BIOLOGICAL FLORA

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

Biological Flora of Britain and Ireland: *Geranium pratense*

No. 305

Richard G. Jefferson[1] | Markus Wagner[2] | Elizabeth Sullivan[3] | Irina Tatarenko[4] | Duncan B. Westbury[5,6] | Paul Ashton[7] | Lucy Hulmes[2]

[1]Bell Cottage, Cumbria, UK; [2]UK Centre for Ecology & Hydrology, Wallingford, UK; [3]The National Trust, Estate Office, Settle, UK; [4]School of Environment, Earth & Ecosystem Sciences, Faculty of Science, Technology, Engineering & Mathematics, The Open University, Milton Keynes, UK; [5]School of Science & the Environment, University of Worcester, Worcester, UK; [6]Land & Property Management, Royal Agricultural University, Cirencester, UK and [7]Department of Biology, Edge Hill University, Ormskirk, UK

Correspondence
Richard G. Jefferson
Email: rjeffegj@sky.com

Abstract

1. This account presents information on all aspects of the biology of *Geranium pratense* L. (Meadow Crane's-Bill). 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. *Geranium pratense* is a perennial gynodioecious forb of neutral grassland. In Britain and Ireland, it is particularly abundant on roadside verges, railway embankments, the margins of watercourses and woodland rides. It is generally intolerant of grazing and is absent or scarce in livestock-grazed grassland. *Geranium pratense* is widespread in England, Wales and Scotland but is scarce in Ireland. It has an extensive native range in Europe and Asia, extending eastwards to Russia, north-western China and Mongolia. It has been widely introduced to new sites within its native range and has been introduced to Canada, the USA and New Zealand.

3. *Geranium pratense* usually occurs on free-draining soils but also infrequently where drainage is impeded. The soils are often nutrient-rich and weakly acidic to weakly alkaline. The underlying geology is usually non-acidic sedimentary rocks or superficial deposits.

4. *Geranium pratense* is protandrous and is pollinated by various insects of the orders Hymenoptera, Diptera and Lepidoptera, particularly bumblebees, solitary bees, hoverflies and butterflies. Eleven species of phytophagous insect have been recorded on *G. pratense* in Britain and Ireland.

5. *Geranium pratense* has little or no capacity for vegetative spread. Primary seed dispersal is ballistic and seeds may be flung over distances of up to several metres. The species has a transient seed bank, that is germination typically takes place in

Nomenclature of vascular plants follows Stace (2019) and, for non-British species, *Flora Europaea*.

the winter and spring after seed production, after the physically dormant seeds have become permeable. Seedling establishment is higher in vegetation-free gaps than in undisturbed grassland vegetation.

6. There has been no significant change in its distribution between the late 1950s and 2019, although since 2000, it has expanded its range, mainly via introductions, in northern and western Scotland, west Wales and in Ireland. Alien sites have increased markedly since the 1960s due to introductions from wildflower seed sowing and spread from gardens.

Meadow Cranesbill. Geraniaceae. *Geranium pratense* L. is a leafy, branched, perennial, gynodioecious herb with a compact, stout, oblique rhizome. Stem (10)30–80(130) cm, pale green, erect or ascending, with short, deflexed eglandular hairs below, dense glandular and eglandular hairs above. Leaves alternate. Lamina (3)7–9 (20) cm long, (6)8–18(22) cm wide, slowly decreasing in size upwards; medium green above, paler beneath, circular, polygonal or reniform in outline, palmately divided more than five-sixths of the way to the base into 5–9 (typically 7) lobes; lobes ovate-rhombic in outline, acute at apex and pinnately lobulate, the lobules with ±oblong, acute or apiculate teeth, appressed hairy on both surfaces. Petioles 6–21(55) cm, hairy. Stipules 4–24(30) mm, narrow and tapered to a fine point. Flowers in pairs on axillary peduncles; peduncles 2–10 cm; pedicels short, one or both shorter than the sepals, reflexed after flowering but becoming erect in fruit. Female flowers smaller than hermaphrodite flowers (on average three-quarters the diameter). Some flowers of intermediate form with 1–9 functional stamens, along with non-functional stamens at various stages of regression. Flowers actinomorphic, protandrous, (28)35–45(50) mm in diameter with female flowers typically smaller than hermaphrodite flowers, bisexual, saucer-shaped. Sepals 5, 7–12 mm, ovate, mucronate (mucro 1.5–3.5 mm), glandular hairy, forming a slightly inflated calyx after flowering. Petals 5, 14–25×8–24 mm, deep violet-blue or white, usually white at extreme base, with translucent, sometimes pinkish veins; base with a dense tuft of hairs on either side; obovate, rounded at apex, claw very short. Stamens 10, 7.5–9 mm, in two whorls; outer whorl, opposite the petals, dehisces first. Swollen glands at the base of each of the inner whorls of stamens comprise the nectary. Filaments abruptly widened at base, more or less deep pink, fringed with hairs below. Anthers dark violet or bluish-black. Ovary superior of five carpels each with two ovules united to a central column. Style 1, >4 mm, stigmas 2.0–2.5 mm, greenish, tinged with pink or dull brownish, purple or crimson. Fruit a dry five-celled schizocarp; immature schizocarps reflexed on reflexed pedicels; mericarps (4)4.5–8(12) mm long×3–4.3 mm wide, rounded at base, smooth, glandular-hairy; beak (20)23–29(35) mm, including distinct stylar portion of 7–8 mm. Seeds oval, dark brown, minutely reticulate and 3–3.5 mm long×2 mm wide.

