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Biological Flora of the British Isles: *Primula veris* L.

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Summary

1. This account presents information on all aspects of the biology of *Primula veris* that are relevant to understanding its ecological characteristics and behaviour. The main topics are presented within the standard framework of the *Biological Flora of the British Isles*: distribution, habitat, communities, responses to biotic factors, responses to environment, structure and physiology, phenology, floral and seed characters, herbivores and diseases, history and conservation.

2. *Primula veris* is a distylous, perennial rosette hemicryptophyte, mostly found in well-drained, herb-rich meadows and grasslands, in scrub or woodland rides and edges, and on calcareous cliffs. It occurs on base-rich loams or clays, on limestone, and sometimes in dunes.

3. Native to the British Isles, it is characteristic of many mesotrophic and calcicolous lowland grassland communities, but it also extends into upland valleys in northern England and Scotland. In Ireland it is also native and most abundant in the central plain. *Primula veris* occurs throughout the temperate areas of Europe as far east as the Russian border.

4. *Primula veris* is a shade-intolerant species that shows reduced performance and flowering under shade or increased competition. The species is not able to penetrate anoxic soil layers and is therefore mostly absent from locations that are characterized by a high water table. It has a well-developed drought tolerance.

5. *Primula veris* is an obligate outbreeder which entirely depends on foraging insects for successful pollination. Although the species shows heterostyly, with two reciprocal morphs (pin and thrum), only relatively low levels of intermorph pollination have been reported. Seed dispersal is restricted to a few centimetres from maternal plants, whereas pollen flow is wider, but still limited to a few metres from parental plants. Both are factors that contribute to a significantly fine-scale spatial genetic structure and small neighbourhood size.

6. At several locations throughout the British Isles, *P. veris* occurs together with *P. elatior* and especially *P. vulgaris*. The hybrid *P. veris × P. vulgaris = P. × polyantha* occurs frequently in mixed populations, whereas the hybrid *P. veris × P. elatior = P. × media* has been rarely reported in Britain.

7. Although *P. veris* is still a widespread grassland herb, it is less abundant in the British Isles and continental Europe than before. This decline can be attributed to changes in land-use practices, such as the loss of traditional hay–meadow management, the loss of grazing and an increase of ploughing, in combination with ongoing destruction and nutrient enrichment of permanent grasslands. However, from 1980 onwards the species has increased substantially in many areas of the UK, largely because its seeds are included in wildflower seed-mixtures that are sown on new or upgraded road and motorway verges, embankments and urban conservation areas.

Key-words: climatic limitation, conservation, germination, grassland communities, grazing, hay-meadows, herbivory, parasites and diseases, reproductive biology, soils

Primulaceae. *Primula veris* L. (Cowslip) is a perennial rosette hemicryptophyte. Rhizome short, stout, ascending, girt at the apex with more or less fleshy scales formed by the bases of withered leaves, furnished with numerous fibrous roots. Leaves (including petioles) 5–15(–20) cm long, 2–6 cm broad at flowering time, enlarging at fruiting time; rugose with the veins impressed above and prominent below, pubescent or glabrescent on the upper surface, thinly greyish or whitish-tomentose to glabrescent on the lower surface. Lamina ovate to ovate-oblong, round or obtuse at the apex, finely toothed, crenate to irregularly erose-crenate at the margin, abruptly attenuates at the base into the petiole and sometimes cordate. Petiole usually shorter than the lamina, membranously winged, sheathing at the base. Cotyledons and leaves with scattered unicellular, capitate glandular hairs on the upper surfaces; similar hairs also occur on the hypocotyl. Scape(s) originating among the leaf axils of rosettes, (5–)10–20(–30) cm tall and markedly pilose, sparsely glandular, farinose entirely when young, distally only later, bearing one or two umbels each with 1–30 flowers or flower buds not all of which may mature, flexible during flowering, rigid during fruiting. Bracts 2–7 mm long, linear-lanceolate, acute or acuminate, hairy. Pedicels 3–20 mm, pubescent, slender, slightly spreading and more or less drooping. Calyx 8–17 mm long, tubular-campanulate, markedly 5-angled, hairy especially along the angles, divided to a quarter of its length into triangular, acute sometimes mucronate teeth, uniformly pale green. Flowers dimorphic. Corolla usually bright-yellow, rarely white, pale cream, fulvous or reddish, with an orange mark at the base of the petals, exannulate, heteromorphic; tube about equalling calyx; limb 10–17 mm in diameter, concave, with obcordate, emarginate lobes; lobes 5–6 mm in width. Stamens with anthers 2 mm long, inserted at the apex of corolla-tube in thrum-eyed flowers, at middle of tube in pin-eyed flowers. Long style equalling the corolla-tube, short style half as long. Capsule 8 mm, shorter than calyx, dehiscing by apical teeth. Seeds 1–1.5 mm in diameter, 0.69–1.24 mg, ovoid, cuboid or subspherical, dark brown to blackish, finely papillate or tuberculate-surfaced, dispersed by a censer mechanism.

Primula veris is a variable species. The delimitation of subspecies is still under debate (Schwarz 1968; Tutin *et al.* 1972; Gutermann *et al.* 1973; Pignatti 1982; Länger & Saukel 1993; Richards 2002). Although Länger and Saukel (1993) distinguish only two subspecies (ssp. *veris* (including ssp. *canescens* and probably ssp. *macrocalyx*) and ssp. *columnae*), most accounts recognize four subspecies and some varieties (see Tutin *et al.* 1972; Richards 2002).

1. *Primula veris* ssp. *veris*. Lamina usually abruptly contracted at base, weakly hairy to glabrescent; petiole winged. Hairs short (0.15–0.3 mm), unbranched and stiff, the terminal cell on leaf hairs typically obpyriform. Flowers small (calyx 8–15 mm, not widely divergent at apex, corolla 9–12 mm in diameter), limb concave and the tube usually longer than the calyx. Throughout most of the European range of the species, excepting the mountains of central and southern Europe, Turkey, the Caucasus and south-central Asia. The typical ssp. *veris*, in the sense of Schwarz (1968), is most abundant,

occurring from Britain, over Belgium towards Germany, the Czech Republic and Poland. It is the only subspecies that occurs in the British Isles (Länger & Saukel 1993).

2. *Primula veris* ssp. *columnae* Ten. (including ssp. *suaveolens*). Lamina ovate, usually cordate, characteristically with a thick covering of white hairs beneath; petiole not or slightly winged. Hairs long (1 mm), partly branched and interwoven, the terminal cell slightly ventricose. Flowers intermediate in size (calyx 16–20 mm, widened at apex and rather hairy, corolla 10–22 mm in diameter), limb almost flat and tube longer than calyx. Mountains of central Spain, central Italy, northern Greece and north-east Turkey.

3. *Primula veris* ssp. *canescens* Opiz. Lamina gradually decurrent into winged petiole, grey-tomentose beneath. Hairs intermediate in length (0.5–0.75 mm), twisted and often branched or interwoven. Flowers intermediate in size (calyx 16–20 mm, corolla 8–20 mm in diameter), limb slightly concave and tube usually equalling the calyx. Lowlands of central Europe, extending to the Alps, Pyrenees and mountains of northern Spain.

4. *Primula veris* ssp. *macrocalyx* Bunge. Lamina narrowed to a long, winged petiole, somewhat hairy to glabrescent beneath. Hairs intermediate in length (0.3–0.5 mm), usually straight, unbranched. Flowers large (calyx 15–20 mm, widened at the apex and often hairy, corolla 18–28 mm in diameter), tube longer than the calyx. South-east Russia (Crimea), Caucasus and south-central Asia, extending to east Siberia.

Primula veris is a native herb of well-drained, herb-rich meadows and grasslands on mesic to calcareous soils. It also occurs in scrub or woodland rides and edges, and on calcareous cliffs where it can be locally abundant. It is, however, less common than formerly, because of ploughing of permanent grassland and the use of fertilizers. In recent years, however, the species has made a notable comeback because of sowing on the embankments and verges of new or upgraded motorways and other trunk roads.

I. Geographical and altitudinal distribution

Primula veris is widespread in lowland areas in the British Isles (Fig. 1). It is recorded in 1632 10-km squares in Great Britain (about 58.2% of the total) (Preston *et al.* 2002). *Primula veris* is more local, or even absent, in much of the west, especially Cornwall, Devon, Wales and Western Scotland (Fig. 1) (Richards 1989). It occurs on the Orkney Islands, the Channel Islands, and the Shetland Islands, but is absent as a native from almost all the Hebridean Islands (Fig. 1). In Ireland, it occurs in 369 places in 10-km squares (about 37.5% of the total) (Preston *et al.* 2002), mainly in the central plain, a characteristic distribution for a calcicole (Fig. 1), but is very rare in the south and north (Richards 1989). It occurs as an escape from cultivation or as a deliberately sown species outside its native range.

The species occurs in most of Europe, north to 63° N in south Sweden and Finland, extends southwards to the Alps, but is absent from much of the Mediterranean region (see Fig. 2; Hultén & Fries 1986). The species occurs in northern
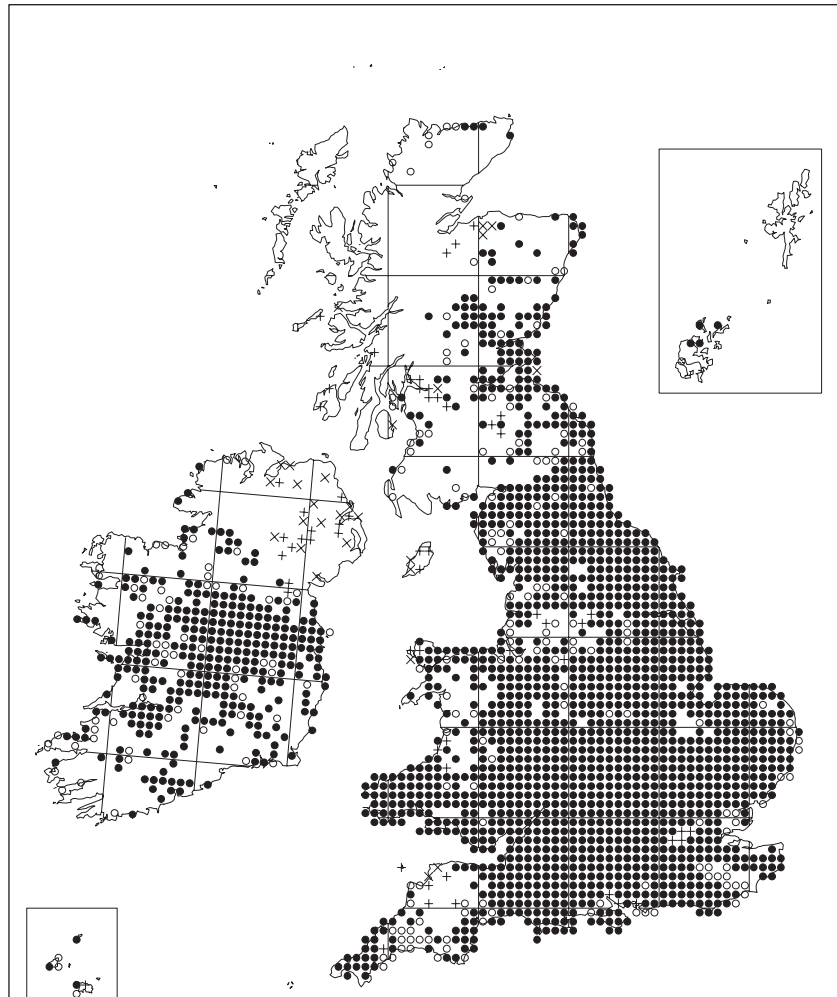
Fig. 1. The distribution of *Primula veris* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. (•) native 1970 onwards; (o) native pre 1970; (+) non-native 1970 onwards; (x) non-native pre 1970. Mapped by Stephanie Ames, Biological Records Centre, Centre for Ecology and Hydrology, mainly from records collected by members of the Botanical Society of the British Isles, using Dr Andrew Morton's DMAP software.

