

Biological Flora of Britain and Ireland: *Fritillaria meleagris*

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Abstract

1. This account presents information on all aspects of the biology of *Fritillaria meleagris* L. (Snake's Head Fritillary). The main topics are presented within the standard framework of the *Biological Flora of Britain and Ireland*: distribution, habitat, communities, responses to biotic factors, responses to environment, structure and physiology, phenology, floral and seed characters, herbivores and disease, history, and conservation.
2. *Fritillaria meleagris* is a perennial spring bulb that grows in wet mesotrophic meadows and wet openings in woodlands. In Britain, it is localised to floodplain meadows but occurs as an intentional introduction in a range of habitats. There are several large populations on the floodplains of the River Thames and its tributaries in Wiltshire, Berkshire and Oxfordshire.
3. *Fritillaria meleagris* occurs on mesotrophic alluvium soils often overlaying calcareous gravel with a relatively wide pH range. It favours a high ground water table during winter months and spring followed by good drainage of the soil throughout the summer.
4. *Fritillaria meleagris* plants regularly experience prolonged dormancy. From 30% to 99% of plants in a population can remain below-ground for more than a year.
5. *Fritillaria meleagris* produces nectar and is mainly pollinated in April by bumblebee queens in England. Other pollinators include insects of the orders Hymenoptera, Diptera and Lepidoptera, particularly bumblebees, hoverflies and butterflies.
6. The release of the seeds from the pod in May–June can take a month. Seeds require warm and cold treatments for the embryo to fully form. Air pockets aid seed flotation on the surface of flood water for up to a month. The seeds of *Fritillaria meleagris* do not form a seed bank, germinating either during flotation or on bare ground.
7. *Fritillaria meleagris* declined in Britain during the 20th century due to agricultural improvement and ploughing of floodplain grasslands. In all, 20 or so remaining populations survive in ancient hay meadows. Several of its British locations receive statutory protection as designated sites. However, recent work suggests

*Nomenclature of vascular plants follows Stace (2019) and, for non-British species, Tutin et al. (1964–1993) and Cherepanov (1995).

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that *F. meleagris* was probably introduced to Britain as an ornamental, and the level of protection it receives is therefore likely to change.

KEYWORDS

conservation, floodplain meadows, germination, pollination, population structure, prolonged dormancy, rare species

Family Liliaceae. *Fritillaria meleagris* L. (Snake's Head Fritillary) is a perennial, bulbous geophyte. Bulb semi-tunicate, 1.5 × 2 cm, consisting of two white storage scales with no extra cover. Adventitious roots at the base of bulb 10–30 cm long, white, few of them contractile. Stem erect, dull-green, waxy, glabrous, non-branched, 20–30(70) cm. 3–6(9) leaves 6–15(20) × 0.4–0.8(1) cm, dull-green on both surfaces, waxy, glabrous, linear veined with obscure veins, entire, attenuate-lanceolate, with maximum width closer to the leaf tip than midway between base and tip, undivided, with attenuate tip. Leaves sessile, spirally arranged along the stem. 1(2–3) flower terminal, peduncle shorter than upmost leaf (bract) during perianthesis, elongates 2–3 times in fruiting. Perianth cup- to bowl-shaped, conspicuously chequered, light and dark purple and cream, sometimes white, 4–6 cm. Perianth segments (tepals) with angular bend of midrib at 1.5–2.5 cm from base, shaping flower as angular-ovoid. Perigonal-type glabrous nectary 1.1 × 0.12 cm on the inner surface of each tepal 0.2–0.4 cm from base (Figure 1e; Stpczyńska et al., 2012). Superior ovary 0.5–0.7 cm, light-green, slender, sessile, glabrous, narrowly cylindrical, with three tinged violet longitudinal

ridges. Fruit loculicidal capsule 1.6–3.2 × 0.8–2.1 cm, erect, with three ribs. Seeds flat, curved-triangular, 0.2–0.5 × 0.3–0.6 cm, with narrow thin edge.

The genus *Fritillaria* includes 140 species worldwide (Day, 2017). *Fritillaria meleagris* L. is the type species of the genus; the type specimen is kept in the Linnaean Herbarium at the Linnean Society of London. The genus is divided into nine subgenera (Rix, 2001), which were confirmed to be monophyletic apart from the subgenus *Fritillaria*, which is polyphyletic and contains two distinctive clades (Day et al., 2014).

Fritillaria meleagris is a relatively uniform species. There are only three subspecies morphologically recognised in Europe, of which *Fritillaria meleagris* var. *contorta* (Baker) W. Mill. is currently accepted as *Fritillaria meleagris*; *Fritillaria meleagris* var. *boissieri* (Costa) Vayr. is a synonym to *Fritillaria lusitanica* subsp. *lusitanica*, and *Fritillaria meleagris* subsp. *burnatii* (Planch.) Rix is a synonym to *Fritillaria tubaeformis* var. *burnatii* (Planch.) Rouy (WCSP, 2014). A one off observation on variability in leaf arrangement is reported from a mountain population of the species in Croatia (Bunovac valley on



FIGURE 1 Flowers and pods of *Fritillaria meleagris*: (a and b) – Double flowers occur in both purple and white phenotypes of the species in most vigorous individuals; (c) peduncle elongated at fruiting; (d) ripe fruit opened; (e) flower showing the elongated nectaries (blue arrow) on the inside of the tepals. Photos: Mike Dodd

South Velebit mountain ridge), where plants have opposite lower leaves and an individual with the upper leaves arranged in a whorl was also recorded there (Kranjčev & Šešok, 2016). Genetic diversity of the species comprises three distinct variants found in Northern Europe/Scandinavia, Eastern Europe and the Russian Federation (Day, 2017). As a rare species, *F. meleagris* is often found in reduced numbers and small population sizes across its range, this has led to fears over a loss of genetic diversity. However, a study of several small populations in western Romania indicated a good prospect of maintaining genetic variability of the species in small populations (Madosa et al., 2016).

Phenotypically, the species varies in colouration of the perianth from white to deep purple. Some populations consist of only purple-flowered plants like one in Poland near Stubno (Zych & Stpczyńska, 2012), and many Russian populations. In Britain, white flowers occur in 0–c. 7% of individuals within a population (King & Wells, 1993). Purple flowers dominate in most populations while the proportion of white-flowered individuals varies from year to year. For example, numbers of white-flowered plants in the population of *F. meleagris* in North Meadow, Wiltshire varied significantly during 20 years of observations: 0%–2.5% in 6 non-consecutive years, 3%–5% in 8 years and 6%–8.5% in 6 other years of monitoring (Figure 2a). Numbers of white fritillaries showed no correlation with the overall population dynamic or with any environmental factors measured on the meadow. Another Fritillary population in Clattinger Farm, Wiltshire which was monitored for 6 years had a much lower number of white-flowered plants varying from 0% to 2.2%. Predominantly, white-flowered populations are rare. These include population on Lugg Meadow, Herefordshire which typically comprises 0%–8% of purple flowers including few mottled flowers with intermediate coloration (Figure 2b).

Here and below, if not specified otherwise, data on populations of *Fritillaria meleagris* in North Meadow and Clattinger Farm on the Upper Thames in Wiltshire, and in Lugg Meadow on the River Lugg near Hereford were collected by the 'Flight of Fritillary' volunteer-based project run by the Open University in 1999–2021 in North Meadow and in 2012–2017 at two other sites (Rothero, 2018). All three monitoring sites are ancient floodplain meadows, traditionally managed for hay in summer and aftermath grazing in autumn-winter. Clattinger Farm floods briefly and occasionally even though it is located only 8 km away from North Meadow, which experiences prolonged episodes of winter floods. Lugg Meadow is located 70 km away from two other sites; it floods regularly for 1–3 months in winter.

White-flowered plants dominated in the now extinct population at Sławno in a coastal region of Poland, which contained only approximately 5% purple-flowered plants; this population is regarded to be anthropogenic in origin (Zych et al., 2013).

Although *F. meleagris* is an iconic species of ancient floodplain hay meadows in Britain, its native status has been the subject of much debate. A recent account on the genetic diversity of the European populations (Day, 2017) did not provide conclusive proof either way and so the most recent flora of the British Isles (Stace, 2019) listed it

as 'doubtfully native' although some botanists have argued strongly for it to be classed as modern introduction (neophyte; Leach, 2010, 2019; Pearman, 2007, 2013; Walker, 2021). The current lack of direct evidence means that a final judgement on its status may be premature and may have to await more conclusive genetic results.

1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

In Britain, *Fritillaria meleagris* is a Nationally Scarce plant (species which are found in between 16 and 100 hectads; hectad is an area 10 × 10 km square) that was considered to be native in wet, species-rich eutrophic meadows on alluvial soils and gravels in lowland England (King & Wells, 1993; Wells, 1994). Most of these populations are located on the floodplains of the River Thames and its tributaries between Cirencester, Oxford and Reading with outlying populations in Suffolk, Herefordshire, Staffordshire and Buckinghamshire although intentionally introduced populations occur in similar meadow habitats in other regions (Figure 3; Walker, 2021). Away from meadows *F. meleagris* has been widely planted as an ornamental and has readily naturalised throughout Great Britain in gardens, semi-wild and wild locations such as roadsides, nature reserves, churchyards, cemeteries, the grounds of large houses and urban areas (Walker, 2021). In Wales and Scotland, most recent records appear to come from private gardens and there is a single record in the Republic of Ireland from a roadside near to Adamstown, County Wexford (Walker, 2021).

F. meleagris is now widely distributed across Great Britain with records from 393 hectads (Figure 3), although only around 20 populations survive in ancient floodplain meadows (Walker, 2021) where they are presumed to be native. It remains very local throughout its range with only 28% of hectads supporting more than one population. Historically, only two hectads near to Oxford (SP50, SP70) contained more than 10 populations (18 and 12, respectively), although all the meadows in SP70 have now been destroyed (Walker, 2021).

F. meleagris is native in south-eastern Europe, from where it spread into north-western parts of Europe after forest grazing and clearance of woodlands (Hollmann, 1972). The native range of *F. meleagris* extends to 52–53°N (Baranova, 1999), whereas populations further north are thought to be introductions, for example, at Kungsängen Nature Reserve near Uppsala, Sweden, at 59°50'N (Zhang, 1983). The species is also naturalised in Denmark, Finland, Norway and the Baltic countries (Tomović et al., 2007), where some isolated populations occur (e.g. Liepinya, 1967).

The species has a mainly western and central European range (Hill et al., 2004; Tomović et al., 2007). In north-western Europe, the largest populations occur along the valleys of the Rivers Loire (France), the Overijssel Vecht (Netherlands) and the Elbe (Germany; Horsthuis et al., 1994). *Fritillaria meleagris* is categorised as a native in France, the Netherlands, Switzerland, Austria and Italy (Friuli-Venezia Giulia) but in Germany it is categorised as a naturalised non-native (originally ornamental; Jäger, 2016) with



FIGURE 2 (a) Predominantly pink-flowered population of *Fritillaria meleagris* in North Meadow, Wiltshire, UK and (b) predominantly white-flowered population in Lugg Meadow, Herefordshire, UK. Photos: Mike Dodd

the possible exception of Jutland (FloraWeb, 2020). It is believed to be extinct in Belgium (Van Landuyt et al., 2006) and the Czech Republic (Botany.CZ, 2020) but still occurs at several locations in Slovakia. In Poland, it is very rare occurring only in the valleys of the Rivers San and Biebrza (Piórecki, 2001). It occurs in Slovenia and northern part of Croatia (in a few locations on Mt Velebit) but its distribution in Dalmatia is uncertain (Ilijanić et al., 1998). The species is also known from Bosnia and Herzegovina, Montenegro (questionable) and Serbia (Tomović et al., 2007). It is widespread in the western and north-eastern parts of Hungary, including some very large populations in the west in the valleys of the small rivers Kerka and Zala (Bódis et al., 2020). In Romania, it was formerly widespread (Bujorean & Grigore, 1965) but many of its habitats were lost to intensive agriculture (Csergő & Frink, 2003). The very eastern edge of the central European range lies in Moldova and western Ukraine (Andrienko & Cherney, 2009).

