × 60–90 µm for the late-flowering and 120–160 × 100–130 µm for the early flowering *O. ustulata* (Mrkvicka 1994).

Stojanow (1916) observed seedlings of *O. ustulata* at a distance of 5–10 cm below the surface in thick humus. The mycorrhizome may grow in the soil for more than 10 years with one segment often (but not always) added each year (Fuchs & Ziegenspeck 1927; Baumann & Künkele 1982). After this initial stage, the root, then the leaf, and finally the tuber are formed; the plant's development has been illustrated by Summerhayes (1951; fig. 1, p. 3). *Orchis ustulata* is thought to have the longest seedling phase in the Orchidaceae, and up to 16 years may pass from germination before it first flowers (Davies *et al.* 1983). Summerhayes (1951) has questioned such estimates of the duration of the seedling stages as being exaggerated. There is at least one site in Estonia where plants grow on a field that was ploughed 6 years previously. Cultivated plants have been claimed to reach flowering within 3 years (Möller 1985), probably owing to the more stable and favourable growth conditions. The initial protocorm/mycorrhizome may attain a length of 20–30 mm before the first root is produced;

this length is remarkable compared with other species with the similar life history of root-aerial shoot-tuber (Rasmussen 1995).

IX. Herbivory and disease**(A) ANIMAL FEEDERS OR PARASITES**

Grazing animals (cattle and sheep) do not avoid *Orchis ustulata* plants and these are certainly not immune to attack by rabbits; cultivated plants are especially susceptible to slug and snail predation. In continental Europe, wild boar also feed on the tubers whilst several carnivorous bugs (Hemiptera) such as *Phymata crassipes* Fabricius have been observed on plants, apparently mimicking the remains of old flowers, but may not be feeding.

(B) & (C) PLANT PARASITES AND DISEASES

No data.

X. History

Linné described *Orchis ustulata* in his *Species Plantarum* in 1753. Before this, however, the species was already known by the 16th century, being described by Fuchs in 1543 (Jacquet 1994). Synonyms include: *Orchis amoena* Crantz 1769, *O. columnnae* F. W. Schmidt 1791, *O. parviflora* Willd. 1805, *Himantoglossum parviflorum* Spreng. 1826 (Procházka 1980) and *Neotinea ustulata* (Bateman *et al.* 1997).

A Mr Stonehouse made the earliest known localized British record for *O. ustulata* by 1650 at 'Scasby-lease', near Doncaster, Yorkshire (How 1650). That this should have been the first is surprising, since in those days the plant would presumably have been much more frequent in the large populations on the southern Downs.

XI. Conservation

Although formerly widespread in the chalk and limestone regions of England, *Orchis ustulata* has suffered one of the severest declines of all wild orchids during the last 50 years and is rare there now (Foley 1994). It may be the most rapidly decreasing plant in Britain (80% decline) having been lost from 210 of 265 formerly occupied 10 × 10 km squares (Preston *et al.* 2002).

In the Netherlands, it has not been recorded since the 1980s and is extinct, or probably so, in the St. Petersburg region of Russia. It is categorized as 'vulnerable' in Estonia and Latvia, 'endangered' in Lithuania, Poland and Denmark (Ingelög *et al.* 1993), 'critically endangered' in Czechia (Holub & Procházka 2000), and given in Red List category 2 for Germany (category 3 for Bayern). The species is protected by law in most of Europe.

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