Spain, but is generally missing in the central part of Spain, although some distinct and isolated populations have been reported, for example in Valle de Tabladillo and La Granja, near Segovia (Castroviejo *et al.* 1997). In Italy, *P. veris* occurs from Piemonte in the Northwest along the Apennines to the Abruzzi Mountains in the South as well as in the region of Udine in the Northeast. The species occurs abundantly in the lowlands of Central Europe, from Germany to Poland (Mirek *et al.* 2002), the Czech Republic, and the Balkan Peninsula (Croatia, Yugoslavia, Albania and northern Greece (Länger & Saukel 1993)), up to the Pannonic lowlands in Hungary and Romania (Länger & Saukel 1993; Diekmann & Lawesson 1999). It extends its range in Central and South-East Russia and the Crimea up to the Urals, the Caucasus, Turkey, Iran and the Altai (Tutin *et al.* 1972), eastwards through Siberia to the Amur north of Manchuria (Hultén & Fries 1986; Richards 2002). The species is absent from Africa, Iceland, northern Siberia and much of the drier areas of central Asia (Richards 2002).

The British altitudinal range extends from sea level to 845 m on Great Dun Fell, Westmorland (Welch & Rawes 1965; Preston *et al.* 2002; Pearman & Corner 2004). In France and Spain, *P. veris* has been found from sea level up to 2300 m in the Pyrenees (Castroviejo *et al.* 1997). In the Alps, it has been reported between 1200 and 2100 m (Hegi 1975), and in

the northern Apennines (Italy) it occurs in calcareous grasslands between 800 and 1500 m a.s.l. In Central Europe, *P. veris* is mostly found between 300 and 600 m in so-called fringe communities (Valachovič 2004), and in Scandinavia its altitudinal range is mostly limited to the lowlands, not exceeding 100 m (Diekmann & Lawesson 1999).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Primula veris is categorized as a member of the Eurosiberian Temperate element by Preston and Hill (1997) and Preston *et al.* (2002). The mean January and July temperatures of 10-km squares where *P. veris* occurs in Britain are 3.7 and 15.2 °C, respectively (Hill *et al.* 2004). The mean annual precipitation is moderate (averaging 900 mm year^{-1}) (Hill *et al.* 2004). Within Great Britain, the cowslip can be found in regions that vary considerably in climatic conditions, from the south-east lowlands, where it is drier, warmer and sunnier and the rainfall is often less than 800 mm, towards its more elevated northern and western limits (upland fringes), beyond the Humber-Severn line, where it is cooler, cloudier and annual rainfall often exceeds 1500 mm. In the Sheffield area, northern
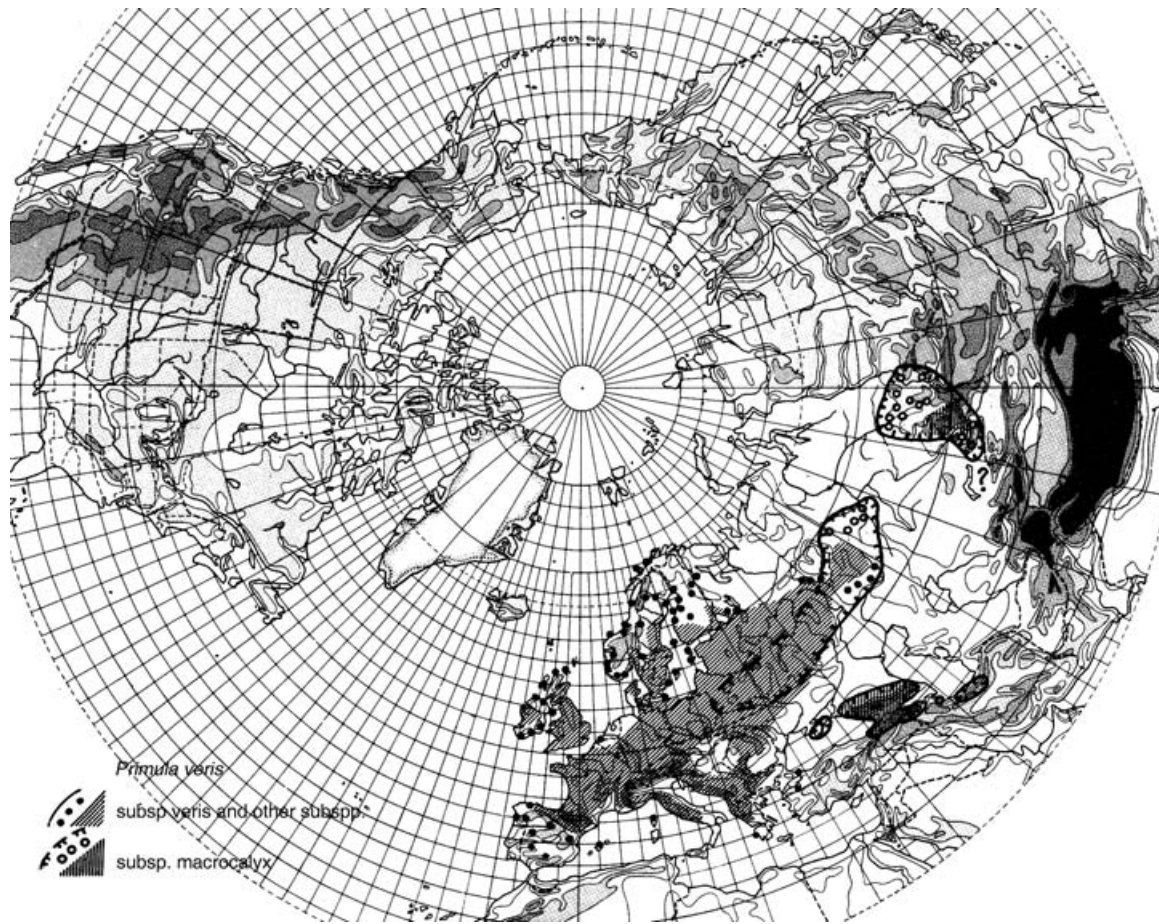
Fig. 2. European distribution of *Primula veris* ssp. *veris* sensu Länger & Saukel (1993). Reproduced from Hultén & Fries (1986) Atlas of North European Vascular Plants North of the Tropic of Cancer, Volume II, by permission of Koeltz Scientific Books, Koenigstein, Germany.

England, *P. veris* is mainly recorded on intermediate slopes corresponding to dale-side habitats, and it is significantly more frequent on unshaded south-facing slopes (Grime *et al.* 2007).

(B) SUBSTRATUM

Primula veris is most abundant on soils derived from a wide variety of more or less calcareous parent materials, such as sedimentary limestones, base-rich chalky boulder clay, loamy soils and sometimes stabilized dunes and cliffs. The species has also been recorded on stabilized scree slopes and lime-stone quarry heaps, lead-mine spoils, railway banks, road verges and, more rarely, in open scrub, mire and on skeletal soils. *Primula veris* occurs on soils with a range in acidity (pH 5.0–8.0), but never establishes on very acid soils (Diekmann & Lawesson 1999; Hill *et al.* 2004; Grime *et al.* 2007). The species further tolerates a wide range of soil moisture, and is characterised by low fertility (Hill *et al.* 2004).

Primula veris may occur on a range of soils, from deep free-draining, alluvial profiles over deep brown soils on clay-lands of the Midlands (which are generally loamy to clayey, and vary considerably in their pH, calcium content and soil moisture), to permanently moist, gleyed and periodically inundated circumneutral soils that can be found throughout

the British lowlands (Rodwell 1992). These soils are associated with a variety of calcareous bedrocks, including the lowland limestones on the Chalk, such as the rendzinas along the North and South Downs, the western oolitic limestones and chalklands, up through the Chilterns to the Lincolnshire and Yorkshire Wolds, where pH ranges from 7.5 to 7.8 (Rodwell 1992). Similar rendzinas occupied by *P. veris* populations are found at the Corallian Limestone of the North York Moors, the Magnesian Limestone of Durham and the Carboniferous Limestone of the Mendips, north and south Wales and Derbyshire Dales (Rodwell 1992; Hill *et al.* 2004).

In addition, *P. veris* occurs on calcareous fixed sands on dunes and coastal plains (Rodwell 2000). Although the surface sand layers at these locations are often darkened by the incorporation of decaying plant material and humus, the amount of organic matter remains very low (2–3%) (Rodwell 2000). Major nutrients, such as nitrogen and phosphorus, are also often limited in these soils. In the north-west of Scotland and the Isles, *P. veris* occurs in 'machair' dune grasslands. At such locations, the amount of calcium carbonate is commonly more than 50% of the sand, sometimes well over 75%, whereas the pH varies between 6.5 and 8.5 (Rodwell 2000). *Primula veris* is only persistent at coastal sites if it is not subjected to saline spray or water (Hill *et al.* 2004).

III. Communities

Primula veris is recorded from 11 grassland communities and 2 sand-dune communities in Britain (Rodwell 1992, 2000); in the following treatment the equivalent European phytosociological alliances are also described.

The species generally reaches its highest abundances in a number of calcicolous grasslands, where it is found in six British communities (Rodwell 1992). In the *Festuca ovina–Avenula (Helictotrichon) pratensis* grassland community (CG2), *P. veris* is a frequent component in the *Succisa pratensis–Leucanthemum vulgare*, the *Holcus lanatus–Trifolium repens* and the *Dicranum scoparium* sub-communities (in 21–40% of the vegetation samples), whereas it is only rarely found in the *Cirsium acaule–Asperula cynanchica* sub-community. Generally, this calcicolous grassland community comprises rich and intimate mixtures of grasses and herbaceous dicotyledons in a continuous, closed sward. Predominant among the grasses are fine-leaved species which form a compact sward. The only sedges to occur with any frequency are *Carex flacca* and *C. caryophyllea*. Among the dicotyledons, hemicryptophytes predominate. The *Festuca–Avenula (Helictotrichon)* grassland shows a wide distribution over the southern lowland limestones, and is always dependent for its maintenance on a certain balance of grazing, traditionally by sheep. Similar grassland communities, in which *P. veris* is frequent, have been widely described from limestones in north-west and Central Europe (e.g. Westhoff & den Held 1969; Oberdorfer 1978; Schaminée *et al.* 1996). In the Galio-Trifolietum, *P. veris* is a distinctive component, together with species such as *Carex flacca*, *C. caryophyllea*, *Sanguisorba minor* and a large number of other hemicryptophytes such as *Plantago media*, *Cirsium acaule*, *Bellis perennis*, *Leontodon hispidus*, *Leucanthemum vulgare*, *Succisa pratensis* and *Prunella vulgaris*. This grassland community occurs on fertile calcareous brown soils in cattle pastures and shows strong similarities with the *Succisa-Leucanthemum* sub-community (CG2b) (Rodwell *et al.* 2007).

Swards in which *Bromus erectus* (*Bromopsis erecta*) makes up more than 10% of the cover and where other grasses usually make a negligible contribution, are typical of the *B. erectus* grassland community (CG3), and contain infrequently scattered *P. veris* individuals. This grassland is generally confined to base-rich soils mostly in the south-eastern part of the country, over Chalk and Oolite. Many of the grasslands assigned to this community have certainly originated from *Festuca–Avenula (Helictotrichon)* grasslands as a result of the reduction of grazing.