In the east, the range of *F. meleagris* is more disjunct. About 600km from the Ukrainian populations, four locations of *F. meleagris* were found in Bryansk Oblast of Russia (Bulokhov et al., 2016), with a further 38 locations being widely scattered across eight other Oblasts in the central part of European Russia (Varlygina, 2008). The most eastern populations of the species

occur in Asia. One population is known from Ishim, Tumen Oblast, Western Siberia, 2,000km away from the Penza and Saratov outposts of the European part of the range. With another gap of 1,000km, 10 populations were recorded in the Altai Krai near the villages Byelokurikha, Amayskiy, Soloneshniy, Sibiryachikha, Khairyuzovka, Kuyagan and in the River Peschanaya valley (Kamelin & Shmakov, 2006; Titova & Kobayakova, 2014). In the Republic of Altai, the species occurs in Maima and Shebalino Districts in the valleys of the Rivers Sema, Peschanaya and Maima, Kan, and Anuy (Ershova, 1996; Krasnoborov, 2007). Most eastern populations of the species were found in the River Biya basin in the valleys of the rivers Setovka, Nanya and Biya (Zolotukhin, 2016, 2017). The species was also recorded in north-eastern Kazakhstan (Flora of Siberia, 1987).

The altitudinal range of *F. meleagris* is broad. It varies from 1.4 m a.s.l. in the Netherlands (Zhang, 1983) and 8–80 m a.s.l. in the British Isles (I. Tatarenko, pers. obs.) to 100–250 m a.s.l. in Serbia (Tomović et al., 2007) and in central European Russia. In Romania, populations were studied at 450 m a.s.l. (Csergő & Frink, 2003). It grows up to 1,200 m a.s.l. in Croatia (Ilijanić et al., 1998). In Asian locations, altitudinal limits of *F. meleagris* vary from 80 m a.s.l. in Tumen Oblast to 200–600 m a.s.l. in the Altai Krai and the Republic of Altai.

2 | HABITAT

2.1 | Climatic and topographical limitations

In the British Isles, *Fritillaria meleagris* is restricted to hectads with mean temperatures of 3.6°C in January to 16.3°C in July and an average annual precipitation of 688 mm (Hill et al., 2004). Comparative climatic values for different parts of the species range are shown in Table 1. *F. meleagris* occurs in a wide range of climates from oceanic in the British Isles to extreme continental in Western Siberia and Altai. In Europe, the temperature range increases with an increasing continentality of the climate. Winter precipitation, either as rain or snow, appears to be an important factor for *F. meleagris* as it requires moist soils in the spring for successful root growth. Although variation in winter precipitation across the species range is substantial (Table 1), in all locations *F. meleagris* occurs in landscape units collecting meltwater and flood water from surrounding areas (see Section 2.2. for details). Lack of summer precipitation appears to have little impact as the species is usually dormant in the summer months.

In Britain, presumed native populations of *F. meleagris* are confined to level floodplains close to rivers. In more topographically complex regions such as the ravines in Orel and Kursk Oblasts, Russia and the Altai mountains, it avoids southerly facing slopes and is largely confined to those facing north-west, west and east (Silantjeva et al., 2011; Zolotukhina & Zolotukhin, 2012).

In Britain, *Fritillaria meleagris* is restricted to very open grasslands with no shade (Trist, 1960; Wells, 1994), although it persists, where

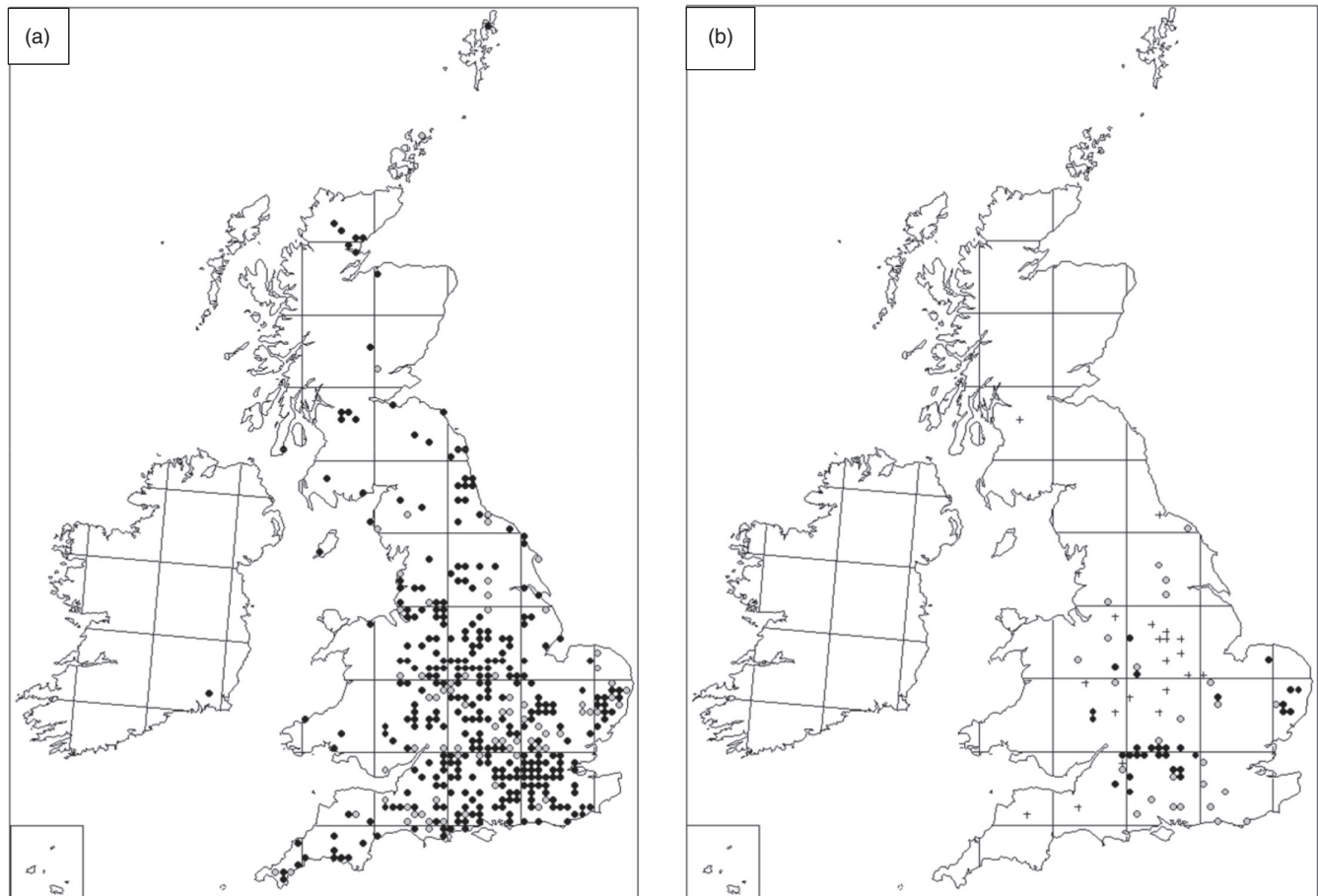


FIGURE 3 The distribution of *Fritillaria meleagris* in the British Isles based on records collated by the Botanical Society of Britain and Ireland (BSBI). (a) the entire range of the species; (b) hectads with populations in unimproved meadows. Black circles indicate hectads where *F. meleagris* occurs in species-rich meadows as a presumed native; grey circles indicate hectads where *F. meleagris* occurs in meadows where it is suspected of having been introduced and crosses indicate hectads where *F. meleagris* occurs in meadows where it is known to have been planted. The maps are taken from Walker (2021) and are reproduced with the permission of the BSBI

City (country)	Mean temperature, °C		Mean precipitation, mm		
	January	July	Annual	Winter	Summer
Birmingham (Great Britain)	3.2	15.7	705	182	180
Upsala (Sweden)	-4.3	16.3	551	113	187
Dombóvár (Hungary)	-1.2	21.5	617	127	199
Cluj-Napoca (Romania)	-2.9	18.9	571	98	230
Lviv (Western Ukraine)	-3.9	17.8	697	123	257
Bryansk (West of European Russia)	-8.5	18.6	597	119	215
Penza (East of European Russia)	-11.5	20.0	540	106	181
Ishim (Western Siberia, Russia)	-17.7	19	549	52	178
Maima (Altai, Russia)	-15.4	20.5	471	58	211

TABLE 1 Climatic measurements in temperature and precipitation across the geographical range of *Fritillaria meleagris* (Climate Data Worldwide, 2020)

planted, in shaded habitats such as private woodlands, plantations and orchards (Walker, 2021). Across its wide geographical range, *F. meleagris* occurs in open habitats more often than in woodlands (Cseregő & Frink, 2003; Horsthuis et al., 1994; Ilijanić et al., 1998; Magnes et al., 2013; Tomović et al., 2007).

2.2 | Substratum

In Britain, *Fritillaria meleagris* grows on alluvium soils overlaying glacial fluvial gravel ranging from 40–60 cm depth in North Meadow to 300–400 cm depth at Clattinger Farm, Wiltshire. These gravels are

TABLE 2 The grassland vegetation types of the British National Vegetation Classification (NVC) that *Fritillaria meleagris* has been recorded in. The table is based on the unpublished set of 187 quadrats recorded by the late Derek Wells (with the assistance of Noel King, Karen Buckley, Lynne Farrell, and Jill Williamson) during surveys of unimproved meadows in lowland Britain for the nature conservancy council between 1970 and 1989. These data are currently held by Natural England; data are reproduced with permission from them. The quadrat data comprised Domin cover abundance scores and were assigned to NVC types by Kevin Walker using Tablefit (Hill, 2015). NVC types assigned to <3 quadrats are excluded from the table

British National Vegetation Classification (NVC) community type	NVC code	% of quadrats (n = 187)	% best-fit mean (SD)
<i>Alopecurus pratensis</i> – <i>Sanguisorba officinalis</i> grassland	MG4	48	64 (10.1)
<i>Lolium perenne</i> leys	MG7	13	59 (8.0)
<i>Anthoxanthum odoratum</i> – <i>Geranium sylvaticum</i> grassland	MG3	8	60 (4.8)
<i>Cynosurus cristatus</i> – <i>Caltha palustris</i> grassland	MG8	8	63 (11.5)
<i>Cynosurus cristatus</i> – <i>Centurea nigra</i> grassland	MG5	7	62 (8.5)
<i>Holcus lanatus</i> – <i>Deschampsia cespitosa</i> grassland	MG9	3	52 (7.4)
<i>Festuca rubra</i> – <i>Agrostis stolonifera</i> – <i>Potentilla anserina</i> grassland	MG11	3	60 (9.2)
<i>Arrhenatherum elatius</i> grassland	MG1	2	56 (5.1)
<i>Filipendula ulmaria</i> – <i>Angelica sylvestris</i> mire	M27	2	52 (29.4)

calcareous in most sites in the Upper Thames valley. The major soil types with which *F. meleagris* is associated (following Avery, 1990 and with sub-types in parentheses) are brown soils (alluvial brown soils, calcareous brown soils, orthic brown soils), lithomorphous soils (rendzinas, sandy regosols) and gleys (alluvial gley soils and orthic gley soils). In Hungary, the species grows on soils with a high clay content (Bódis et al., 2020).

The aquifers in the gravels beneath many of its British floodplain sites keep the soils permanently moist which is reflected in high Ellenberg soil moisture (F) indicator score of 8 (Hill et al., 2004). Plants favour high soil-water content during the autumn, winter and spring months as their roots are very sensitive to desiccation, whereas good soil drainage is needed in the summer when plants are dormant. As a consequence, on floodplains, plants avoid areas where the ground water table persists at the same depth through the driest period of the year (Tatarenko et al., 2013; Zhang & Hytteborn, 1985). This explains why *F. meleagris* favours the lower parts of slopes in river valleys across its geographical range (Baranova, 1999; Kiseleva et al., 2010; Rotov, 1972; Zolotukhina & Zolotukhin, 2012). In steppe regions, populations usually occur in the upper parts of ravines and eroded depressions where snow is deposited in the winter and meltwater keeps the ground moist in the spring (Lepeshkina & Voronin, 2015; Zolotukhina & Zolotukhin, 2012). On the floodplain of the Kungsängen Nature Reserve in Sweden, *F. meleagris* often grows on sedge tussocks which are free-draining in the summer months (Zhang, 1983). In hilly areas, the steeper gradients provide sufficient drainage for *F. meleagris* to grow in wet meadows and bogs (Csörgő & Frink, 2003; Zolotukhin, 2016, 2017).

In Britain, *Fritillaria meleagris* typically grows on free-draining to moderately permeable, well-structured and non-compacted clay or silty alluvial soils. Its presence usually indicates soils of intermediate fertility (Ellenberg nutrients [N] indicator value of 4–5; Hill et al., 2004). For example, the available phosphorus concentrations range from 7.7 mg/kg PO₄-P at Clattinger Farm to 23 mg/kg PO₄-P at Lugg Meadow and up to 16–29 mg/kg PO₄-P at North Meadow, Wiltshire. *F. meleagris* also grows on undisturbed nutrient-rich

chernozem soils with a humic layer of up to 1–1.5 m deep at Streletskiy Uchastok in the Central Chernozem State Biosphere Nature Reserve, Kursk Oblast, Russia (Vlasov et al., 2014). In Hungary, *F. meleagris* was associated with an average organic matter content of 8.1 ± 4.6 (m/m)% across 13 locations (Bódis et al., 2020).

F. meleagris is an indicator of weakly acid to weakly basic conditions (Ellenberg Soil Reaction [R] indicator value of 7) and is never found on very acid soils (Hill et al., 2004). For example, the minimum soil pH (H₂O) at 10 cm depth was 6.2 at North Meadow and 5.7 at Lugg Meadow. On the long-term Park Grass Experiment at Rothamsted, UK, *F. meleagris* is restricted to just one of the 20 different nutrient treatments. It grows on Plot 17, which is treated annually with sodium nitrate at 48 kg/ha/yr (but no added phosphorus or potassium) growing at pH 5.8 (M. J. Crawley, pers. comm.). In Kursk Oblast, *F. meleagris* is associated with chernozem soils with a pH of between 6 and 7. Likewise *F. meleagris* occurs on peaty soils in the upper part of the river Sard valley in Romania also with a pH ranging between 6.4 and 7.2 (Csörgő & Frink, 2003). In Hungary, the species grows in slightly more acid conditions (pH_[KCl] = 5.1 ± 0.8, range 3.9–6.3) and with a lower CaCO₃ content (<0.05%; Bódis et al., 2020).

3 | COMMUNITIES

In Britain, the majority of presumed native populations of *Fritillaria meleagris* occur in species-rich mesotrophic *Alopecurus pratensis*–*Sanguisorba officinalis* grassland (NVC MG4) of the National Vegetation Classification (NVC; Rodwell, 1992; Jefferson & Pinches, 2011; Table 2). Recently, it has also been recorded from a newly described wet grassland closely related to MG4–*Alopecurus pratensis*–*Poa trivialis*–*Cardamine pratensis* grassland (MG15; Wallace & Prosser, 2017). Both these grasslands are closely associated with the Alopecurion swards in The Netherlands, most notably Fritillario–Alopecuretum Calthetosum, Fritillario–Alopecuretum pratensis and Fritillario–Alopecuretum Cynosuretosum (Schaminée et al., 1996, cited by Wallace & Prosser, 2017). Where these grasslands have

been agriculturally improved it can persist in species-poor *Lolium perenne* leys (NVC MG7) and it also locally abundant in drier *Cynosurus cristatus*-*Centaurea nigra* grassland (NVC MG5) or where water levels are impeded or water tables higher *Cynosurus cristatus*-*Caltha palustris* (NVC MG8). It occurs much more locally in a range of other grassland, mire and scrub communities (Table 2).

Most frequent associates of *F. meleagris* represent top five communities listed in Table 2: *Festuca rubra*, *Holcus lanatus*, *Ranunculus acris*, *Trifolium repens*, *Plantago lanceolata* and *Rumex acetosa*. Some of the associates represent MG4 plant community more specifically: *Alopecurus pratensis*, *Sanguisorba officinalis*, *Filipendula ulmaria* (Table 3). *Taraxacum officinale* scores high associate frequency partly as a member of MG4 plant community, partly as an indicator of bare ground in the habitat. The latter is particularly important for *Fritillaria*'s seedlings establishment.

In Germany and Switzerland, *F. meleagris* is a characteristic species of the *Calthion* alliance (Wallace & Prosser, 2017) and *Molinio-Arrhenatheretea* (Csergő & Frink, 2003; Horsthuis et al., 1994; Ilijanić et al., 1998). However, its phytosociological range is much broader. In the Netherlands, it also grows in *Arrhenatherum pubescens*-*Alopecurus pratensis* grassland, whereas in Sweden, it grows in a sedge-rich community dominated by *Carex cespitosa* (Zhang, 1983). In Serbia, it occurs in association with *Querceto-Fraxinetum serbicum mixtum* and *Querceto-Carpinetum*, as well as in wet meadows (Tomović et al., 2007). In south-east Austria, *Fritillaria meleagris* is associated with *Pruno-Fraxinetum*, *Pseudostellario-Carpinetum*, *Galio palustris-Caricetum ripariae*, *Lysimachio vulgaris-Filipenduletum caricetosum acutiformis*, *Iridetum sibiricae*, *Serratulo-Festucetum commutatae*, *Silaetum pratensis* and *Festuco pratensis-Alopecuretum pratensis* (Magnes et al., 2013).

In Romania, *F. meleagris* has been recorded mainly from open moist oak forests (Bujorean & Grigore, 1965; Gubesch & Morari, 1974; Maloş et al., 1967), *Salix cinerea* scrub (Bujorean & Grigore, 1965; Gubesch & Morari, 1974; Ularu & Parascan, 1970) and wet meadows on floodplains that were formerly forested (Gubesch & Morari, 1974; Popescu, 1967; Ularu & Parascan, 1970). Populations were associated with a soil moisture gradient from *Junco-Molinietum* Preising 1951, *Cirsietum rivularis* Nowinski 1926 and the wettest *Caricetum acutiformis* Egger 1933 (Csergő & Frink, 2003). In the Alps, *F. meleagris* grows in alpine pastures (Rix, 1968). In Hungary, *F. meleagris* is typically a riverine woodlands made up of willow, poplar, alder, oak, elm and ash and persists once sites have been cleared of trees (Kevey, 2008; Mesterházy, 2013). However, the largest populations occur in *Arrhenatherum elatius* dominated hay meadows as well as mesotrophic wet meadows and *Molinia caerulea* fens that develop following woodland clearance in river valleys (Bódis et al., 2020).

In the Carpathians of Western Ukraine, *Fritillaria meleagris* occurs in floodplain forests of union *Alnion incanae* Pawlowski 1928 and on wet meadows that have established on sites cleared of trees; in Zhitomir and Kiev Oblasts it grows in meadows with granite outcrops along the River Ros (Andrienko & Cherney, 2009; Chervona Kniga Ukraini, 2019). In Bryansk Oblast, Western Russia, it occurs

TABLE 3 The main associates of *Fritillaria meleagris* in lowland meadows in Britain. The figures are based on the 187 quadrats described in Table 2. Only species recorded in more than 20 quadrats (>10%) are shown

Species	% of quadrats (n = 187)
<i>Festuca rubra</i>	92
<i>Taraxacum officinale</i> agg.	80
<i>Holcus lanatus</i>	77
<i>Ranunculus acris</i>	75
<i>Plantago lanceolata</i>	73
<i>Rumex acetosa</i>	72
<i>Trifolium repens</i>	67
<i>Alopecurus pratensis</i>	65
<i>Trifolium pratense</i>	63
<i>Filipendula ulmaria</i>	62
<i>Lolium perenne</i>	61
<i>Anthoxanthum odoratum</i>	60
<i>Lathyrus pratensis</i>	53
<i>Ranunculus bulbosus</i>	48
<i>Agrostis stolonifera</i>	45
<i>Dactylis glomerata</i>	42
<i>Cerastium fontanum</i>	40
<i>Sanguisorba officinalis</i>	40
<i>Centaurea nigra</i>	34
<i>Leucanthemum vulgare</i>	29
<i>Bellis perennis</i>	29
<i>Poa trivialis</i>	29
<i>Cynosurus cristatus</i>	28
<i>Ranunculus repens</i>	27
<i>Silaum silaus</i>	25
<i>Deschampsia cespitosa</i>	24
<i>Lotus corniculatus</i>	24
<i>Bromus racemosus</i>	23
<i>Cardamine pratensis</i>	19
<i>Rhinanthus minor</i>	18
<i>Carex flacca</i>	17
<i>Vicia cracca</i>	17
<i>Schedonorus pratensis</i>	17
<i>Scorzoneroides autumnalis</i>	17
<i>Lysimachia nummularia</i>	16
<i>Prunella vulgaris</i>	16
<i>Briza media</i>	14
<i>Ophioglossum vulgatum</i>	13
<i>Luzula campestris</i>	11
<i>Trisetum flavescens</i>	11
<i>Phleum pratense</i>	11

in spruce plantations, along the edges of mixed pine-birch-aspen woodlands and along abandoned tracks on wet soils (Bulokhov et al., 2016).

In Asia, *F. meleagris* occurs in wet meadows and fens in river valleys and, in smaller numbers, in wet forests and shrublands (Krasnoborov, 2007; Zolotukhin, 2017). In the republic of Altai, it is associated with the forest belt, growing in Heteroherbae–*Carex cespitosa* communities in river and stream valleys. Small numbers of plants occur in post-woodland meadows (Ershova, 1996). In Maima River basin in the republic of Altai, *F. meleagris* occurs in communities with *Scirpus sylvaticus*, *Carex acuta* and *C. leporina* growing together with *Caltha palustris*, *Fillipendula ulmaria*, *Geum rivale*, *Leucanthemum vulgare*, *Prunella vulgaris*, *Silene flos-cuculi*, *Sanguisorba officinalis* and *Trollius asiaticus* (Fedotkina, 2005). In a few places, it also occurs as an ephemeral in gaps and openings in floodplain willow woodland as well as in *Salix-Prunus padus* woodland on the terrace of the river Biya valley (Zolotukhin, 2016).

4 | RESPONSE TO BIOTIC FACTORS

In Britain, *Fritillaria meleagris* is a light-loving species that is rarely found where relative illumination in summer is <40% and consequently it has an Ellenberg light (L) indicator value of 8 (Hill et al., 2004). *F. meleagris* avoids competition for light with other species in both meadows and forests by completing its above-ground growth over around 8 weeks during the spring. Shading from tall herbaceous vegetation in the summer has no negative effect on *F. meleagris* (Zolotukhina & Zolotukhin, 2012).

Fritillaria meleagris does not appear to be adversely affected by cutting as it usually completed its growth by the time meadows are cut for hay from early to mid-July onwards. Mowing in June can be beneficial in helping seed dispersal over larger distances as a greater proportion of seeds will be retained in the pods at the time of the cut. The most positive effect of mowing and aftermath grazing, however, is the reduction in plant litter and the density of grasses, which otherwise prevent seedlings of *F. meleagris* establishing among the sward. A deep litter layer will physically block contact between the seeds and the soil as well as reducing light if seeds have managed to germinate. Dense vegetation also severely restricts the seedlings' ability to form a renewal bulb due to competition for light. This was confirmed in an experiment where seeds of *F. meleagris* were sown in 10 pots with meadow species already established, and 10 pots with bare soil and no plants growing. Seed germination rate was similar in both treatments but no seedlings survived until next year in the 'meadow' pots, whereas 80% of seedlings continued to grow in pots with no competition from other species (I. Tatarenko, pers. obs.).

5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

In Britain, *Fritillaria meleagris* forms extensive populations in old, traditionally managed floodplain meadows such as at North Meadow in Wiltshire where it has been recorded in 45%–75% of 320

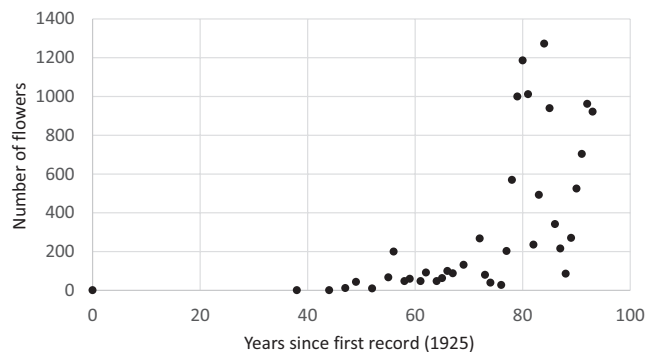


FIGURE 4 The number of flowers of *Fritillaria meleagris* recorded on Portholme meadow, Huntingdonshire, UK, since it was introduced in 1925; adapted from Walker (2021)

1 × 1 m quadrats regularly surveyed across the meadow. Frequency in other British meadow sites varies from 28% in Lugg Meadow in Herefordshire, 34% in Ducklington Mead in Oxfordshire and 72% at Clattinger Farm in Wiltshire (H. Wallace & I. Tatarenko, unpubl. data). The establishment of new colonies appears to take a considerable amount of time because of the very low rates of seed dispersal, and vegetative spread which is usually <0.5 cm per year. The life cycle of the species, including prolonged dormancy (Tatarenko, 2019), can lead to an exponential increase in population size as well as substantial annual fluctuations. For example, on Portholme Meadow in Huntingdonshire where *F. meleagris* is likely to have been introduced around 1925 it took around half a century for the populations to reach 200 flowers and a further 25 years for numbers to exceed 1,200 (Figure 4). However, the distribution of *F. meleagris* on this meadow shows that seed can be transported up to 500 m during floods or possibly in hay attached to agricultural machinery (Walker, 2021). In floodplain meadows in Britain density of *F. meleagris* range from 1 to 69 (average 12) plants per 1 m², although its cover rarely exceeds 1%–2% due to its grass-like leaves. This was confirmed by the survey of Fritillary sites in lowland England during the 1970s (as described in Table 2) in which *F. meleagris* never exceeded a Domin cover abundance of 4 (5%–10%) and had a cover of <1% in 69% of quadrats and a cover of 1%–4% in a further 23% of quadrats (Derek Wells, unpubl. data).