Primula veris is also a minor component of the *Brachypodium pinnatum* grassland community (CG4), including all swards in which *B. pinnatum* makes up more than 10% of the cover and where other grasses usually make a negligible contribution. It comprises vegetation types that are similar to the *Festuca–Avenula (Helictotrichon)* grassland, but are somewhat poorer overall in species. As in the *Bromopsis erecta* community, the dominance of *Brachypodium pinnatum* is associated with an absence of grazing in predominantly calcicolous swards. In all the three sub-communities belonging to this community, the *Avenula (Helictotrichon) pratensis–*

Thymus praecox (polytrichus), the *Centaurea nigra–Leontodon hispidus* and the *Holcus lanatus* sub-community, *P. veris* can usually be found in low abundance. Grasslands similar to those described here, with the occurrence of the cowslip, have been reported from France (Allorge 1921), The Netherlands (Westhoff & den Held 1969) and Germany (Ellenberg 1978).

Primula veris is a minor component of the *Bromus erectus (Bromopsis erecta)–Brachypodium pinnatum* grassland community (CG5). This grassland community is very much centred on the Oolite of the Cotswold scarp and Northamptonshire/Lincolnshire, and is closely related to some Continental Mesobromion swards, such as the *Gentiano – Koelerietum* (Westhoff & den Held 1969; Ellenberg 1978; Oberdorfer 1978; Schaminée *et al.* 1996). In the latter, *P. veris* represents a constant component, and other species such as *Gentianella germanica*, *G. ciliata*, *Galium pumilum* and *Cirsium acaule* are distinctive associates of this community (Schaminée *et al.* 1996).

On moister and more mesotrophic calcareous soils on more flat or gently-sloping sites, where the *Avenula (Helictotrichon) pubescens* grassland (CG6) typically develops, *P. veris* is a constant element and can be locally abundant, especially in the *Dactylis glomerata – Briza media* sub-community. In this grassland community, the vegetation is usually dominated by various mixtures of *Festuca rubra* and generally smaller amounts of *Helictotrichon pubescens* and *H. pratensis*.

Primula veris reaches high constancy in the rare *Sesleria albicans (caerulea)–Scabiosa columbaria* grassland (CG8), in which its frequency ranges between 21% and 80% of the vegetation samples. In these closed swards, in which *S. albicans* is usually the most abundant grass, *Carex flacca* and *C. caryophyllea* are also very common. Typical associates in such swards are *Thymus polytrichus*, *Helianthemum nummularium*, *Sanguisorba minor*, *Plantago lanceolata*, *Lotus corniculatus*, *Campanula rotundifolia* and *Linum catharticum*. This community is restricted to free-draining, calcareous soils over Magnesian Limestone in the cool, dry climate of lowland Durham, and is generally maintained by grazing.

In mesotrophic grasslands, the cowslip is found in five communities (Rodwell 1992). *Primula veris* is a scarce member (occurring in 1–20% of the vegetation samples) of the *Centaurea nigra* and *Urtica dioica* sub-communities belonging to the *Arrhenatherum elatius* grassland community (MG1). In this grassland community, coarse-leaved tussock grasses are always conspicuous and generally dominant. The *Centaurea* sub-community is closely associated with moist calcareous soils on steep rocky slopes of Carboniferous and Magnesian limestone, whereas the *Urtica* sub-community, which is much more abundant in Britain, is prominent in areas of intensive arable agriculture. This community, in which *P. veris* represents a minor component, is very similar to the Arrhenatheretum of western Europe, where it is also widespread (Tüxen 1937; Schaminée *et al.* 1996).

In some upland valleys in northern England, *P. veris* is an infrequent and scarce member (in 1–20% of the vegetation samples) of the *Briza media* sub-community of the *Anthoxanthum odoratum–Geranium sylvaticum* grassland (MG3), typically developing on brown soils on level to moderate sloping

sites. This community shows clear affinities with other meadow types in the Arrhenatheretalia allocated to the Polygono-Trisetion, which replaces the Arrhenatherion at higher altitudes in central Europe.

Primula veris reaches higher abundances in the species-rich *Alopecurus pratensis–Sanguisorba officinalis* grassland (MG4), where it is found at 21–40% frequency. In this grassland community, herbaceous dicotyledons are always an important component of the herbage. Apart from *P. veris*, other rosette species, such as *Leontodon autumnalis*, *L. hispidus*, *Plantago lanceolata* and *Bellis perennis* are also often prominent in the short sward. This lowland grassland community is characteristic of areas where traditional hay-meadow management has been applied to seasonally-flooded land, and the repeated deposition of silt generally has resulted in accumulation of deep alluvial profiles under the meadows. This traditional hay–meadow grassland community, with *P. veris* as a minor component, is often reported from similar lowland grasslands in large parts of Western Europe (e.g. Westhoff & den Held 1969; Schaminée *et al*. 1996).

Throughout the British lowlands, *P. veris* is frequently present in the dicotyledon-rich *Cynosurus cristatus–Centaurea nigra* (*Centaureo–Cynosuretum*) grasslands (MG5). In the *Lathyrus pratensis* and the *Galium verum* sub-communities it is found at 21–40% frequency, whereas in the *Danthonia decumbens* sub-community, the species occurs much less frequently (1–21% of the samples). Within this grassland community, dicotyledons generally comprise a substantial proportion of the herbage, in which rosette hemicryptophytes, such as *P. veris*, are particularly prominent. This is a typical grassland of traditional seasonally-grazed hay-meadows. It is, however, becoming increasingly rare as a result of changed farming practices, a factor that is largely responsibe for the decline of *P. veris* in Britain during recent decades (see also XI). No equivalent vegetation type has been described from continental Europe.

Primula veris is an infrequent and scarce member of the *Holcus lanatus–Deschampsia cespitosa* community (MG9), a coarse sward dominated by *D. cespitosa* and other large tufted or tussocky grasses, such as *Holcus lanatus*, *Dactylis glomerata* and *Arrhenatherum elatius*. This community is virtually ubiquitous in suitable sites throughout the lowlands on permanently moist, gleyed and periodically waterlogged circumneutral soils. Lowland grassland types showing high similarities with this community, with the presence of *P. veris*, have been described from various parts of the Continent (e.g. Westhoff & den Held 1969).

Primula veris is a member of the *Festuca rubra – Galium verum* fixed dune grassland (SD8). Within this community, it is a minor component (in 1–20% of the vegetation samples) of the *Luzula campestris*, the *Bellis perennis–Ranunculus acris* and the *Prunella vulgaris* sub-communities. Generally, such dune vegetation comprises *Festuca rubra* and a variety of other grasses, dicotyledons and mosses that make up a closed sward. Within these grasslands, *Ammophila arenaria*, *Poa pratensis* and *Holcus lanatus* are a constant feature. Of the large number of dicotyledons, *Galium verum*, *Plantago lanceolata*, *Bellis perennis*, *Achillea millefolium*, *Thymus polytrichus*

and *Viola riviniana* often predominate. This grassland community can be found on suitable stable dunes and sand plains all around the British coast, especially at the more southerly coasts. In the north-west of Scotland and the Isles, these grassland communities, especially the *B. perennis–R. acris* and *P. vulgaris* swards, represent a typical component of the machair landscapes.

The species is a more frequent component of the *Ammophila arenaria–Arrhenatherum elatius* dune grassland (SD9) (occurring in 21–40% of the vegetation samples), which includes rank, tussocky swards in which both *Festuca rubra* and *Ammophila arenaria* are very common. Within this community *P. veris* is also a constant member of the *Geranium sanguineum* sub-community (in 21–40% of the vegetation samples). Compared with other dune grasslands, a noticeable feature of this community is the common occurrence of *Arrhenatherum elatius*. Within these swards, a wide variety of dicotyledonous herbs occurs, such as *Heracleum sphondylium*, *Achillea millefolium*, *Veronica chamaedrys*, *Galium verum*, *Ononis repens* and *Plantago lanceolata*, but bryophytes are usually few. This community is typically confined to less heavily grazed stretches of more fixed, calcareous coastal sands, occurring rather locally on dune systems all around Britain, though much more commonly along the seaboard of north-east England.

Finally, *P. veris* often occurs in large and dense stands in semi-natural grassland vegetations on roadside verges and embankments (Richards 2002). These semi-natural grasslands often show affinities with several of the above described grassland communities.

Outside Britain, *Primula veris* also occurs in the sub-Atlantic and central-European oak or oak-hornbeam forests of the Carpinion betuli (Nimis & Bolognini 1993; Pott 1995; Stortelder *et al*. 1998; Diekmann & Lawesson 1999). This association generally occurs on meso- or eutrophic more clayey-loamy soils, where the groundwater is near the soil surface, but fluctuates considerably in depth throughout the year. Dominant tree species are *Fraximus excelsior* and *Quercus robur*, but *Prunus avium*, *Acer pseudoplatanus* and *Carpinus betulus* are also regular components of this community. In Central Europe, *P. veris* occurs within the Primulo veris–Carpinetum community in the lowlands of southern Moravia and northern Hungary (Ellenberg 1988; Neuhäusl & Neuhäuslová 1968; Knollová & Chytrý 2004). The cowslip is also a widespread element of the xerothermic or thermophilous mixed Oak woods (Quercetalia pubescenti-petraeae), which are among the floristically richest habitats in Central Europe (Ellenberg 1988). The distribution of these mixed Oak woods extends from southern France (e.g. Buglossoido-Quercetum), over the calcareous soils of the southern Alpine valleys (e.g. Lithospermo-Quercetum), towards Central Europe, with its centre of distribution in south-east Europe. In the Bakony Mountains (Western Hungary), the cowslip is also a typical component of mixed oak forests in which *Quercus cerris* is interdispersed with *Fraximus ornus* and *Acer campestre* (Kálmán *et al*. 2004). In central and eastern-Europe, but also in Britain, Ireland, France, Belgium and the Netherlands, *Primula veris* is a typical component of the Prunetalia spinosa (Weber 1997;

Stortelder *et al.* 1998). This association is mainly found on shallow soils over limestone that are not influenced by the ground water table (Stortelder *et al.* 1998). Although *P. veris* is a typical associate of this vegetation, it rarely occurs under high abundances, and individuals often disperse from nearby more open locations. Other distinctive species of this association are *Prunus spinosa*, *Crataegus monogyna*, *Rosa canina*, *R. agrestis*, *Ligustre vulgare*, *Viburnum lantana*, *Viola canina*, *Orchis purpurea*, *Sanicula europea* and *Brachypodium pinnatum*.

Diekmann and Lawesson (1999) reported that in northern Germany and Denmark *P. veris* is associated with the limestone beech forests (Cephalanthero-Fagion). In the Baltic, the cowslip is a constant component of species-rich wooded meadows and alvar forests. Here *P. veris* co-occurs with *Orchis mascula*, *Sesleria caerulea*, *Filipendula vulgaris*, *Galium verum*, *Hepatica nobilis*, *Melica nutans*, *Brachypodium pinnatum*, *Calamagrostis arundinacea* and *Carex montana* (T. Kull, pers. comm.). *Primula veris* is also reported from mesic wooded meadows in Southern Sweden (the so-called '*Sesleria* meadows', *sensu* Tamm 1972), where scattered trees such as *Quercus robur* and *Betula pendula* represent a typical aspect of these communities. In these meadows, *Viola canina*, *Anthoxanthum odoratum*, *Potentilla erecta*, *Persicaria vivipara*, *Galium verum*, *Alchemilla* sp., *Filipendula vulgaris* and *Melampyrum nemorosa* are distinctive associates (Tamm 1956).