The number of plants in populations vary considerably from site to site. Small populations are often under 200 plants but may range up to 2,000 plants (Walker, 2021). The largest British population occurs at North Meadow, Wiltshire, where an estimated million plants are present in some years (Wolstenholme, 2011). An even larger population (>>1,000,000 flowering individuals) is known from Krówniki in southeast Poland (Zych & Stpiczyńska, 2012). A large population also occurs in the Kungsängen Nature Reserve in Sweden where *F. meleagris* colonised the meadow from a nearby botanic garden (Zhang, 1983). Population sizes vary from 79 to 1,801 in Mátra Mountains in Hungary (Bódis et al., 2020) and the largest population in Russia occurs on the steppes in the Petrin Log ravine in Streletskiy site of Tcentralno-Chernozemniy Zapovednik where around 600,000 plants extend over 8 ha (Vlasov et al., 2014; Zolotukhina, 2007). Siberian populations are much smaller; the

overall number of plants in nine locations in the Altai Krai is estimated to be <1,000 (Shmakov & Silantjeva, 2016).

Magnes et al. (2013) found no differences in abundance of *Fritillaria meleagris* in meadows, scrub and woodlands. In some populations, species density measured 30–40 plants per square metre (Bulokhov et al., 2016). Uneven distribution of the species across the sites can be caused by microtopography including tussocks of *Carex caespitosa* (Zhang, 1983). The availability of bare ground for seed germination was considered to be a key factor in determining the spatial distribution of the plants in bryophyte-covered areas of *Caricetum acutiformis* or patches of bare soil in *Cirsietum rivularis* community (Csörgő & Frink, 2003).

In most populations, the number of flowering individuals is usually exceeded by vegetative plants. On North Meadow long-term monitoring showed that the ratio of vegetative to flowering plants varied between 2.4 and 5.6 over 20 years. This is in line with records from continental populations where a ratio of between 1.9 and 3.2 has been found over 4 consecutive years (Zolotukhina & Zolotukhin, 2012) and 3.4–4.3 in 2 years at a different site (Lepeshkina & Voronin, 2015). In some populations, such as in Clattinger Farm, vegetative plants outnumber flowering individuals by 6–13 times; this ratio declined to 2.3–3.2 only twice during 6 years of observations (Figure 5). In a population in the Upper Şard valley in Romania in 2003, the ratio reached 8–18 (Csörgő & Frink, 2003), and in two populations in western Hungary it was 1.8 and 5.3 in 2017 (Bódis et al., 2020). One of the largest ratios ever recorded was in Kursk Oblast, Russia, where it varied from 9.2 to 28.4 over 5 years (Zolotukhina & Zolotukhin, 2012). Very occasionally, the number of flowering plants can outnumber vegetative individuals. This was recorded once in 20 years of population monitoring at North Meadow. In four other years, the numbers were almost equivalent. In a population near to Tüskeszentpéter in Hungary flowering plants comprised 55% in 2017 declining to 31% in 2018 (J. Bódis, pers. comm.). Numbers of both vegetative and flowering plants can fluctuate significantly from year to year. In a forest habitat in Hungary the ratio of vegetative to flowering plants varied between 9.9 and 62 in 4 years and there was no flowering plant in 1 year (Bódis et al., 2020). The ratio of vegetative to flowering plants in

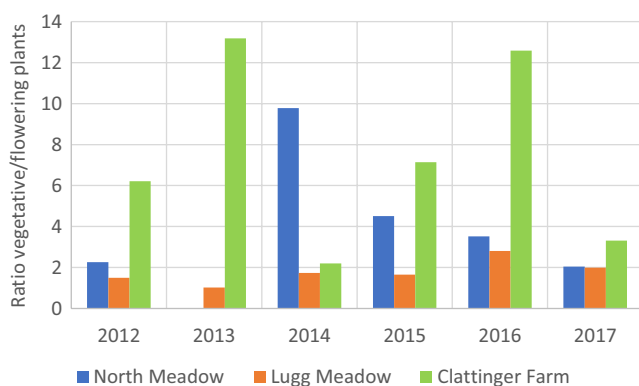


FIGURE 5 Changes in the ratio of vegetative to flowering individuals of *Fritillaria meleagris* in three British floodplain meadows monitored over 6 years

Lugg Meadow in Herefordshire was found to be less dynamic compared to the other two populations shown in Figure 5.

The overall numbers of plants in 130 permanent 1 × 1 m quadrats continuously monitored in North Meadow over 20 years varied from a minimum of 9 in 2013 to a maximum of 1034 in 2019 (Figure 6).

5.2 | Performance in various habitats

Differences in the height of *Fritillaria meleagris* across a range of British populations were largely explained by the frequency of flooding and the amount of macronutrients deposited by floodwaters. Sites that are very rarely flooded and therefore have very low nutrient inputs, such as Clattinger Farm, Wiltshire, have much shorter plants than populations growing on regularly flooded sites such as Lugg Meadow (Figure 7). However, leaf production (number of leaves) measured across three British sites (North Meadow, Clattinger Farm, Lugg Meadow) was not significantly different (I. Tatarenko, unpubl. data) unlike at two sites in Hungary (J. Bódis, pers. comm.).

Plants from shaded habitats are taller than individuals growing in the open (Rotov, 1973). After comparing 26 morphometric characters of flowering *F. meleagris* in several populations in the Carpathian mountains, Andrik (2013) showed that plants from shaded habitats in the forests had flowers that were twice as heavy, and with a Leaf Area Index (LAI) that was 1.6 times larger than plants from open meadows. In contrast, the size and weight of the bulbs were slightly larger in the open, meadow populations. Plants in populations disturbed by trampling by grazing animals were 20% shorter than in undisturbed shaded areas (Andrik, 2013). In Romania, taller plants in wetter conditions produced larger flowers, whereas no such correlation was seen in the plants from a drier part of the soil moisture gradient, although the potentially confounding influence of soil nutrients were not tested (Csörgő & Frink, 2003).

5.3 | Effect of frost, drought, etc

In most parts of its range, *Fritillaria meleagris* avoids frost by remaining dormant below-ground during the winter months. However, in the areas with an extremely continental climate, such as Western Siberia and Altai, its distribution is restricted to river valleys that are sheltered from the most severe winter frosts (Ershova, 1996). In the Mountainous Altai, *Fritillaria meleagris* is often associated with wet soils in river valleys close to where snow beds and ice blankets cover the ground long into the summer months (Ershova, 1996).

Long-term flooding inhibits the development of ground frost in areas where there is little or no snow cover during the winter months. In Britain, floodplain habitats of *Fritillaria meleagris* can be flooded for 2–5 months during the autumn and winter. These floods also reduce the amount of surface litter and create patches of bare ground required for successful seed germination and seedling establishment. Floods in late March and April delay the growth of *F. meleagris* by 2–3 weeks (I. Tatarenko, pers. obs.). Conversely spring

FIGURE 6 The number of vegetative and flowering individuals of *Fritillaria meleagris* recorded in 130 permanent 1 × 1 m quadrats in North Meadow, Wiltshire, UK in 1999–2021

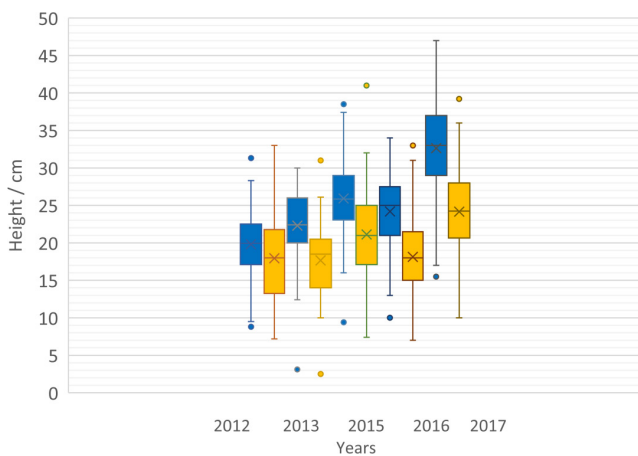
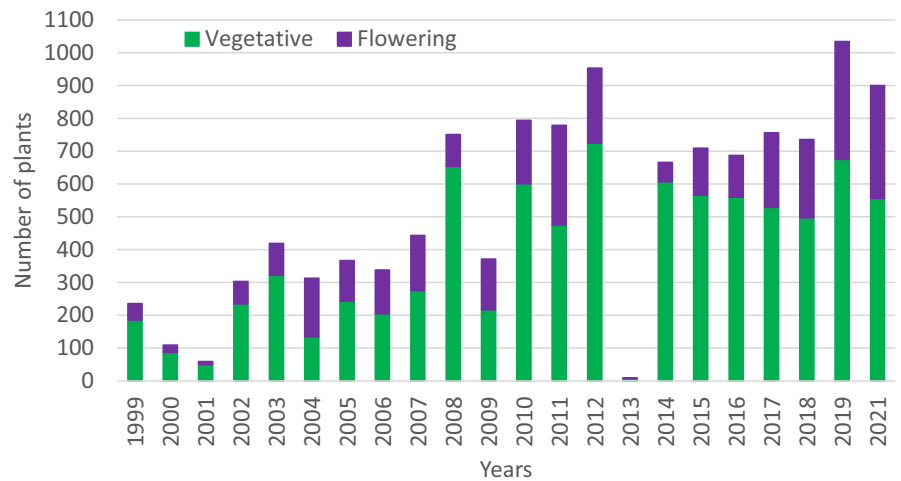


FIGURE 7 The height of flowering plants of *Fritillaria meleagris* growing in two floodplain meadows: Lugg Meadow (blue boxes) floods regularly and receives nutrients with sediments; Clattinger Farm (amber boxes) floods very occasionally, lacking sediments. Observations took place in 2012–2017, excluding 2014

floods deposit nutrients which are readily available to the growing plants resulting in their larger sizes.

The North Meadow population was severely affected by an exceptionally prolonged flood that lasted for 10 months from late April 2012 to February 2013. As a consequence, almost the entire population of 1,500 individuals within a series of permanent plots remained dormant with only 9 individuals appearing above-ground in 2013. Prolonged dormancy was also observed following a period of exceptionally low soil temperature in the winter and early spring of 2013. This is thought to have blocked the chemical signal that breaks dormancy and commences the beginning of sprouting of the bulbs. During this period (15 January–April 15, 2013), there was only 1.7 day degrees above 6°C for the period, which was 26 day degrees lower than the next lowest value for the same time period, observed in 2006 (M. Dodd, unpubl. data). It was not clear if it was this, one of the extreme factors mentioned above, or their combination which caused the mass prolonged dormancy in the population. An additional biotic factor which affected the appearance of *Fritillaria meleagris* in 2013 was a 20 cm thick mat of stolons formed on the ground and water surface by an extensive

growth of *Agrostis stolonifera* during the autumn 2012. The mat could have an extra insulating effect on the soil temperature keeping it locally even lower than regional values (I. Tatarenko, pers. obs.).

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

The bulb of *Fritillaria meleagris* consists of two free storage scale leaves. Seedlings and juvenile plants have only one storage scale as a bulb. The first green leaf is produced in juvenile plants in the year following seed germination. It assimilates nutrients much more efficiently than the cotyledon to form a larger 1-scale bulb of up to 5–7 mm in diameter. The plant grows monopodially until its apical meristem forms the first above-ground stem (Zhang, 1983; Baranova, 1999; I. Tatarenko, pers. obs.). During the third year, in good growing conditions, the plant forms an above-ground stem bearing 3–4 spirally arranged leaves. At this stage, the plant switches to sympodial growth forming a renewal 2-scale bulb 8–12 mm in diameter from a top lateral meristem (Baranova, 1981, 1999; I. Tatarenko, pers. obs.).

The roots increase in size and number as the plant develops. Around 20 roots are present by the time that plants produce leafy stems. Large flowering individuals with bulbs up to 2 cm in diameter usually have around 40–60 roots that are between 20 and 60 cm long. During the spring, thick contractile roots also appear that regulate the position of the bulb. The optimal bulb depth appears to be 10–15 cm, but in floodplains where sediment is deposited during the spring bulbs can be found to a depth of 20–30 cm. The deep burial of bulbs is thought to reduce the growth of lateral meristems resulting in poor vegetative reproduction (Baranova, 1999). In very wet soils such as at Kungsängen Nature Reserve in Sweden bulbs are located at a much shallower depth between 5 and 8 cm (Zhang, 1983).

The bulbs grow along a vertical shoot axis. The internodes can be very short and if the position of the bulb below-ground is relatively shallow a renewal bulb sits in between the scales of the old bulb (Figure 9a). If the location of the bulb is too deep, a renewal bulb can be formed on the top of the old one (Figure 10a). Lateral spread

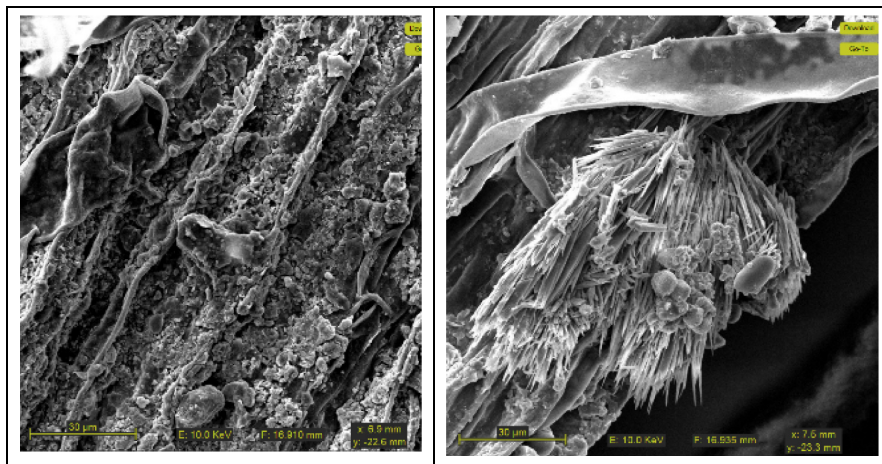


FIGURE 8 A microbial community living on the exoderma of the wintering roots of *Fritillaria meleagris*. SEM images courtesy of the Open University OpenLab

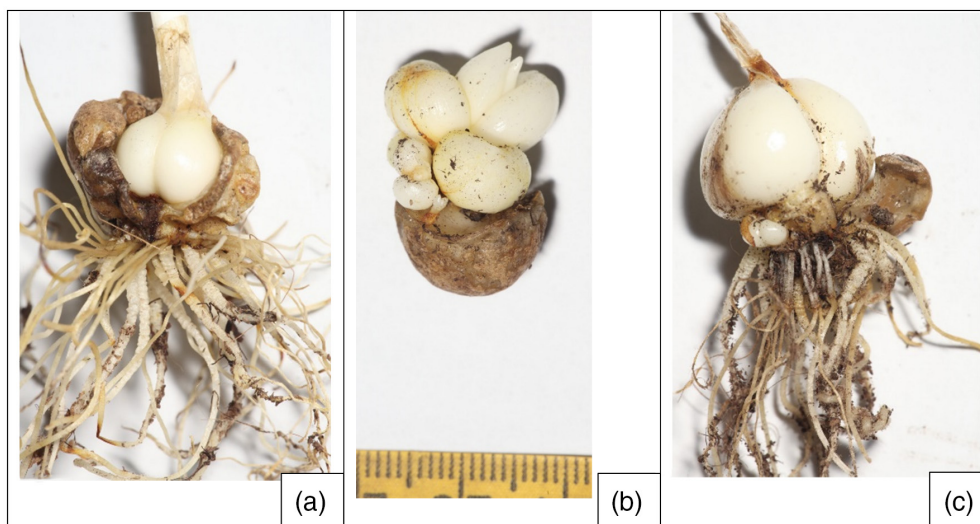


FIGURE 9 Bulbs of *Fritillaria meleagris* cultivated by the Royal Horticultural Society and showing: (a) the renewal bulb growing with the remains of the previous year's bulb and thick contractile roots among the thin feeding roots; (b) three bulbils of different sizes formed along the edge meristem of an old bulb; (c) a dormant plant with no above-ground shoot and a small bulbil forming from the axillary bud on the main shoot. Photos: Mike Dodd

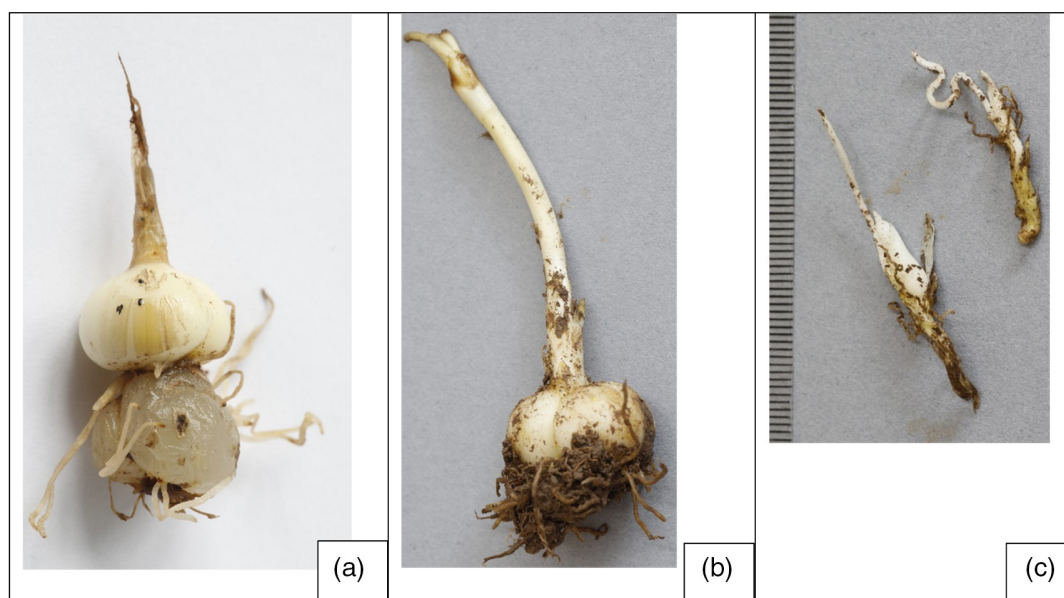


FIGURE 10 Dormant plants of *Fritillaria meleagris* collected from Lugg Meadow, UK, in 2018: (a) a new bulb formed during dormancy with no external shoot growth; (b) a new bulb with shoot growth that stopped before the leaves reached the soil surface; (c) shoots with long tubular sheaths that failed to reach the soil surface and therefore did not produce a leaf blade. Photos: Mike Dodd

of the plant is negligible and excludes any possibility of the ramets occupying new areas in the habitats.

In nutrient-poor soils, plants tend to grow monopodially forming a single root leaf each year and a small 1-scale bulb for several years (Tatarenko, 2019). Following an environmental stress (such as a prolonged flood) and dormancy, many plants return to monopodial growth state as a way of saving energy—a strategy that is widely used by orchids (Tatarenko, 2014). Under stress, the adult plants of *F. meleagris* form a single root-leaf that is much bigger than in juvenile plants. This leaf can reach a width of 2 cm and length up to 20 cm, compared to 0.2–0.3 cm width and up to 10 cm length in juvenile plants. Some plants produce a leaf blade from the top of one of the storage scales which results in a plant having two root leaves (Tatarenko, 2019). The presence of two-leaved plants in a population is not high but has been observed to be consistent over a number of years at North Meadow, Clattinger Farm and Lugg Meadow.

One-leaved plants have been generally regarded as 'juvenile' following Zhang (1983). Monitoring of individual plants at Lugg Meadow over 7 years revealed that adult plants, both vegetative and flowering, can occasionally emerge bearing a single leaf (Tatarenko, 2019). This has been described for other species as a retrogression in a life cycle as adult plants general have larger leaves than juveniles (Silvertown et al., 1993). The width of the leaf can be used as an indicator of age; single leaves 2–5 mm wide are likely to belong to juvenile plants, leaves wider than 9 mm are likely to indicate adult plants. Single leaves 6–9 mm wide could represent either juvenile or adult groups—a fact that should be taken into account when studying populations of *F. meleagris* (Tatarenko, 2019).

Zhang (1983) suggested an additional age category—'sub-adults'—for plants with 2–3 leaves. However, the monitoring of individuals on Lugg Meadow revealed annual variation in the number of leaves making this category problematic as a character in population studies (Tatarenko, 2019). Therefore, the age categories which can be used with a sufficient level of confidence are as follows:

- *Juvenile*—non-flowering plants with a single leaf 0.2–0.5 cm wide and up to 10–13 cm long;
- *Adult vegetative*—non-flowering plants with 3–9 leaves arranged along the stem, or a two-leaved rosette, or a single large leaf 1.0–2.0 cm wide and up to 15–20 cm long;
- *Flowering*—plants with 1–2 flowers and with 3–9 leaves arranged on the stem.

Plants with aborted flowers have also been reported, that is, where a flower bud produced in the autumn does not complete its development into a flower in the following spring. The sequence of the age-states described above from single-leaved juveniles to many-leaved adults only occurred in 6% of the plants observed in Lugg Meadow. Those plants continued to increase their size and number of leaves through subsequent years. Seven juvenile plants formed an increasingly large single leaf for 3–5 years before producing a

flowering stem. Such a large single leaf was named a 'feeding leaf' as the leaf size was similar in size to several narrow stem-leaves combined. Often plants which re-emerged from a prolonged dormancy also had a 'feeding leaf'. During 7 years of observation on Lugg Meadow, 29% of adults had at least one reversal from having an aerial leafy stem back to a single leaf in the subsequent year. In some plants, several such reverses were recorded (Tatarenko, 2019).

6.2 | Mycorrhiza

To date, no species of *Fritillaria* has been shown to possess a mycorrhizal association with a fungus. In *Fritillaria meleagris*, even prolific root growth in spring shows no sign of mycorrhizal colonisation with the roots remaining intact during 2 months of growth. Dormant plants maintain a vernal cohort of 30–50 roots over the summer. These have abundant fungal presence in the root hairs along with a superficial spread of mycelium on the roots. Some microbial growth has been observed along the cell walls in roots' exoderma forming a characteristic pattern (Figure 8). These connections to the soil microorganisms were observed at morphological/microscopic level; further investigations of symbiosis of *Fritillaria meleagris* with soil fungal and microbial communities are therefore required.

6.3 | Perennation: Reproduction

Fritillaria meleagris is a typical geophyte as described by Raunkiaer's classification of life-forms. The bulb is the primary mode of perennation. Nutrients stored in the bulb are used for fast growth of the above-ground shoot in spring.

The annual cycle of growth can change if a plant fails to produce above-ground organs in spring. Absence of above-ground organs for more than a year is called 'prolonged dormancy' (PD), and by 2018 it has been recorded in 108 species from 21 families (Zhmylev et al., 2018). PD has been observed in *Fritillaria meleagris* in the wild in Sweden (Zhang, 1983) and 3-year dormancy has also been reported for cultivated plants of a close species *Fritillaria meleagroides* (Markov & Idrisova, 1996). Monitoring of individual plants in Lugg Meadow over 7 years (2012–2019) revealed that PD is common in *F. meleagris* with 37% of individuals remaining below-ground for 1 year and 26% for 2 years (Tatarenko, 2019). A tiny proportion of plants (0.6%) remained dormant for 7 years. Only 9% experienced no PD. Overall, 167 variants of annual sequences of dormant and active individual plants were observed in 231 adult plants of *F. meleagris*. Dormancy was also common in juvenile plants, with 59% entering PD after their first appearance, whereas 12% grew for 2 years before entering PD. Most plants re-emerged from PD as non-flowering plants, either with a single, large feeding leaf or a stem with 3–4 narrow leaves; only a few plants flowered immediately following re-emergence (Tatarenko, 2019). Excavation of dormant plants in 2018 revealed that PD is expressed differently in individual plants. The plant shown in Figure 10a had been dormant for 2 years since

flowering in 2015 during which time it had formed a new bulb. The dormant plant shown in Figure 10b had last flowered in 2017 and in 2018 bud growth had been initiated but stopped 5 cm below the ground surface, probably because all of its roots had died. Some plants were found to have branched below-ground to form smaller bulbs (Figure 10c); these were classed as dormant as no above-ground organs had been formed. These findings show that PD does not happen uniformly in *F. meleagris* (Tatarenko, 2019).