Primula veris represents a typical component of the forest association Orchio-cornetum, which is mainly found on shallow soils over limestone that are not influenced by the ground water table (Stortelder *et al.* 1998). This association is reported from Belgium, the Netherlands, Germany and northern France, and is tightly linked with coppice and wood edges (Stortelder *et al.* 1998). Apart from *P. veris*, *Orchis purpurea*, *Hypericum hirsutum*, *Ophrys insectifera*, *Cephalanthera damasonium*, *Rosa arvensis*, *Arum maculatum*, *Viola reichenbachiana*, *Listera (Neottia) ovata*, *Polygonatum multiflorum*, *Paris quadrifolia*, *Primula elatior* and *Platanthera chlorantha* represent distinctive components of this forest community.

Primula veris is also often associated with the *Primula–Schoenus ferrugineus* association (calcareous fens), occurring either in moist, soligenous mire sites or at locations characterized by strongly shifting water tables (Tyler 1981). This association is generally found in Scandinavia, the Baltic and Central Europe, where *Schoenus ferrugineus*, *Liparis loeselii*, *Primula farinosa* and *Tofieldia calyculata* are distinctive associates.

IV. Response to biotic factors

One of the major biotic factors promoting survival or loss of *P. veris* populations is human activity and the occurrence of this species is closely associated with historical land-use practices such as mowing and grazing. Although the species is capable of persisting several years and even decades after management has ceased (Brys *et al.* 2004; Ehrlén *et al.* 2005; Lehtilä *et al.* 2006), it responds rapidly to environmental changes and/or vegetation succession (Brys *et al.* 2005; Endels *et al.* 2005; Lindborg *et al.* 2005). Abandonment of traditional grazing or mowing, and closing shrub or tree canopy quickly
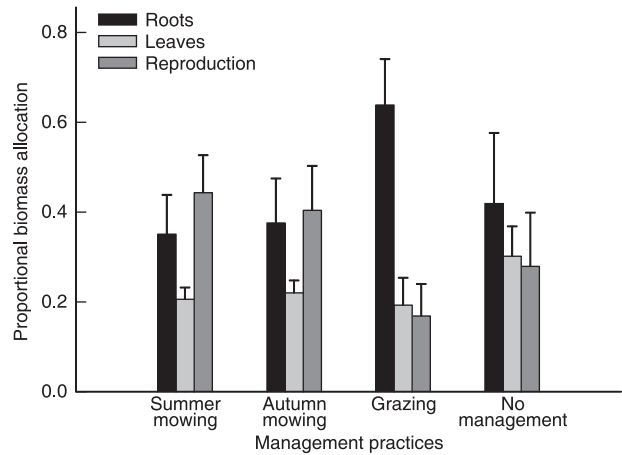

Fig. 3. Mean proportional biomass allocation (± SE) to roots, leaves and reproductive tissue obtained from 20 reproductive *Primula veris* individuals under four management treatments (summer mowing, autumn mowing, grazing and no management) in a calcareous grassland in Belgium (Voeren). At the end of April, each individual was dug out and oven dried for 24 h at 70 °C, after which the roots, leaves and flower stalks were weighed. Summer and autumn mowing took place at the end of July and mid-October, respectively, and grazing was applied by cattle from the beginning of July until the end of September.

result in lower performance and reduced population growth rates of *P. veris* (see V B).

Although grazing has undoubtedly contributed to the maintenance of *P. veris* in a large part of its distribution area in the past, the timing and intensity of grazing affect its performance and population dynamics. Intense grazing by cattle early in the growing season causes a lower proportional biomass allocation to reproductive tissue, a lower number of flowers per plant and reduced leaf area (Figs 3 and 4; R. Brys and H. Jacquemyn, unpubl. data). Experiments in which a proportion of the leaves was removed at different times in the growing season showed that removal of 50% of the leaves during flowering (early defoliation) negatively affected current reproductive performance (fruit set and total seed production) and future growth, whereas removal of leaves later in the season (removal of 50% of the leaves during fruit development) only reduced future flowering probability and growth (middle defoliation), or did not affect any fitness component (late defoliation, removal of 50% of the leaves during fruit maturation) (García & Ehrlén 2002). Both observations thus suggest that damage to above-ground tissue during the growing season not only results in the destruction of flowering stalks and fruits, but also in reduced flowering probabilities and performance of adult individuals in the next growing season depending on the developmental stage of the plant (García & Ehrlén 2002; Brys *et al.* 2004). These responses may, at least partly, be explained by the fact that the species invests considerable resources in above-ground growth and carbohydrate production each spring (Syrjänen & Lehtilä 1993), and because the starch content in its roots is very low during flowering (Mestenhauser 1961).

Herbivores also exert indirect effects through the creation of gaps, which serve as safe sites for seed germination. However,
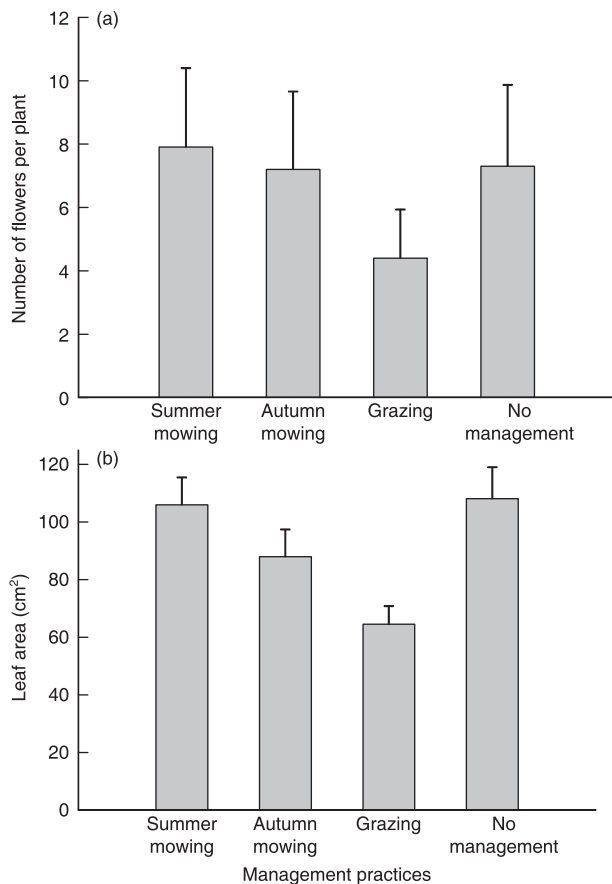
Fig. 4. (a) Number of flowers and (b) leaf area produced by 20 reproductive *Primula veris* individuals under four management regimes (summer mowing, autumn mowing, grazing and no management) in a calcareous grassland in Belgium (Voeren). Summer and autumn mowing took place at the end of July and mid-October, respectively, and grazing was applied by cattle from the beginning of July until the end of September. Means (± SE).

if gaps in the vegetation become too large, frost and drought reduce recruitment (Ryser 1993). The Common Vole, *Microtus arvalis* (Pallas), also promotes germination of *P. veris* seeds, as it creates gaps in the vegetation especially around the burrows and along its runways (Gigon & Leutert 1996).

V. Response to environment

(A) GREGARIOUSNESS

If conditions are favourable, *P. veris* can develop large and conspicuous populations with high densities. Although *P. veris* is never a dominant species in the vegetation, adult rosette densities between 10 and 34 individuals per m^2 have been found (Kéry *et al.* 2003; Brys *et al.* 2004), whereas seedlings may reach densities up to 100–200 m^{-2} (R. Brys and H. Jacquemyn, unpubl. data). Because of the limited seed dispersal capacity (see VIII C), seedlings generally occur clustered around adult plants (R. Brys & H. Jacquemyn, pers. observ.). Occasionally, clusters of *P. veris* may arise as a result of vegetative propagation, although this seems to be limited (Tamm 1972; Van Rossum & Triest 2007; see also VI C).

(B) PERFORMANCE IN VARIOUS HABITATS

Although *Primula veris* occurs in a broad range of habitats, it often shows reduced performance under shade or increased competition. Flowering frequency and the number of flowers and flowering stalks produced per plant significantly decrease after abandonment of traditional grassland management (Brys *et al.* 2004; Ehrlén *et al.* 2005; Lindborg *et al.* 2005) or closing tree canopy (Tamm 1972; Whale 1984; Endels *et al.* 2005). Individuals that are still able to flower under shaded conditions often have insufficient reserves to enable the scape to become sclerified, ultimately leading to its collapse (Keith-Lucas 1968). Increasing shade also reduces seed maturation, resulting in significantly lower seed production rates compared to unshaded individuals (Keith-Lucas 1968; Whale 1984). Succession to forest further results in reduced population growth, mainly due to decreased sexual reproduction and seedling recruitment, and increasing mortality. This leads to skewed population structures with an excess of old adults (Brys *et al.* 2004; Endels *et al.* 2005; Lehtilä *et al.* 2006). Such 'regressive' population structures have also been found in small and remnant populations of *P. veris* growing in small landscape elements deprived of any disturbance regime in the western part of Belgium (Brys *et al.* 2003). These observations also agree with findings of Tamm (1972), who showed strong reductions in the abundance, the number of flowering individuals and their longevity once the species was overshadowed by trees and shrubs, or even by tall broadleaved grasses such as *Brachypodium sylvaticum*. In contrast, the species also responds quickly to increasing light after canopy removal or opening of the vegetation, resulting in an immediate response of increased flowering and both increased growth and seedling recruitment the year after (Endels *et al.* 2005). Nonetheless, *P. veris* can be found in forest edges and relatively open forests or woods with a long tradition of coppicing on limestone pavements, where the species is able to flower abundantly and reproduce successfully.

Primula veris is a characteristic of nutrient-poor habitats (Ellenberg value for nitrogen = 3; Hill *et al.* 2004). Experiments that artificially increased nitrogen (commercial solid NH$_4$NO$_3$) deposition resulted in declining population sizes (Brys *et al.* 2005), which were mainly the result of reduced flowering probabilities, seed production, recruitment and establishment of seedlings. Long-term projections (Brys *et al.* 2005) also showed that populations subjected to the highest N enrichment (9 gN m^{-2} year^{-1}) will become extinct within 30 years (mean annual population decline of 18.2% and 15.5% and mean time to extinction of 13.7 and 24.4 years under mowing and grazing, respectively) (Brys *et al.* 2005), whereas populations that receive no fertilizer treatment will increase in population size.

(C) EFFECT OF FROST, DROUGHT, ETC.

Effect of frost

There is little evidence of mortality of adult plants due to frost. *Primula veris* is adapted to long and cold winters with

deep soil frost and to late and quick spring warming (Hegi 1975; Länger & Saukel 1993; Diekmann & Lawesson 1999).

At the core of its range within Britain, the mean number of days of ground frost during January ranges between 18 and 21, indicating frequent frosts during winter. Late frost may, however, cause damage of flowers and flowering stalks and consequently decrease reproductive output later in the growing season (Inghe & Tamm 1988).

Effect of waterlogging and drought

Primula veris is mostly absent from grasslands characterized by a high water table (Grime *et al*. 2007). Whale (1983b) showed that the mean dry mass of new *P. veris* recruits decreased significantly with an experimentally raised water table after three months of growth. Such a reduced biomass increment during early growth may in turn reduce an individual's ability to compete and/or become successfully established. Moreover, roots are not able to penetrate into anoxic layers and therefore are shorter and only penetrate the upper soil layers under saturated soil conditions. Such a restriction or cessation of root growth under waterlogged conditions is characteristic of waterlogging-intolerant species.

Compared to the related *Primula vulgaris* and *P. elatior*, *P. veris* is the most drought tolerant (Gilbert 1903; Woodell 1969; Whale 1984), as it tolerates lower soil water potentials than both other species before its photosynthetic rate is appreciably affected (Whale 1983b). Although Inghe and Tamm (1988) often observed temporary wilting of *P. veris* rosettes in dry summer periods in southern Sweden, they did not detect a significant impact on survival probabilities of such individuals. Under exceptionally dry and hot conditions during flowering, flowers are, however, found to wilt much faster, resulting in a significant reduction of fruit and seed set (pers. observ.).

Effect of shade

Primula veris has an Ellenberg value of 7 for light, indicating that it is a typical species of well lit places, but that it can also survive under partial shade (see V B). Based on experimental measurements of CO_2 exchange in *P. veris*, *P. vulgaris* and *P. elatior*, in which incident radiation was gradually reduced by means of shading screens, Whale (1982, 1983a) showed that *P. veris* was the least, and *P. vulgaris* the most shade tolerant species with *P. elatior* intermediate between the two (see also VI E).

VI. Structure and physiology

(A) MORPHOLOGY

Primula veris is a rosette hemicryptophyte (Clapham *et al*. 1987). The mature vertical rhizome is short, stout, and girt at the apex with the broad withered basal remains of old foliage (Fig. 5). The rhizomes produce numerous fibrous roots, thrusting through living leaf bases, and can be up to 15 cm long. Roots contain starch grains that may vary in size from 4 to 10 μm (Länger & Saukel 1993).
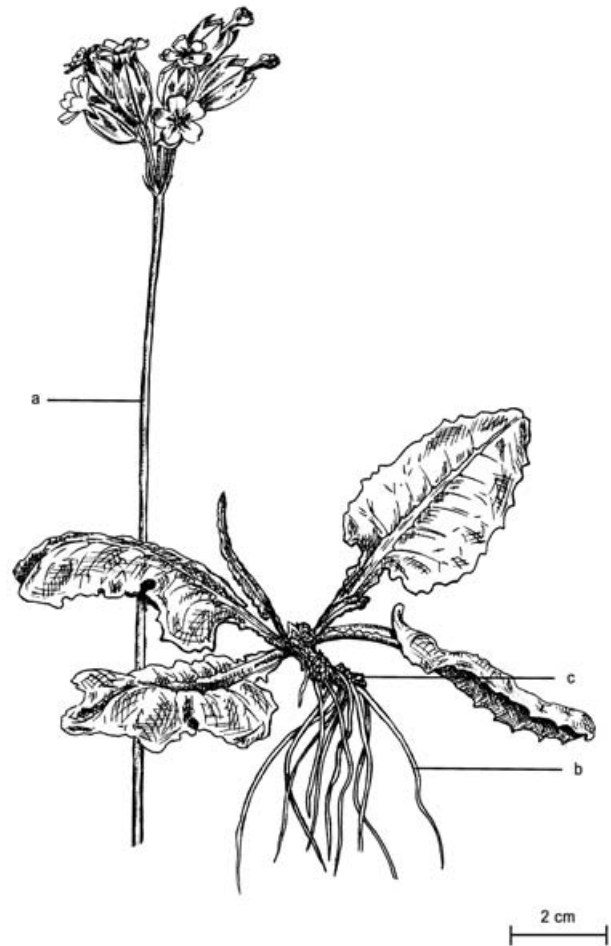

Fig. 5. Adult plant of *Primula veris* in April. (a) Flowering scape, (b) fibrous roots and (c) vertical rhizome.

A rosette of *P. veris* bears successive leaves, which enlarge throughout the growing-season until fruiting. Older leaves gradually senesce, first turning yellow and then rotting to leave a brown fibrous coating around the base of the stem. The overwintering leaves are dull green, short, sheathing and unexpanded. The mean number of stomata (± SE) in an area of leaf lamina of 0.096 mm^2 for five leaves of *P. veris* was 2.8 ± 0.4 and 13.9 ± 1.3 on the abaxial and adaxial surfaces, respectively (Whale 1982). An intercalary primordium may give rise either to a new vegetative rosette or to an inflorescence. Scapes, originating in the axils of leaf bases, are pilose and grow out in April, usually bearing one or two umbels with up to 30 flower buds (Fig. 5). Scapes are flexible during flowering, but become more rigid as the fruits develop.

(B) MYCORRHIZA

Arbuscular mycorrhizas have been reported in *Primula veris* (Nespiak 1953; Stelz 1968; Harley & Harley 1986).

(C) PERENNATION: REPRODUCTION

Primula veris is a long-lived perennial. In a Scandinavian population Ehrlén & Lehtila (2002) estimated an average life

span of 52.3 years. Reproduction occurs mainly through seeds. However, under unfavourable conditions, individuals may produce lateral rosettes throughout the growing season. Rosettes occur clustered and densely packed around the mother plant and remain attached to the parent axis (Tamm 1972; Grime *et al.* 2007). Branching of the rhizome has been observed in a small fraction of the genets and only over very short distances (Van Rossum & Triest 2007). Seedlings can reach maturity and start to flower from their third or fourth year of growth onwards (R. Brys and H. Jacquemyn, unpubl. data).

(D) CHROMOSOMES

Like all other members of the section *Primula*, *P. veris* is diploid with a somatic chromosome number of $2n = 22$ (Clapham *et al.* 1987).

(E) PHYSIOLOGICAL DATA

Primula veris uses the C_3 pathway of carbon fixation. The seasonal dynamics of photosynthetic CO_2 uptake were studied by Whale (1983a) in the field from the assimilation of $^{14}CO_2$ from a labelled air supply. Photosynthetic parameters were obtained from light response curves at different times of the year and for different temperatures. The peak in the light saturated rate of CO_2 assimilation (A_{max}) in *P. veris* (10.5 ± 0.4 μmol m^{-2} s^{-1}) occurred at the beginning of April, when plants start flowering, and declined during the growing season. *Primula veris* thus shows an increased carbon gain early in spring that exploits the high spring light phase before expansion of the vegetation canopy. This high light phase largely coincides with flower and fruit production, and a substantial carbon gain in spring could guarantee the initiation of flower primordia and/or increase the proportion of dormant flower buds developing (Whale 1983a). The light saturation point for *P. veris* occurred at a quantum flux density (**Q**) of 1160 μmol m^{-2} s^{-1}, and its calculated quantum efficiency was 20 ± 3 nmol CO_2 μmol photon^{-1} (mean ± SE). Compared to the related *Primula elatior* and *P. vulgaris*, *P. veris* is least well-adapted to survive moderate shade, as a consequence of its relatively low quantum efficiency, high light saturation point and high dark respiration rate (2.7 ± 0.2 μmol m^{-2} s^{-1} measured in the laboratory).

The response of photosynthesis in *P. veris* to imposed soil water deficits has also been experimentally assessed (Whale 1983a). Non-flowering potted plants were watered and allowed to drain to field capacity. The pot and soil were then sealed from the above-ground parts of the plant and individuals could then transpire freely with no replenishment of water lost. Plants were allowed to wilt for one day after which they were re-watered. At frequent intervals during this drying/rewetting cycle, plants were weighed to determine water loss through transpiration. Light response curves for the aerial parts of the plants were obtained from measurements of CO_2 exchange by means of infrared gas analysis. As water content fell, quantum efficiencies, dark respiration and photosynthetic rates all rapidly declined in *P. veris*, but recovery of the maximum photosynthetic rate (A_{max}) on rewetting was achieved within 48 h. As the intensity of soil drought increased, stomatal conductance and maximum photosynthetic rate declined, but compared to the related *P. vulgaris* and *P. elatior*, this decrease was much slower (Whale 1983a). Based on the cumulative water loss on a leaf area basis relative to the proportion of photosynthetic maximum maintained, *P. veris* also transpired the least water compared to *P. vulgaris* and *P. elatior*, making it the most drought tolerant species of the three.

(F) BIOCHEMICAL DATA

Primula veris roots contain up to 29.5 mg g^{-1} dry mass triterpene saponins, mainly primulasaponin A (on average) and primulasaponin B, as well as the phenolic glycosides, primulaveroside and primveroside, which are used medically to treat inflammation, laryngitis and bronchitis (Calis *et al.* 1992; Muller *et al.* 2006; Okrslar *et al.* 2007). Flowers also contain triterpene saponins, phenolic glucosides, and flavonoids: 3′, 4′, 5′-trimethoxyflavone (Huck *et al.* 1999, 2000), quercetine and its derivatives, kaempferol, and 3-limocitrin glucoside (Hegnauer 1990). Similar lipophilic flavonoids, with the exception of methoxyflavones, as well as 3′, 4′-dihydroxyflavonglucoside were detected in leaves of *P. veris* (Hegnauer 1990; Harborne 1994; Budzianowski *et al.* 2005). Ethanolic extracts are also obtained from the leaves for the treatment of epilepsy and convulsions (Jager *et al.* 2006).

VII. Phenology

Primula veris rosettes lose old leaves during winter. The production of new leaves occurs in late winter (February–March). They expand throughout the growing season and achieve peak biomass in summer. Especially under dry and hot conditions, a substantial number of leaves senesces at the end of the growing season (August–October), but the majority remains until new leaves are developed in late winter (Grime *et al.* 2007).

Flowering primordia generally appear in late autumn (Poshkurlat 1962), but flower buds on unextended scapes become visible at the end of March and the beginning of April (pers. observ.). Flowering takes place from the beginning of April to the middle of May. In a subsample of 27 *P. veris* populations in Switzerland, Kéry *et al.* (2003) observed that thrum plants produced significantly more flowers per inflorescence than pin plants (on average 6.31 and 5.78, respectively). Peak flowering occurs at the end of April, and the number of flowering plants within a population may vary strongly between years and sites (Inghe & Tamm 1988). A 9-year study of a large *P. veris* population in a calcareous grassland in the eastern part of Belgium revealed that the proportion of adult flowering individuals varied greatly from year to year, with some remarkably good (1999, 2005 and 2007) and bad (2001 and 2002) years (Fig. 6). Within this site, the proportion of flowering individuals was significantly lower under grazing than under summer mowing (on average 13.3% and 44.4%, respectively) (Fig. 6). Flowering frequencies of adult individuals were on average 0.47 ± 0.02 and 0.17 ± 0.02, under summer
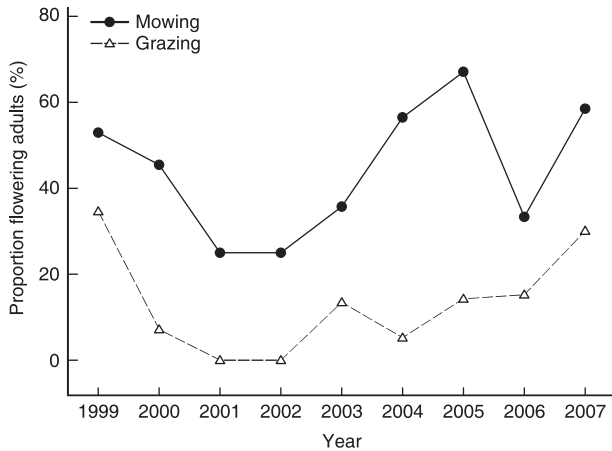
Fig. 6. Proportion of flowering *Primula veris* adults over a 9-year period (1999–2007) under grazing and summer mowing management in a calcareous grassland in Belgium (Voeren). Mowing took place at the end of July and grazing was applied by cattle from the beginning of July until the end of September.

mowing and grazing, respectively, indicating that an adult plant flowered 2.7 times more frequently under mowing than under grazing over this nine-year study period (R. Brys and H. Jacquemyn, unpubl. results). Seeds ripen 8–10 weeks after fertilization and seed shed takes place from mid July to September onwards.