Fritillaria meleagris reproduces vegetatively in two ways: by the growth of lateral shoots (Turrill, 1951) and by 'bulb division' (King & Wells, 1993). The latter refers to the production of bulbils on the bulb scales. In wild populations of *Fritillaria meleagris*, a clonal growth was observed by Zhang (1983) at Kungsängen Nature Reserve in Sweden where 14% of studied plants showed a vegetative sprout of bulbils from the bulbs. There were no other observations in the wild because of the protected status of the species; however, the formation of bulbils on the scales of old bulbs is well known in cultivation (Baranova, 1999; Petrić et al., 2011; Figure 9b). Neither way of vegetative propagation in *F. meleagris* leads to noticeable clonal spread (Hill et al., 2004) as the distance between daughters and parent plants is usually less than 0.5 cm (Zhang, 1983). This limited spread produces very dense clones of up to 10–30 shoots within 4–9 cm² (Tatarenko, 2019). In clones, ramets became dormant and then re-emerged from PD at the same time (t-test, $n = 40$, $p = 0.0001$). On Lugg Meadow, Herefordshire, the predominantly white-flowered population showed a higher rate of plants forming clones than in the purple-flowered populations (I. Tatarenko, pers. obs.).

The lateral meristems in *F. meleagris* are mainly inactive (Baranova, 1999). As a result, the axillary buds on the main shoot do not develop fully. Usually buds are only produced from the apical meristem unless these are damaged or remain dormant. If this happens, then the axillary buds can develop into the bulbils (buds) and shoots. An axillary bud was observed to develop on a dormant plant in cultivation (Figure 9c). Some dormant plants at Lugg Meadow were found with shoots branching and growing below-ground (Figure 10c). A different individual produced four adult ramets while growing below-ground for 6 years (Tatarenko, 2019). Another mode of vegetative reproduction observed mainly in cultivation is the production of adventitious bulbils from the lateral meristems of the storage scale-leaves of the bulb (Figure 9b). Each scale can produce up to six bulbils and each bulbil comprises a shoot with 3–6 storage scales tightly arranged around a shoot axis with no other leaves present.

Tissue culture has been used for a long time to propagate *Fritillaria meleagris* for conservation purposes (e.g. Kukulezanka et al., 1989; Zăpârțan, 1997). Scale sections taken from bulbs have been frequently used to produce somatic embryos and bulbils (Laslo et al., 2011; Petrić et al., 2011). Other parts of the plants, such as leaf bases (Subotić et al., 2010), mature zygotic embryos (Petrić et al., 2011) and floral buds (Muraseva et al., 2015) have also been used to propagate *F. meleagris* successfully.

The annual production of seed appears to be the main mode of reproduction in natural populations of *F. meleagris*. Seeds germinate

in the winter or spring within a year of being shed from the pod. Seeds remain viable for one, or more rarely 2 years (Sedelnikova, 2003; Vetchinkina, 2010). In optimal conditions, adults start to flower in their fifth or sixth year after seed germination (Zhang, 1983). On infertile soils, the pre-flowering period of ontogenesis can take much longer. The overall life span of *F. meleagris* has been estimated as 25 years (Horsthuis et al., 1994) but field observations suggest that it can live much longer. The mortality rate of adult plants appears to be very low: for example, only one of 126 plants died during monitoring over 6-year observation period at Lugg Meadow, UK (Tatarenko, 2019).

6.4 | Chromosomes

$2n = 24$ (Darlington, 1937).

Polyploidy was not recorded in *F. meleagris*, it is extremely rare in the genus *Fritillaria* in general with only triploid plants occasionally found (Darlington, 1937). The genus *Fritillaria* has one of the largest genomes known in the plant kingdom (Bennett & Leitch, 2012). Genome size of a diploid plant is 1C-value 47.3 pg (Leitch et al., 2007). Species of *Fritillaria* have a large range of genome sizes, with 1C-value varies from 29.7 pg to 100.1 pg (Day et al., 2014).

6.5 | Physiological data

Fritillaria meleagris has C3 type photosynthesis. Low temperatures are required for the germination of *F. meleagris* seeds (Vetchinkina, 2010). The chilling of *F. meleagris* bulbs formed in vitro has been shown to have a strong positive effect on the breaking dormancy (Nikolic et al., 2008). The rooting rate after 6 weeks of chilling was significantly higher (60.4%) when compared to controls grown under standard conditions (32.4%). Shoot and root lengths were also higher in chilled bulbs. Marković et al. (2020a) investigated the effect of gibberellic acid (GA₃) and gibberellin biosynthesis (GA) inhibitors—ancymidol (A) and paclobutrazol (P) on changes in soluble sugar content in dormant bulbs. The main sugar in *F. meleagris* bulbs was glucose while fructose content was lower. GA₃ treatment at 24°C for 5 weeks had the most pronounced effect on bulb weight, sprouting and sugar content compared to 7°C and a control. The sensitivity of bulbs to GA inhibitors differed in effect on sugar content in bulbs. The effect of soaking bulbs in GA₃ solution (1, 2 and 3 mg/L) combined with low-temperature treatment (7°C) was even more pronounced (Marković et al., 2020b).

6.6 | Biochemical data

The medicinal properties of species of *Fritillaria* have been recognised within traditional Chinese medicine for over 2,000 years (e.g. Zhang et al., 2010). The Genus *Fritillaria* has also been studied in Europe from phytochemical and pharmacological perspectives

(Saklani et al., 2011). Most of these studies have focussed on alkaloids within the bulbs. It is known that bulbs of *Fritillaria meleagris* contain the poisonous alkaloid imperialine ($C_{27}H_{43}NO_3$) which can induce vomiting and potentially cardiac arrest (Bauer et al., 1958; Forsyth, 1954). In all, 10 new and 3 very rare steroidal glycosides have been isolated from the bulbs of *F. meleagris*; these were classified as spirostanol derivatives, furostanol derivatives, pseudo-furostanol derivatives and cholestane derivatives of the steroidal alkaloid glycosides. These chemical compounds had a negative effect on the growth of human leukaemia and adenocarcinoma cells (Matsuo et al., 2013). It seems likely that these poisonous chemicals prevent soil invertebrates from damaging the bulbs.

7 | PHENOLOGY

Individuals of *Fritillaria meleagris* comprise a bulb and a series of shoots and adventitious roots that are replaced annually. The bulb is a main mode of perennation during summer, autumn and winter months while active growth of the above-ground shoot is observed in March, April and May. Like other geophytes in relatively moist climates, *F. meleagris* produces a new renewal bud during summer months. By the end of the summer, a flower bud has formed inside this renewal bud together with a renewal bud of the II order, which will sprout in the year after next (Baranova, 1999). Root growth occurs in both the spring and autumn with the spring cohort usually being 2–3 times bigger than those produced in the autumn. The autumn roots support rapid shoot growth in the following spring. No morphogenetic changes have been observed in the buds or roots during winter months, even in mild winters. It takes 18–20 months from initiation of the shoot apex below-ground to the production of an above-ground shoot. The shoot apices start to emerge in August and September and are covered by two leaf primordia for 6 months over the winter. These continue to develop in March forming a bulb with two scale storage leaves. By the end of May, the renewal bud usually consists of three sheath leaves enclosing a shoot apex. Development of the bud continues during the summer when no above-ground organs are present; the entire shoot including the flower bud is fully formed in a bud by the end of summer (Baranova, 1991; I. Tatarenko, pers. obs.). Roots are produced at the base of the bulb in September and October. These autumn roots persist over the winter ensuring that the above-ground organs develop rapidly in the spring when compared to individuals that lack them. The spring roots are produced in March and early April ahead of the bud sprouting. These vernal roots are more numerous (50–70) and longer (up to 20–30 cm) than the autumnal roots (2–10, up to 5–10 cm). Several contractile roots appear among vernal roots to maintain the bulb position in the soil at between 10 and 20 cm depth. The roots persist for about a year. In Britain, the above-ground growth occurs in late March, April and May. An episode of earlier development of leaves in late February and March was recorded in wet grassland at Aubert Ings in Yorkshire (K. Walker, pers. obs.). A root leaf or leafy stem appears above the ground in late-March or early-April. Shoots extend

above-ground for 3–5 days with the flower buds opening 2–3 days later. Flowers remain open for 4–9 days (M. Dyson, unpubl. data) with nectaries producing nectar throughout anthesis. Once the flower has been pollinated, the tepals drop to the ground and the flower stalk elongates upwards around 5–10 cm above the flower height. The seeds ripen by the beginning of June and seed dispersal lasts for around 2–3 weeks. For germination, seeds require at least 3 months of warmth followed by exposure to cold temperatures (see 'Seed production'). The seeds germinate from February to April. Seedlings keep green cotyledons for 1–2 months and form 1-scale bulb before going into dormancy.

In Britain, the flowering period is determined by spring temperatures: in warm springs, *F. meleagris* will start flowering in the first or second week of April, whereas in cold springs flowering is delayed till the end of April or the beginning of May especially if combined with flooding. Most continental populations flower at the end of April or in early May. In the mountains of Croatia, flowering takes place at the end of April until mid-May, a month later than lowland populations (Kranjčev & Šešok, 2016). Further east in the Altai region *F. meleagris* flowers in early May and the growth is completed by the end of June (Shmakov & Silantjeva, 2016). A study of herbarium specimens ($n = 64$) collected in the Pannon Ecoregion in Hungary identified the earliest flowering date as 28th February and the latest as 24th May with fruit set between 24th April and 24th May (Bódis et al., 2020).

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

Fritillaria meleagris was originally thought to be a dichogamous (protogynous), fully out-crossing and mainly bumblebee-pollinated species (Hedström, 1983). However, later studies showed that the flowers are in fact homogamous with the stigma becoming receptive at the same time as the anthers dehisce pollen (Zych & Stpiczyńska, 2012). On North Meadow, UK, the flowers remained open for 4–7 days (median = 6, $n = 29$). Pollen production lasted for between 3 and 6 days with a median of 5 days ($n = 29$; Figure 11). In a Polish population, nectar was available to pollinators for a similar number of days (5–6; Zych & Stpiczyńska, 2012).

In April 2016, an experiment was carried out at North Meadow, UK, to assess self-compatibility. In this study, 50 flower buds were 'bagged' to exclude pollinators using a 1 mm² mesh and compared with 50 flowers that were left unbagged. All the unbagged flowers that survived ($n = 34$) produced mature seed pods, whereas no pods were produced on flowers with bags. This suggests that flowers do not spontaneously self-pollinate. In a few cases, two flowers were unwittingly bagged together but none of these produced pods suggesting that cross-pollination between flowers does not occur in the absence of pollinators. Although self-pollination is rarely observed, artificial crosses can result in the production of fully developed seeds (Zych & Stpiczyńska, 2012). This means that although the flowers are self-compatible they almost always require pollinators to transfer

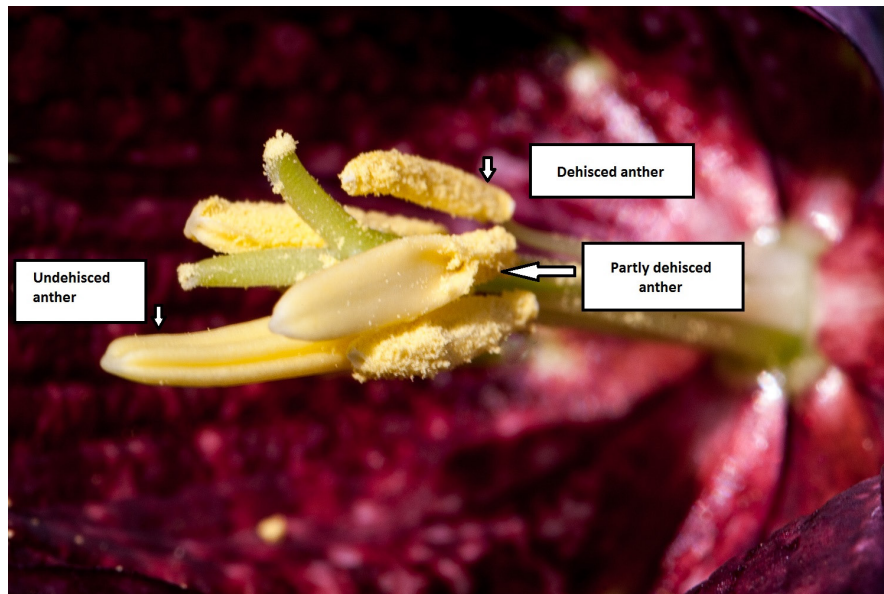


FIGURE 11 Asynchrony in pollen presentation in a flower of *Fritillaria meleagris*. Photo: Miranda Dyson