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

Reproduction of *Primula veris* is amphimictic. It is an obligate outbreeder and entirely depends on foraging insects for successful pollination (Darwin 1877). *Primula veris* flowers are fragrant, produce copious nectar, and are visited by a variety of insects (see Table 1). It is successfully pollinated by insects with long probosces that are able to exploit the nectar (Proctor & Yeo 1973). Nonetheless, *P. veris* flowers are also frequently visited by small insects, such as thrips (*Taeniothrips* spp.) and small beetles (*Meligethes* spp.) (Darwin 1877; Woodell 1960a; pers. observ.).

As in other *Primula* species, distyly is controlled by a 'supergene', involving at least seven loci, including those for style length, anther height, and size of pollen and stigmatic papillae. This complex acts together to produce two super-alleles, S and s, in which the allele determining the thrum morph is dominant (Bateson & Gregory 1905; Richards 1997). With this system pin plants are thus homozygous recessive (ss) and thrums are heterozygotes (Ss). Homozygous thrums (SS) do not normally occur under field conditions since illegitimate pollination in the thrum morph generally fails to produce any seeds (Wedderburn & Richards 1990).

Heterostyly in *P. veris* was first investigated and thoroughly described by Darwin (1862) in the mid-nineteenth century. He illustrated and described the dimorphic flowers of *P. veris* in detail, noting that there were not only intermorph differences in style length and stamen position, but also associated dimorphisms in corolla and stigma shape, length of stigmatic papillae, and size and shape of pollen grains. Generally, pin stigmas are globular and the surface is rough while thrum stigmas are somewhat flattened and have a central depression, so that the longitudinal axis is much larger than that of pin stigmas (Darwin 1862). The anthers of the morphs do not differ in size (Darwin 1877). Average pollen size for pins is 18.1 µm (range 13.6–23.4 µm), whereas that for thrums is 29.5 µm (range 25.4–33.2 µm) (Ornduff 1980; Morozowska

Table 1. Pollinators recorded for *Primula veris* L.

Species/classification	Source	Species/classification	Source
HYMENOPTERA		COLEOPTERA	
Apidae		Nitidulidae	
Bombus hortorum L.	1, 2, 3	*Meligethes nigrescens* Sr.	1, 3
B. lapidarius L.	1, 2, 3	*M. solidus* Kug.	1
B. pascuorum S. (=*B. agrorum* F.)	1, 2, 3	*M. erichsoni* Bris.	1
B. muscorum L.	1, 2, 3, 7, 8	*M. erythropus* Marsh	1
B. terrestris L.	2, 3, 7, 8	*M. obscurus* Ev.	1
B. rajellus K.	2	*M. aeneus* F.	1
Andrenidae		*M. pedicularius* G.	1
Andrena gwynana K.	2	*M. difficilis* Heer.	1
Anthophoridae			
Anthophora pilipes F.	2, 4, 5, 8	LEPIDOPTERA	
Anthophora acervorum L.	1, 2	Noctuidae	1
Halictidae		*Cucullia verbasci* L.	
Halictus albipes F.	2	Pieridae	6
H. cylindricus F.	2	*Gonepteryx rhamni* L.	
DIPTERA			
Bombyliidae			
Bombylius discolor Mik.	2, 4, 5, 8		

Information obtained from: 1, Darwin (1877); 2, Knuth (1909); 3, Christy (1922); 4, Proctor & Yeo (1973); 5, Lack (1982); 6, Müller (1883); 7, Weiss (1904); 8, Woodell (1991).

& Idzikowska 2004). The smaller pin pollen is thought to attach more easily on the short thrum papillae than on the much longer pin papillae and *vice versa* (Richards 1989). Pin individuals produce on average 211 000 pollen grains per flower, whereas thrums produce on average 87 000 (Ornduff 1980), resulting in an average pin : thrum ratio of pollen production per flower of 2.4 : 1. Pollen grains from pin individuals are mainly 6-colpate, whereas those of thrum flowers are 8-colpate (Erdtman 1952; Moore *et al.* 1991; Morozowska & Idzikowska 2004). Ornamentation of pin pollen grains is microreticulate, with lumina up to 0.8 μm wide, and thrum pollen grains are reticulate and eureticulate with lumina that are 1.1–1.7 μm wide (Nowicke & Skvarla 1977; Morozowska & Idzikowska 2004). Thrum pollen germination, following legitimate pollination, was greatest at 6 °C, while pin pollen germinated best at 15 °C (McKee & Richards 1998).

Although the incompatibility genes are closely linked to those controlling heteromorphic features, there is no evidence that these heteromorphic features are directly involved in the functioning of the incompatibility in *Primula* (Wedderburn & Richards 1990). The incompatibility system is limited to the stigma and style, and penetration of stigmatic papillae by pollen tubes is affected by self-recognition reactions of both the pollen tubes and stigmatic papillae (Wedderburn & Richards 1990). Following illegitimate pollination, pollen tubes generally become swollen and sinuous, whereas the stigmatic papillae often show localized callose responses inhibiting further pollen tube growth (Richards & Ibrahim 1982; Richards 1997). Nonetheless, Darwin (1877) had reported that the incompatibility system in *P. veris* was not strict and weaker in pin than in thrum individuals. About 14.5% of the total number of ovules set seed after illegitimate pin × pin crosses, whereas an average seed set of only 0.6% was found following thrum × thrum illegitimate crosses (Wedderburn & Richards 1990). For both floral morph types, illegitimate pollen germination and pollen tube growth was significantly stimulated by increasing temperature (highest at 26 °C) (McKee & Richards 1998). Richards & Ibrahim (1982) also found that selfing is very unlikely under natural conditions, and inbreeding depression was reported in selfed pin offspring by Darwin (1876), which suggests that crossing of pin morphs may be successful in producing a limited number of viable seeds.

In contrast to the optimal disassortative pollen flow hypothesis in heterostylous species, Ornduff (1980) showed very low levels of intermorph pollination of pin individuals and moderate levels of intermorph pollination in the thrum morph in two natural cowslip populations in Britain. Moreover, pin stigmas bore between 92% and 97% illegitimate pin pollen and between 8% and 3% legitimate thrum pollen, whereas in thrum stigmas 34% and 69% of the pollen load was composed of thrum pollen and 66% and 31% was composed of pin pollen (Ornduff 1980). Woodell (1991) documented comparable levels of legitimate pollination of pin flowers that ranged between 2% and 16%, and even lower levels on thrum stigmas ranging between 1% and 6% in five natural *P. veris* populations in Britain. These observations suggests that the reciprocal positioning of stigmas and anthers does not limit interference

of pollen removal with pollen deposition within the same morph and that it does not promote disassortative pollen transfer, as would be theoretically predicted. Such asymmetric pollination in combination with a weak self-incompatibility system is one of the most likely mechanisms to cause deviations in morph ratios (e.g. Barrett *et al.* 1989). Nonetheless, several studies in a large number of *P. veris* populations in England (*n* = 18; Antrobus & Lack 1993), Switzerland (*n* = 76; Kéry *et al.* 2003) and Belgium (*n* = 69; Brys *et al.* 2003) did not find a substantial deviation towards any morph at population level. Only Lees (1971) reported a small, but significant excess of thrum plants in a *P. veris* population in Scotland, which he interpreted as possibly due to a heterozygote advantage.

Pollen flow patterns within *P. veris* populations have been measured by Richards & Ibrahim (1978) by counting legitimate pollen loads on stigmas of naturally pollinated plants in two large populations in Britain (Northumberland). Average pollen dispersal distances varied between 1.11 and 2.63 m, with 95% of the pollen travelling 3.5–12 m, and were not significantly different between morphs. Leptokurtic pollen dispersal and small pollen dispersal distances (Richards & Ibrahim 1978; Richards 1997) are consistent with gene dispersal distances as reported by Van Rossum & Triest (2007) (on average 1.98 m). Legitimate pollen transfer also decreased with decreasing plant densities (Richards & Ibrahim 1978), and pollen dispersal was less at higher plant densities (Richards 1997). This also agrees with observations of Van Rossum *et al.* (2004), who showed increasing levels of (biparental) inbreeding at high plant densities, which they, at least partly, attributed to pollinator behaviour combined with restricted seed dispersal. On the other hand, Antrobus & Lack (1993) and Morozowska & Krzakowa (2003) argued that long-distance pollen dispersal across populations is one of the most plausible explanations for the low genetic differentiation (F_{ST} < 0.102) that they observed among *P. veris* populations in the Oxford region and western Poland, respectively. Because *P. veris* flowers at the time that queen *Bombus* spp., *Anthophora* spp. and early emerging *Bombyliidae* are searching for nests, it can be reasonably expected that they cover a wider area than during the normal foraging behaviour of workers later in the flowering season, which may explain the observed levels of genetic differentiation.

(B) HYBRIDS

Although British populations of *P. veris*, *P. vulgaris* and *P. elatior* tend to be separated by ecological differentiation (Valentine 1961), all three species are known to hybridize in some mixed natural populations (Valentine 1975).

The hybrid *P. veris* × *P. elatior* (= *P. × media* Peterm.) (see Fig. 7a) occurs only rarely in Britain (Valentine 1952) and is restricted to some wild populations occurring in wet meadows and woods in East Anglia (Christy 1897; Hill 1907; Jermyn 1974; Valentine 1975; Simpson 1982; Wells 1983). Its distribution in Britain is shown by Taylor and Woodell (2008). Outside Britain, natural *P. × media* hybrids have also been found in Czechoslovakia (Valentine 1966), Belgium and northern France

Fig. 7. The hybrids (a) *P. × media* (Peterm.) (*P. veris × P. elatior*) at Maintenon (Eure-et-Loire, France), and (b) *P. × polyantha* (Mill.) (*P. veris × P. vulgaris*) at Maulden (Bedfordshire, UK). Both photographs are of spontaneous hybrid individuals in natural populations in the field.

(R. Brys and H. Jacquemyn, unpublished results). *Primula veris* and *P. elatior* only occasionally meet in damp meadows or alluvial forests, flower at different times, and there are strong internal barriers to hybridization (Valentine 1952), factors which may explain the rarity of this hybrid. Experimental interspecific crosses (both *P. veris* ♀ × *P. elatior* ♂ and *P. elatior* ♀ × *P. veris* ♂) result in very small and light seeds with only very few seeds containing traces of endosperm at maturity (Valentine 1955; Woodell 1960b). Only 0.5% of the seeds obtained from *P. veris* ♀ × *P. elatior* ♂ crosses germinated successfully, whereas none of the seeds originating from *P. elatior* ♀ × *P. veris* ♂ germinated (Valentine 1955).

The hybrid *P. veris* L. × *P. vulgaris* Huds. (= *P. × polyantha* Mill.; False Oxlip) (see Fig. 7b) is predominantly found on woodland rides and edges, in scrub, hedgerows and on roadside verges throughout the area where the distributions of the two parents overlap (Richards 1989; Preston *et al.* 2002). Although the parent plants have different ecological requirements, several sympatric populations are known that show an overlap in their flowering period both in England (Clifford 1958; Woodell 1965; Mowat 1961; Valentine 1975; Richards & Ibrahim 1978; O'Mahony 2004) and Europe, such as in Austria (Hegi 1975); France (pers. observ.) and Hungary (Bauer & Cservenka 2002; Kálmán *et al.* 2004). Hybrids tend to occur as scattered individuals in natural populations, rather than in large masses (Pugsley 1927; Valentine 1955). Experimental interspecific crosses showed that most of the resulting seeds,

both from *P. veris* ♀ × *P. vulgaris* ♂ and *P. vulgaris* ♀ × *P. veris* ♂ crosses, are empty at maturity, but some have little endosperm and a few an embryo, which rarely reaches mature size (Valentine 1955). Generally, only seeds resulting from *P. veris* ♀ × *P. vulgaris* ♂ crosses are able to germinate (on average 37%) (Valentine 1955). Flowers of the hybrids are intermediate in colour and size between the two parental species, and they are produced in pedunculate inflorescences similar to their cowslip parents (Clifford 1958; Hegi 1975; Gurney *et al.* 2007). Investigation of floral variation in the hybrid zone of both species revealed strict reciprocity between anther and stigma heights of both parental species, but reciprocity was strongly broken in the F_1 hybrids (Kálmán *et al.* 2004). Artificial pollination experiments between *P. veris*, *P. vulgaris* and their interspecific hybrids proved that both the F_2 generation and the backcrosses can be formed relatively easily (Valentine 1955; Woodell 1960c). Nonetheless, despite the possibility of introgression, all the observations on natural *P. veris × P. vulgaris* hybrid zones drew attention to the rarity of F_2 and backcross plants (Clifford 1958; Mowat 1961; Woodell 1965), which can, at least partly, be explained by the strongly broken reciprocity in F_1 hybrid flowers (Kálmán *et al.* 2004).

Simpson (1982) recorded the tertiary hybrid *P. veris × P. vulgaris × P. elatior* (= *P. murbeckii* Lindq.) at two sites in west Suffolk. A single vigorous plant found in east Cambridgeshire in 1993 appeared to be the result of the long-distance
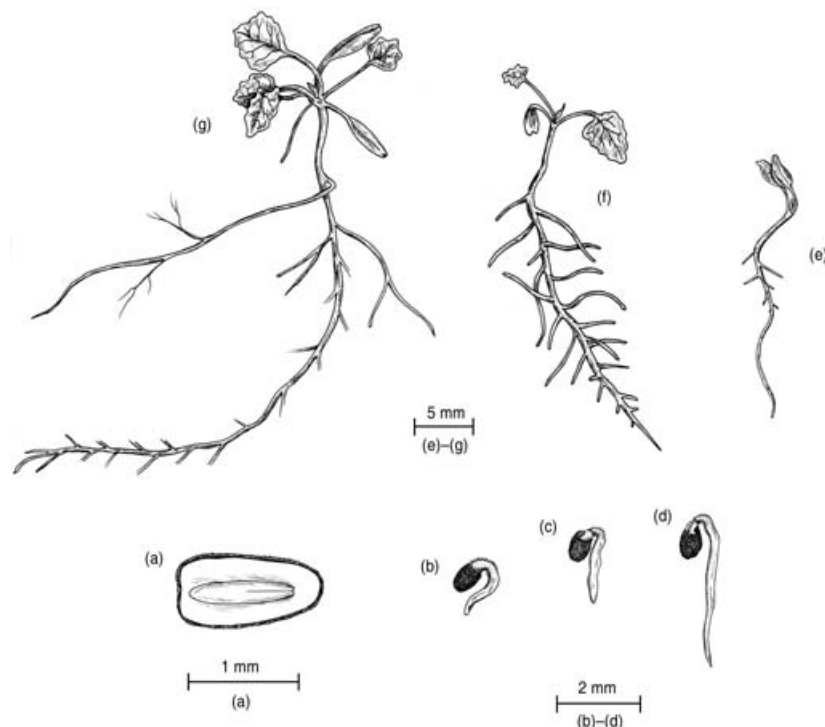
Fig. 8. Seed, and stages in the germination and early development of *Primula veris*: (a) ripe seed; (b–d) radicle emergence; (e) cotyledons expanded; (f–g) first pairs of leaves apparent.

fertilization of a wild oxlip by the pollen of a garden Polyanthus, *P. veris × P. vulgaris* (Preston 1993). The British distribution of *P. murbeckii* is shown by Taylor and Woodell (2008).

(C) SEED PRODUCTION AND DISPERSAL

Each flower produces a capsule that bears finely papillated dark brown to blackish seeds that are on average $1.7 × 1.4$ mm (Grime *et al*. 2007). Mean seed mass varies between 0.69 and 1.24 mg (Grime *et al*. 2007; Kéry *et al*. 2000; Lehtilä & Ehrlén 2005). The embryo is straight, elongated, located in the middle of the seed, and pressed into the surrounding nuclear endosperm (Fig. 8; Corner 1976).

Experimental legitimate pollination results in an average seed set of 76% of the total number of ovules (Wedderburn & Richards 1990). Although Kéry *et al*. (2000) and Brys *et al*. (2003) did not observe significantly different seed production rates between pin and thrum individuals in a large number of natural cowslip populations, Darwin (1877) reported that in some cases, the legitimate cross of thrum ♀ × pin ♂ appeared to be more fertile than the reciprocal in terms of seed production rates per capsule, which he attributed to the much smaller cross sectional area of conducting tissue available for pollen tube growth in styles of pin flowers.

Across 26 fragmented *P. veris* populations in Belgium, the proportion of flowers that developed successfully into fruits varied between 0% and 81% (mean = 61%), the number of fruits per plant varied between 0 and 108 (mean = 18.9), and the average number of seeds per fruit ranged from 1 to 61 (mean = 27.9). The number of seeds per fruit and seed mass were negatively correlated (McKee & Richards 1998; Kéry *et al*. 2000; Brys *et al*. 2003), so that as seed set at fruit level increases, individual seed mass decreases, suggesting resource limitation at fruit level (Tremayne & Richards 2000). Proportional fruit set and seed production increased significantly with increasing population size (Kéry *et al*. 2000, 2003; Brys *et al*. 2003; Van Rossum *et al*. 2006), whereas population density was positively related to the number of fruits per plant, and negatively to the number of seeds per fruit and per plant (Kéry *et al*. 2000; Van Rossum *et al*. 2006).

Supplemental hand-pollination in open flowering *P. veris* individuals did not indicate that there were any fitness costs associated with sexual reproduction (García & Ehrlén 2002). Lehtilä & Syrjänen (1995) even demonstrated a significant increase of survival, size, and reproductive success of supplemental hand-pollinated plants in the subsequent years. A flower removal experiment of Lehtilä & Ehrlén (2005) also showed that when all but one flower was removed from each inflorescence, seed mass significantly increased (by 33%) compared to control plants. These variable and somewhat contradictory observations suggest that possible trade-offs might depend largely on the environmental conditions.

Although the majority of seeds is shed after fruits opened in July or August, a minority may be retained for a longer period in the ripe capsules (pers. observ.). Scapes may persist erect throughout the winter bearing capsules with these unshed, unimbibed viable seeds. In general, seeds are easily dispersed for short distances by wind and raindrops propelling them from the opened capsules (van der Pijl 1982). Once they reach the ground, seeds are unlikely to blow or roll in dense grass sward. By using sticky tapes radiating 5 m from isolated seed producing plants, Richards and Ibrahim (1978) showed that average seed dispersal distances were very small and remarkably similar in two British *P. veris* populations

(respectively 0.12 and 0.11 m). It is unlikely that seed dispersal by animals is important, as mature seeds neither bear structures to attach to animals nor have the gelatinous projection of the seed-coat (elaiosome) attractive to ants, as is found in *P. vulgaris*. To our knowledge, there are no data available that have shown endozoochory of *P. veris* seeds. Water transport is probably the most important agent in spreading the species over greater distances. Such transport may, for instance, explain recent colonization patterns of *P. veris* populations several kilometres downstream from its nearest source population on riverine flood plain meadows along the Meuse in Belgium (K. van Looy, pers. comm.).

(D) SEED GERMINATION AND VIABILITY

Although some *P. veris* seeds germinate soon after being shed under natural conditions, the majority of seeds overwinters and germinates in spring (from the end of April until mid-May onwards) (Muller 1978; pers. observ.).

Although Morozowska (2002) found that the majority of seeds obtained from natural populations in Poland appeared to be viable by a tetrazolium test (mean 88%, range 83–92%), seed germination rates were surprisingly variable. Poor germination rates are usually due to dormancy (Thompson *et al.* 1997). Grime *et al.* (2007) and Milberg (1994) reported that fresh cowslip seeds are strictly dormant at the time of dispersal and need cold stratification to activate germination. Because seeds contain water-soluble inhibitors, dormancy of *P. veris* seeds is not broken after ripening under dry conditions (Grime *et al.* 2007). In order to stimulate germination, seeds require light (Pons 1991; Milberg 1994) and prefer a narrow range of temperatures (optimum of 16.1 °C; Fig. 9; Milberg 1994). Seeds of *P. veris* subjected to higher temperatures are likely to re-enter dormancy (Milberg 1994). After 16 months' burial, 85% of *P. veris* seeds remained viable (Milberg 1994). This suggests that a large fraction of the seeds may ultimately
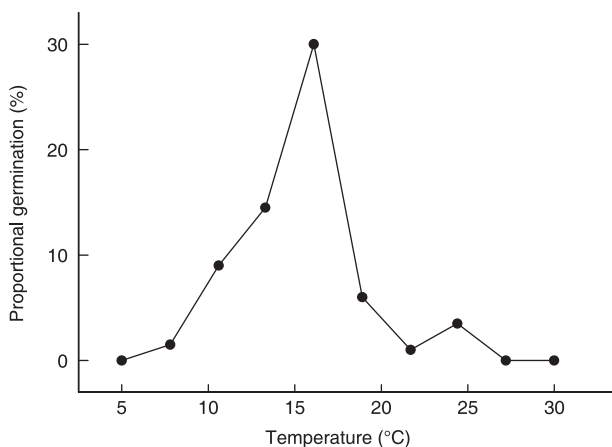
accumulate in the soil. Large amounts of viable *P. veris* seeds are indeed recorded in the persistent soil seed bank (Milberg 1992, 1994; Milberg & Hansson 1994). Thompson *et al.* (1997) therefore classified *P. veris* as a species that forms a short-term persistent seed bank, with a mean seed bank density of 183 m^{-2}. Treatment of cowslip seeds with gibberellins significantly increased germination success (Kéry *et al.* 2000; Morozowska 2002). GA$_3$ treatment was most effective at a germination temperature of 10 °C with a seven days pre-chilling, resulting in germination rates of 92.6–99.3%, whereas this was only 63.3–92.0% at a temperature of 20 °C (Morozowska 2002).

Germination rates (scored as radicle emergence) and early growth of seedlings at the soil surface did not respond significantly to increasing water table height (Whale 1983b). Although high water tables may allow optimal germination rates, this advantage is tempered by the increased likelihood of fungal infection, which is common under natural conditions (Keith-Lucas 1968; Abeywickrama 1949). In contrast, *P. veris* seedlings appear to be highly susceptible to prolonged periods of drought, which is an important cause of mortality during juvenile development (pers. observ.). Ryser (1993), who studied seedling establishment and survival in artificial gaps in a nutrient-poor limestone grassland (*Mesobrometum*) in northern Switzerland, reported that shelter by neighbouring plants appeared to be advantageous for the establishment of *P. veris*.

Seedling establishment under field conditions is positively associated with seed mass, with 57% more seedlings produced from heavier seeds (average seed mass = 1.24 mg) than from lighter ones (average seed mass = 0.73 mg) (Lehtilä & Ehrlén 2005). Kéry *et al.* (2000) also reported that germination success increased with increasing seed mass, and that seeds originating from large populations had a higher germination success, a higher chance of seedlings surviving until the following autumn and a cumulative higher offspring size than seeds from small populations.