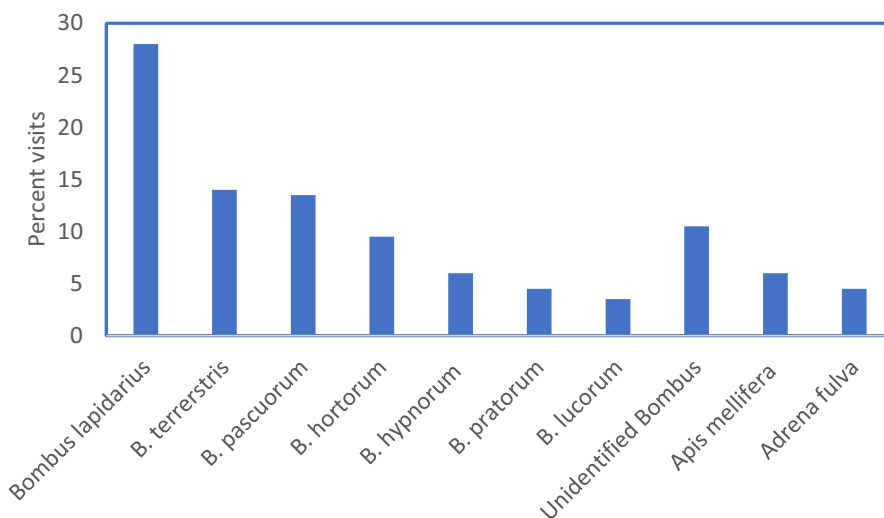


FIGURE 12 Visits of bee species to flowers of *Fritillaria meleagris* at North Meadow, UK. (M. Dyson, pers. obs.)

pollen to the stigma, either from the same or a different flower. The easily accessible nectar and pollen attract a variety of pollinators to the flowers of *Fritillaria meleagris*. Nectar production in the flowers of *F. meleagris* was measured in Polish populations and over its flowering time a single flower secreted on average 10.9 ± 13 mg of nectar (mean and *SD*; $n = 182$). The sugar concentration of the nectar was in the range of 3% and 75% with an average concentration exceeding 50%. Nectar production changed depending on the stage of anthesis, being highest during full anthesis (21.8 ± 16.1 mg; 70.5%, mass and concentration, respectively) and lowest at the end of anthesis (1.3 ± 2.7 mg; 16.9%, mass and concentration, respectively; mean and *SD*). In *F. meleagris*, nectar was composed of almost equal quantities of sucrose, glucose and fructose and this balance did not change in successive stages of anthesis (Rix & Rast, 1975; Stpczyńska et al., 2012).

The flowers of *Fritillaria meleagris* are thought to be one of the main food sources (nectar) for bumblebee queens in April when few other plants are in flower in meadows. In the springs of 2016

and 2017, pollinators of *F. meleagris* were identified and counted in North Meadow, UK. A total of 200 bees were observed visiting flowers of which 93% were bumblebees belonging to seven species (Figure 12). In 2016, 86% of the invertebrates seen foraging flowers were bumblebees; 7% were *Adrena fulva* (Tawny Mining-bee) and 7% were *Apis mellifera* (Honey Bee). No other invertebrates were observed on or inside flower. The most common species of bumblebee seen on flowers during April and May was *Bombus lapidarius* (Red-tailed Bumblebee) which accounted for 28% of visits to flowers (Figure 12). The caste of the bumblebees was not noted in 2016. However, during 2017, the behaviour of 47 bumblebees foraging on flowers was studied in detail at the same site and 66% of these ($n = 31$) were queens belonging to seven different species. Although it was not possible to track the entire foraging journey of all individuals, 43% were observed visiting 10 or more flowers on each journey with one individual visiting 56 flowers before leaving the meadow. Fifty-seven percent of the bees seen foraging flowers were carrying pollen loads (Figure 13). The flowers of *F. meleagris* at North



FIGURE 13 *Bombus lapidarius* with a pollen load visiting a flower of *Fritillaria meleagris* at North Meadow, UK. Photo: Miranda Dyson

Meadow are primarily pollinated by bumblebees, especially early in the season when queens are establishing new colonies and are reliant on *F. meleagris* flowers for both pollen and nectar (M. Dyson, unpubl. data). In a study in Poland, bumblebees comprised 81% of the visits to flowers, thereby further confirming their status as the main pollinators of *F. meleagris* (Zych et al., 2013). In Hungary (near Gyékényes), *Bombus lapidarius* (1 worker), *B. ruderarius* (2 workers), *B. sylvarum* (1 worker) and *Osmia cornuta* (1 female) were recorded as pollinators of *F. meleagris* in 2017 (Bódis et al., 2020). In a Polish population where *F. meleagris* flowers later small solitary bees of the genera *Andrena* and *Lasioglossum* were found carrying almost three times larger pollen loads than bumblebees or honeybees, suggesting they could be more effective pollinators later in the season (Zych & Stpiczyńska, 2012).

It has been suggested that populations with predominantly white or purple flowers would differ in their pollination rates because they occur in different habitats or because bumblebees were more attracted to one colour than another. This hypothesis was tested by comparing the number of ripened pods in predominantly white- (Lugg Meadow) and purple-flowered (Clattinger Farm) populations that also differed in terms of flooding regime, ground water-table fluctuation, soil composition and vegetation type. Despite all these differences, the fruiting pattern was very similar over 2 years (2014 and 2015). Individuals of *Fritillaria meleagris* formed no pods in more than 70% of surveyed 1 × 1 m quadrats in both populations, about 20% of quadrats had only 1 pod, and few quadrats on both sites had more than 4 pods. Average fruit production was 0.51 pod/per 1 m² on Lugg Meadow, and 0.52 pod/per 1 m² in Clattinger Farm (I. Tatarenko, unpubl. data). This supports observations in Warsaw

Botanic Garden where bumblebees did not distinguish between white and purple flowers in an artificial mixed population (Zych & Stpiczyńska, 2012).

8.2 | Hybrids

None known.

8.3 | Seed production and dispersal

After the flowers are pollinated, the tepals fall and the stem elongates upwards by between 5 and 10 cm, thereby increasing the height at which seeds are dispersed from the terminal pod (Figure 1c). The size of the mature pod varies from 1.1 cm to 2.4 cm in diameter and from 1.6 cm to 4.7 cm in length; the dry weight of a pod is between 0.1 and 0.25 g. On average, 138 seeds are produced in each pod (I. Tatarenko, unpubl. data), although previously published values are lower at between 50 and 100 seeds per capsule (Gibbons, 1990; Oswald, 1994; Turrill, 1951). In 2017, 77% of flowers produced fertile pods in a sample of 50 marked flowering plants on North Meadow, UK. The mean pod length was 1.69 ± 0.30 cm (range: 0.88–2.3 cm) and the mean number of developed seeds per pod was 91.5 ± 31.5 (range: 31–157). The number of undeveloped seeds per pod was 36.2 ± 20.9 (range: 7–99; M. Dyson, unpubl. data).

In one study in Hungary, the ratio of pods to flowers was 86.8% and 80.9% in two populations with no statistically significant difference between the two populations in terms of seed number. The mean number of developed seeds per pod was 139.6 ± 25.8 ($n = 20$, range: 87–214), and mean number of undeveloped seeds per pod was 15.8 ± 10.3 ($n = 20$, range: 5–43; Bódis et al., 2020).

In floodplain meadows, anecdotal evidence suggests that seeds of *Fritillaria meleagris* are dispersed mainly by wind and water (Rotov, 1972; Walker, 2021). The seeds are released sequentially as layers from within a loculicidal capsule. As it dehisces, the valves gradually become wider or even bend down (Figure 1d). The seeds are usually dislodged from the pod when the stems are knocked by mammals or shaken by wind. The average dispersal distance is very short, usually 10–30 (40) cm, although strong winds can carry seeds up to 2–3 m (I. Tatarenko, pers. obs.). The appearance of new colonies on floodplains well away from known populations suggests that long-distance dispersal in flood-waters can occur and this may be the origin of many of the floodplain populations along the River Thames in Britain (Walker, 2021). In Tula Oblast in Russia, establishment of new populations of the species was recorded along a small stream all originated from a single long-existing population located upstream (S.S. Isaev and T.I. Varlygina, pers. comm.). The seeds of *F. meleagris* have excellent buoyancy; in mesocosm experiments seeds floated on the water surface for 2 months with no sign of physical damage.

8.4 | Viability of seeds: Germination

Seed embryos usually account for around 4% of the total seed mass, although seeds show a significant variation in the development of embryos with about 20% of seeds in a population have no or very poorly developed embryos. In Britain, well-developed seeds varied in size from 0.18×0.15 cm (0.9 mg) to 0.61×0.52 cm (4 mg; Figure 14). Very similar figures have been obtained from a population in Sweden (0.3–0.6 cm, 0.5–2.0 mg; Zhang, 1983). Seeds cultivated in Siberia were over twice as heavy as these natural populations (5.45 mg; Sedelnikova, 2003). The weight of the seed (2.1–4 mg) appears to have little effect on the distance that seeds are dispersed (Csontos, 2001).

Seed embryos of *F. meleagris* are still immature when dispersal commences at the start of June (Nikolaeva et al., 1999). The embryos are linear and only about a twelfth to a fifth the size of the endosperm (Batygina, 1985). Both warm and cold temperature treatments are required for embryos to break deep and complex morphophysiological dormancy (Nikolaeva et al., 1985).

Seed dormancy was investigated on seeds obtained from plants cultivated in the Main Botanic Garden, Moscow, Russia (Vetchinkina, 2010). Seeds from ripened pods were sown on media (Murashige & Skoog, 1962) and cultivated for 5–7 weeks at 20–22°C and 2, 9 and 12 weeks at a 3–5°C. Control seeds were kept at 3–5°C and only 2.63±0.2% of embryos had developed after 3 weeks. At 20°C, 77% of embryos had developed well after 3 weeks and by the fifth and seventh weeks they reached two-thirds of their maximum size and stopped further development until the cold treatment. Further development was stimulated by cold temperatures of 3–5°C and a 3-month treatment was found to be more effective than shorter periods. After 3 months of exposure to cold temperatures, 88% of embryos completed their development (Vetchinkina, 2010). In a separate study, seeds sown in soil in a botanic garden in Western Siberia germinated at 35%–48% (Sedelnikova, 2003). In our mesocosm experiment, seeds sown in the soil at a depth of 1 cm germinated 2–4 weeks later when compared to seeds floating in water. The overall germination in both flooded and non-flooded treatments reached 70% (I. Tatarenko, pers. obs.).



FIGURE 14 Variation in seed sizes in *Fritillaria meleagris* population in North Meadow, UK. Seeds were collected in 2018. Photo: Mike Dodd

8.5 | Seedling morphology

Seeds can germinate while on the water surface (Figure 15a) or under the water (Figure 15b). Seedling establishment, either from the floating or from ground germination, requires available bare ground. Seedlings of *Fritillaria meleagris* are very difficult to spot in among dense herbage in natural habitats due to their thread-like cotyledons that are only 1–1.5 mm diameter. Consequently, their development has been studied in mesocosms at the Open University campus, Milton Keynes, UK. Each seedling produces a short radicle and a tubular thread-like cotyledon 1–1.5 mm in diameter, up to 5–10 cm long (Figure 15c) and is very curved if seed germinated on the water surface. The tubular cotyledon encloses an apical meristem which produces a primary storage scale-leaf—a bulb just 1.5–3 mm in diameter. These seedlings can float on the surface of flood-waters for up to a month following germination and root immediately once the water recede. The seedling produces a radicle which forms the primary root 3–7 cm long. The cotyledon dies off by mid-April to mid-May, depending on the time of seed germination which may vary from February to April. Overall, the seedling stage lasts for about 2 months (I. Tatarenko, unpubl. data).

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

All the above-ground organs of *Fritillaria meleagris* (flowers, stems, leaves) are predated by the Lily Beetle (*Lilioceris lili* Scopoli, Chrysomelidae, Coleoptera; Cox, 2007). A high proportion of flowers were observed to be damaged by insects in a population in Bryansk Oblast, Russia (Bulokhov et al., 2016). Caterpillars (species unknown) were also observed grazing on green pods and unripened seeds at Clattinger Farm and North Meadow, UK. Grazing by caterpillars was observed on individual plants and occasionally on a group of plants. In the former, the pods were damaged from the side, with the seeds specifically targeted. In the latter, the grazers removed the top halves of the pods together with the seeds. Such damage affected <1% in population in North Meadow, UK, in 2018 (I. Tatarenko, unpubl. data).

In Britain, seed predation appears to vary considerably across sites and years. In 2014, counts of ripened and unripened (green) pods in two sites revealed a stronger negative impact of invertebrate grazers at Lugg Meadow, where only 34% of green pods ripened compared to 45% at Clattinger Farm. However, in 2015, the relative number of ripe pods was much lower in both sites but more similar (23% and 26%, respectively, I. Tatarenko, unpubl. data). In Britain, Wood Pigeon (*Columba palumbus* L.), Red-necked Pheasant (*Phasianus colchicus* L.) and European Rabbit (*Oryctolagus cuniculus* L.) have also been reported as causing significant damage to some populations by systematically removing flowers of *F. meleagris* (Price, 1983; Trist, 1981); however, their impact on reproduction success has yet to be studied.

FIGURE 15 (a) Germinating seed of *Fritillaria meleagris* floating on the water surface and (b) under water. (c) Seedlings of *F. meleagris* that germinated as floating seeds and rooted into soil once the water-level receded below the soil surface. Photos: Mike Dodd

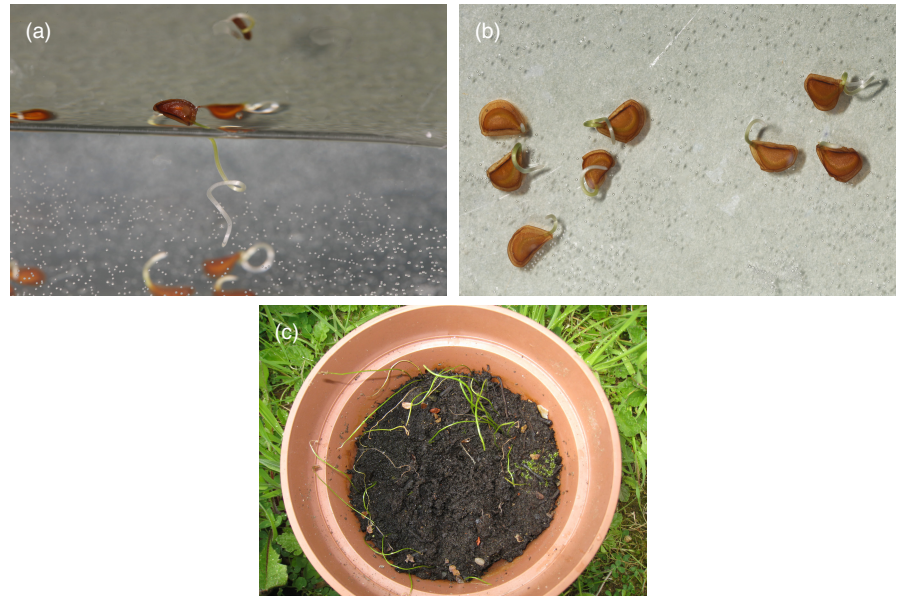


FIGURE 16 Fungal mycelium covering the dry fruits of *Fritillaria meleagris*, North Meadow, Wiltshire. Photo: Irina Tatarenko

9.2 | Plant parasites

An unknown fungus has been observed on the pods of *Fritillaria meleagris* at North Meadow, UK. The seed pods were covered with dark-brown mycelium with fruiting bodies occasionally found across the meadow (Figure 16). As many as 57 species of fungi have recorded on the dead leaves and stems of *F. meleagris* (Ellis & Ellis, 1997).

9.3 | Plant diseases

None known.

10 | HISTORY

There is currently no fossil evidence to confirm the presence of *F. meleagris* in the British Isles before it was first reported from the

wild in 1737 (Godwin, 1975; Pearman, 2017). Consequently, its origin has been the subject of considerable debate with two rival hypotheses as to when (and how) it arrived in the British Isles (Walker, 2021). One view, very persuasively argued by Oswald (1994), suggests that it colonised naturally during the current post-glacial via the land-bridge that extended across the current North Sea basin. This 'Greater Rhineland' range was then gradually cut-off from mainland Europe by rising sea levels, isostatic adjustments and possibly finally by tsunamis created by the Storegga submarine landslip around 8,200 years ago. For a long time, it has been assumed that populations in species-rich ancient grasslands on floodplains in southern and eastern England were relicts of this wider distribution and therefore that it should be treated as a native British species. Further support for this view comes from its habitat associations in Europe and Asia where it frequently grows in woodlands on floodplains (Krasnoborov, 2007; Tomović et al., 2007; Zolotukhin, 2017). Over large parts of this range humans have cleared these woodlands but *F. meleagris* has colonised the grasslands that have taken their place (Ershova, 1996; Gubesch & Morari, 1974; Popescu, 1967; Ularu & Parascan, 1970), possibly benefitting from increased pollination and seed dispersal in more open landscapes. The widespread adoption of hay-making over the last two millennia will have further benefitted *F. meleagris* as it has set plentiful seed before the hay was traditionally cut. *F. meleagris* could therefore have migrated to the British Isles during the current post-glacial, survived the widespread clearance of woodlands on floodplains and then been maintained by traditional hay meadow management till modern times.

The alternative view relies on documentary evidence and argues that *F. meleagris* was introduced to Britain by early horticulturalists for cultivation in botanic gardens during the sixteenth and seventeenth centuries. One of the earliest European texts on plants (Gerarde, 1597) mentions *F. meleagris* growing on the floodplain meadow in France, from where it was taken to other countries for ornamental reasons. The first published record in the wild in Britain

came much later, in 1737, when it was described as 'observed above 40 years.... in Maudfields' in Middlesex (Pearman, 2007). By the 1820s, it had been recorded from meadows in a further five counties but most tellingly the largest populations in Wiltshire, most notably North Meadow, were not discovered till the 1880s (Pearman, 2013; Walker, 2021). This seems remarkably late for such a conspicuous and attractive species and has led many botanists to the conclusion that it was simply not present in the wild before the eighteenth century by which time the vast majority of native British plant species were first recorded. Added weight to this argument comes from the lack of cultural references to *F. meleagris* in British art, literature, architecture, folklore and place names which would have undoubtedly occurred if it had been known from the Classical period onwards (Harvey, 1996).

The argument that its sheer abundance on many British sites strongly supports it being a native species has also been weakened by recent observations on meadows in England and Sweden where it is known to have been introduced. At Kungsängen meadow in Sweden, for example, numbers now equal those at North Meadow even though it is known to have colonised the meadow from a nearby botanic garden in 1747, which is coincidentally close to when it was first recorded in Britain. This suggests that all the British populations could have easily reached their present size within the last 300 years under a hay meadow management regime (Walker, 2021).

In other habitats in Britain, *Fritillaria meleagris* has been introduced for ornament or has escaped from ornamental habitats to colonise semi-natural habitats, possibly as seed or bulbs washed down rivers or in garden waste discarded on roadsides or in other habitats. A recent study of 593 populations across Britain and Ireland showed that 80% were associated with non-meadow habitats where it had been planted or naturalised, mainly in urban areas (21%), gardens and parkland (15%), churchyards and other religious buildings (14%), and along roadsides (7%; Walker, 2021). Some, if not all, of these roadside populations are likely to have originated from discarded garden waste.

Molecular study of *F. meleagris* populations across its geographical range by Day (2017) found considerable genetic similarity between British and Northern European populations of the species which seems to support the neophyte status of *F. meleagris* in the British Isles. On the other hand, natural colonisation of the British Isles is expected to be linked to north European populations of any species. Further genetic studies are required to get more conclusive evidence of the origin of British populations.

11 | CONSERVATION AND MANAGEMENT

Fritillaria meleagris is considered to be a rare and threatened species across its entire geographical range. In Britain, it is considered to be a Nationally Scarce species (Stewart et al., 1994) with a threat status of Vulnerable (Cheffings et al., 2005) before its national status was changed from native to alien. As a consequence, it no longer receives an official threat status (e.g. it is included on the 'Waiting List' by Stroh et al., 2014), although it remains a key flagship species for the

conservation and restoration of floodplain meadows in the British Isles (Walker, 2021).

Fritillaria meleagris is protected at the national level in several countries including Belgium (Van Landuyt et al., 2006), Hungary (Bódis et al., 2020), Romania (Oprea, 2005), Ukraine (Andrienko & Cherney, 2009) and Poland (Piórecki, 2005). In Russia, it is included in the national Red Data book of the Russian Federation (Varlygina, 2008) and 11 regional Red Data Books. In the Netherlands, *F. meleagris* showed one of the highest vulnerability indices among rare plants in the region (Kwak & Bekker, 2006).

In Britain, *Fritillaria meleagris* occurs in Lowland Meadows as listed on Annex 1 of the EU Habitat and Species Directive (92/43/EEC). These species-rich floodplain hay meadows experienced a severe decline since the 1940s as a result of agricultural intensification (draining, ploughing, reseeding) with estimates of losses ranging from between c. 50% and 98% (Ridding et al., 2015). The majority of surviving meadows supporting NVC MG4-type grassland (Rodwell, 1992) were designated as Sites of Special Scientific Interest (SSSI) or other protected areas (Jefferson & Pinches, 2011). As a consequence of these losses, the number of populations of *F. meleagris* declined dramatically and there are now only around 20 populations in floodplain meadows where they are presumed to be native (Walker, 2021). The management and conservation of these remaining floodplain meadows is conducted by a range of organisations including the Wildlife Trusts, Natural England, RSPB, private companies, community groups, individual landlords and farmers. Six percent of the existing populations of *Fritillaria meleagris* have been planted in grasslands as part of conservation and restoration schemes (Walker, 2021).

In Hungary, the species occurs in a wide range of habitats of high conservation status in Europe based on the Annex II of Council Directive 92/43/EEC (the 'Habitats Directive') of the European Commission. These include in order of frequency: Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (Alno-Pandion, Alnion incanae, Salicion albae; 91E0), Alluvial meadows of river valleys of the *Cnidion dubii* (6440), Lowland hay meadows (*Alopecurus pratensis*, *Sanguisorba officinalis*) (6510), Alkaline fens (7230), Riparian mixed forests of *Quercus robur*, *Ulmus laevis* and minor, *Fraxinus excelsior* or *angustifolia* along the great rivers (91F0), Hydrophilous tall herb fringe communities of plains and montane to alpine levels (6430) and *Molinia* meadows on calcareous, peaty or clayey-silt-laden soils (*Molinia caerulea*) (6440) (Bódis et al., 2020).

The majority of the presumed native populations of *Fritillaria meleagris* in Britain occur in protected conservation areas, mainly designated Sites of Special Scientific Interest (SSSI), but also National Nature Reserves (NNRs) and local nature reserves (Walker, 2021). In European Russia, *F. meleagris* habitats are protected in the Central Chernozem Zapovednik (Kursk Oblast), in Prioksko-Terrasnyi Zapovednik (Moscow Oblast) and National Park 'Orlovskoe Polesiye' (Orel Oblast). In Altai, one location of the species is protected as the Nature Monument 'Steppe near the village Sibiryachiha' (Silantieva et al., 2011). Wet meadows with *F. meleagris* are listed in the Green Book of Siberia as protected plant communities (Ershova, 1996).

In Britain, *Fritillaria meleagris* occurs in floodplain meadows traditionally managed for hay and aftermath grazing. In continental Europe, it grows in hay meadows which are managed with a single summer cut. Since the species completes its above-ground growth by the beginning of June the hay cut, which normally happens in late June or July, has no negative effect on populations and, on the contrary, benefits the species in dispersing seed and removing litter and standing biomass, thereby creating microsites for germination and reducing the abundance of potential competitors.

Thick litter deposit which builds up in the absence of a hay cut negatively affects seed germination and seedling establishment. In one of two locations of *F. meleagris* in Orel Oblast, Russia conservation measures include three hay cuts during summer months to prevent litter from building up. As a result, the fritillary population density reaches up to 87 plants per sq. m (Lepeshkina & Voronin, 2015). Mowing is the most recommended management regime for the species' conservation (Varlygina, 2008).

Woodland populations of *F. meleagris* in continental Europe occur in the openings and gaps where management for conservation of the species includes clearing shrub undergrowth. Woodland populations would also benefit from coppicing which improves light availability for the ground flora.

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CONFLICT OF INTEREST

None of the authors have a conflict of interest.

AUTHORS' CONTRIBUTIONS

I.T. wrote the manuscript; K.W. compiled the information on the species' range, conservation and plant communities in the British Isles; M.D. wrote the Section about species pollination.

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The study does not include data.

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