Although the probability of seedling emergence is negatively related to seed density, the absolute number of seedlings increased with the density at which seeds were experimentally sown under natural field conditions (Brys *et al.* 2005; Ehrlén *et al.* 2005). This suggests that there is no saturation of seeds, even at densities that are many times larger than the normal seed rain, and that density-dependent interactions among seeds or emerging seedlings at realistic densities are not a major determinant of plant densities in *P. veris*.

(E) SEEDLING MORPHOLOGY

The first stage of germination is marked by swelling of the seed, which results in partial rupture of the testa at the top of the seed (Fig. 8). Germination is epigeal (Grime *et al.* 2007). On germination, the radicle bursts through a split in the seed coat, develops ephemeral root hairs and becomes anchored in, or to, the substratum. The radicle develops into the primary root system of the plant. The hypocotyl is glabrous or has some glandular hairs towards the tip (Muller 1978). During

Fig. 9. Germination of seeds of *Primula veris* at constant temperature (adapted from Milberg 1994). In total 150 seeds were used at each temperature. Prior to the experiment, seeds had been cold-stratified on wet filter paper in a plastic pot sealed with parafilm for 4 months in 2 °C in darkness.

an upward elongation of the hypocotyl, the cotyledons tend to remain in the testa, after which they expand and separate, shedding the seed coat. Seedlings have two spathulate cotyledons (3.5 mm each) developing an ovate shape (5.5 mm) with a rounded-truncate tip (Muller 1978); stomata are found on both surfaces of the cotyledon. The tip of the cotyledon bears forwardly-directed, regularly-spaced glandular hairs (three-celled), which are very sparse at the base of the cotyledon. Similarly, abnormal gland-like structures are common on the root surface of the seedling. Two types of hairs are found on the epidermis of developing seedlings; most of the hairs on the upper epidermis are three-celled, in contrast to those on the lower epidermis which are generally five-celled. The first developing leaves are ovate with a cordate base and a hairy petiole. The tips of the leaves are rounded and sinuate-crenate.

IX. Herbivory and disease

(A) ANIMAL FEEDERS OR PARASITES

Apart from the impact of herbivory by large mammals (see IV), leaves of *Primula veris* are also frequently predated by several insects and molluscs (García & Ehrlén 2002). Lehtilä & Syrjänen (1995) documented several thrips (*Thysanoptera* spp.) and species of geometrid larvae (*Geometridae* spp.) frequently feeding on leaves *P. veris*. It is also frequently infested by a number of leaf miners (summarized in Table 2).

Insects and molluscs are also often reported to cause substantial losses of flowers during the flowering season. Breadmore and Kirk (1998), for instance, reported substantial flower damage (10%) of *P. veris* individuals in a limestone grassland in central England, mainly caused by slugs. Visible signs of floral damage were also observed in 37% and 67.% of flowering individuals in two natural *P. veris* populations in South Sweden (Ehrlén *et al.* 2005; Lehtilä & Ehrlén 2005). Moreover, in individuals having damaged flowers, on average

50% of their flowers were lost. Given that destruction of flowering stalks and flowers does not result in compensatory flower production later in the growing season, this inevitably results in reduced seed set and may thus cause reduced recruitment success (García & Ehrlén 2002).

Reproductive output may further be diminished as a result of pre-dispersal seed predation. One of the most important seed predators of *P. veris* is the larva of the plume moth *Amblyptilia punctidactyla* Haworth (Pterophoridae) (Leimu *et al.* 2002). The intensity of pre-dispersal seed predation varies largely between populations and years, and significantly increases with the size of the flowering plants and with increasing canopy closure (Leimu *et al.* 2002; Kolb *et al.* 2007). *Primula veris* seeds are also an important host food for the caterpillar of *Hamaeris lucina* Linnaeus (the Duke of Burgundy, Lycaenidae) (Emmet & Heath 1989; Asher *et al.* 2001; Leon-Cortes *et al.* 2003). In the UK, *H. lucina* can be found on *P. veris* populations, feeding on fruits during the night (Emmet & Heath 1989; Tomlinson & Still 2002), but the butterfly is in serious decline, perhaps because of the more intensive management of some grasslands and the neglect of others (Fox *et al.* 2006). Less frequently, *P. veris* fruits can also be attacked by the larvae of *Falseuncaria ruficuliana* Guenée (Tortricidae) (Emmet 1988). This rare species is occasionally found in some *P. veris* populations in Sweden (Leimu *et al.* 2002). Finally, Hurst and Doberski (2003) also documented that the beetle *Pterostichus madidus* Fabricius (Carabidae) consumed both unimbibed and imbibed seeds of *P. veris*, both under laboratory and field conditions in Britain.

(B) PLANT DISEASES

Primula veris is the primary host of the leaf spot white mould *Ramularia primulae* Thüm. (Capnodiales), an oligophagous damaging foliar disease (Ellis & Ellis 1997). This anamorphic fungus causes round or angular, pale brown spots on leaves of

Table 2. Leaf miners recorded from *Primula veris* L.

Species/classification	Source	Species/classification	Source
LEPIDOPTERA		**COLEOPTERA**	
Noctuidae		Chrysomelidae	
Apamea crenata Hufnagel	1	*Apteropeda orbiculata* Marsh.	5
Heloiphobus reticulata Goes.	2	Curculionidae	
Noctua orbona Hufnagel	1, 3	*Sciaphilus asperatus* Bonsd.	6
N. fimbriata Schreber	2	*Orthochaetes insignis* Aubé	5
DIPTERA			
Agromyzidae			
Phytomyza (= *Chromatomyia*) *primulae* Rob.	4		
Liriomyza huidobrensis Blanchard	5		
L. trifolii Burgess	5		
L. bryoniae Kaltenbach	5		
L. strigata Meigen	5		
Anthomyiidae			
Delia echinata Séguy	5		

Information obtained from: 1, Allan (1949); 2, Noble (1975); 3, Heath & Emmet (1979); 4, Spencer (1972); 5, Hering (1957); 6, Hoffma nn (1950).

the cowslip and other Primulaceae (such as *P. elatior* and *P. vulgaris*), each surrounded by a bright yellow or pale orange border. The centres of these spots sometimes drop out, leaving shot-holes. To a lesser extent, *Ramularia interstitialis* (Berk. & Broome) Gunnerb and Constant is also hosted by *P. veris*, causing yellowish spots fading outwards without definite margin and a white felty mycelium at the leaf underside (Ellis & Ellis 1997). *Primula veris* can also be seriously injured by the smut fungus *Urocystis primulae* (Rostr.) Vánky (Urocystidiales), infecting the ovary of *P. veris* by means of an embedded sorus and a conidial anamorph (Legon & Henrici 2005; Spooner & Legon 2006). The downy mildew *Peronospora oerteliana* J.G. Kühn (Peronosporales) has occasionally been found on leaves of *P. veris*, forming effuse colonies on the lower surface of leaves (Ellis & Ellis 1997). *Primula veris* is also sporadically attacked by the *Pseudomonas syringae* pathovar. *primulae* (Hall), a rod-shaped, Gram-negative bacterium with polar flagella.

X. History

Primula veris is native to the British Isles and was first recorded in 1568 in Lancashire (Clarke 1900). A seed from medieval material at Shrewsbury has been identified as either a cowslip or oxlip seed, and is the only known (sub-)fossil record for either species from the British Isles (Godwin 1975).

There are several explanations for the origin of the name Cowslip. Generally it is assumed that it is a polite form of Cowslop, derived from 'cow dung' or 'cow pat', which originates from a conception that the cowslip sprang up in the meadow at places where a cow had lifted its tale (Grigson 1996). Another explanation is that this name is a corruption of 'Cow's Leek', *leek* being derived from the Anglo-Saxon word *leac*, meaning a plant. There are, however, several names for *P. veris*. In old Herbals the plant has been called as 'Herb Peter' and 'Key Flower', because the pendent flowers suggest a bunch of keys, the emblem of St. Peter. Additionally, in the Norse mythology, the flower was a dedicated symbol of Frcya, the Key Virgin, and it was believed that through this flower, one could be admitted to her treasure palace. This pagan story became changed in time to be the Virgin Mary, so it also got the name of 'Our Lady's Keys' and 'Key of Heaven'. Other folk names given to *P. veris* are 'Palyswort', 'Fairy cups', 'Tisty-Tosty', 'Plumrocks', 'Password', 'Paigle', 'Peggle' and 'Crewel'.

In olden days, *P. veris* flowers were in great demand for homely remedies, to make wine, tea and ointment of special value in strengthening the nerves and the brain, relieving restlessness and insomnia, and as an excellent sedative and an antispasmodic. Old herbalists, such as John Gerard, classed *P. veris* and *P. vulgaris* together as 'Petty Mulleins', and credited both species with much the same properties, but *P. veris* was significantly more powerful and was generally preferred. Gerard (1597) also recommended both the flowers and leaves of both species, boiled in wine, as a remedy for all diseases of the lungs, whereas the juice of the root itself, snuffed up the nose, was recommended for migraine.

XI. Conservation

Although *P. veris* is not listed as a rare or scarce species (Hill *et al.* 2004), its occurrence in the UK was formerly more common than today (Preston *et al.* 2002). The New Atlas of the British and Irish Flora records it in 1413 10-km squares since 1987, compared with 1638 before 1969 (Preston *et al.* 2002), a decline of 13.7%. The Change Index (Telfer *et al.* 2002), quantifying the relative magnitude of change of the period 1930–1969 with 1987–1999, of *P. veris* in Britain is −0.32 (Preston *et al.* 2002). This slight overall decline can be attributed to the fact that the cowslip is mostly associated to Mesobromion or calcicolous grassland communities that are traditionally maintained by means of hay-meadow treatment or grazing, with no or only light application of natural organic manures (see also III). These types of grasslands are, however, becoming increasingly rare and locally distributed as a result of agricultural improvement (Rodwell 1992). Since the 1980s, however, the species has increased substantially in many areas of the UK, largely because its seeds are included in wildflower seed mixtures that are sown on new or upgraded road and motorway verges, embankments and urban conservation areas, in an effort to increase the distribution of the cowslip again (Preston *et al.* 2002; Richards 2002). These introductions, and other escapes from cultivation, may explain the rather slight relative decline as shown by the New Atlas change index (Preston *et al.* 2002) and the fact that the species has shown no further decline in the UK between 1986 and 2004 (Braithwaite *et al.* 2006). Such recent non-native populations have only been identified on the distribution map (Fig. 1) outside the core range of the species.

In many areas of its original distribution (also on the Continent), the occurrence and abundance of *P. veris* declined mainly as a result of changed land-use practices, ongoing fragmentation and increased nutrient influx from the surrounding landscape (Mennema *et al.* 1985; Fischer & Stöcklin 1997; Brys *et al.* 2003; Kéry *et al.* 2000, 2003; Lindborg *et al.* 2005). Because many of the fragmented *P. veris* habitats are small, they are consequently highly vulnerable to edge effects, such as nutrient influx (Kéry *et al.* 2000; Brys *et al.* 2003; Lindborg *et al.* 2005). A mixture of relatively intense grazing, creating conditions suitable for seedling establishment and growth, and more relaxed grazing allowing seed production, might be the optimal management strategy to maintain viable *P. veris* populations in the long-run (Brys *et al.* 2005; Ehrlén *et al.* 2005). Such a management regime could be achieved through between-year variation in grazing pressure, small-scale spatial heterogeneity in terms of more open areas and grazing refuges near thorny shrubs (such as *Prunus spinosa*, *Rosa* spp., *Crataegus monogyna* etc.), or through late summer grazing as in traditionally managed hay meadows.

Acknowledgements

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