Geranium L. is currently estimated to have 436 species worldwide (The World Flora Online, 2022), largely confined to temperate climates (including tropical mountains) as natives, but with a plethora of species, hybrids and cultivars grown for ornament around the world (Cullen et al., 2011; Yeo, 2001). Edwards et al. (2023), for example, list 55 cultivars of *G. pratense* for sale. Section Geranium, by far the largest within the genus, includes the morphologically and genetically similar *G. pratense*, *G. rotundifolium*, *G. collinum*, *G. sylvaticum* and *G. columbinum* (Esfandani-Bozchaloyi et al., 2018). Genetically, *G. sylvaticum* and *G. pratense* appeared to be very close (0.93 Nei's genetic identity) due to shared common alleles (Shi et al., 2021). Several subspecies and varieties of *G. pratense* have been described from the mountainous parts of the species' range. The Himalayan form has been described as subsp. *stewartianum* Y. Nasir, a Turkish form as subsp. *finitimum* (Woronow) Knuth and a Caucasian form as subsp. *ruprechtii* Woronow. In Siberia var. *longebracteatum* Serg., var. *alpestre* Krylov, f. *rigidulum* Serg., var. *typicum* Krylov, f. *mollis* Serg., var. *dissectum* Serg. have been described (Sergievskaya, 1935). Based on morphological characters, the two latter varieties have since been circumscribed as a separate species, *G. sergievskajae* (Peschkova) Troshkina (Troshkina, 2016).

Genetic variation in *G. pratense* was studied in road-verge and riverside populations in Northern England, UK (Adenegha, 2022). Samples for measuring genetic diversity were collected at the large scale across six regions in England: Tyneside, Cumbria, Durham, Yorkshire, Lancashire and Cheshire; and at the medium scale in three river valleys: the River Ribble, the River Wharfe and the River Hodder (the lower reaches of a tributary to the Ribble). Small-scale sampling focussed on 21 populations along the River Ribble. Genetic variation was measured in 1087 samples using polymorphic microsatellites with 10 different markers. Measurements of heterozygosity suggested inbreeding in populations along the River Ribble and in NE England. Cumbrian and northeast English populations had unique genotypes not found in populations from Lancashire. Allelic richness was also, on average, greater in the two most northerly locations. Cumbria had the highest number of specific alleles.

Proportion of the total genetic variance contained in a subpopulation relative to the total genetic variance (F_{ST}) can range from 0 to

1. The overall pairwise F_{ST} score for populations of *G. pratense* between all regions was low (0.04; $p < 0.001$), characterising high gene flow and low population differentiation at the big scale. Similar observations apply at the medium spatial scale. Pairwise F_{ST} scores between the River Ribble and River Hodder were low (0.02, $p < 0.001$), and even lower between the River Ribble and the River Wharfe (0.01, $p < 0.001$). When examining genetic variation at the local spatial scale along the River Ribble, allelic richness was higher upstream than downstream. By contrast, allelic richness is high and remains at equilibrium in roadside populations, perhaps because of bidirectional pollinator movement within ecological corridors such as roads (Adenegha, 2022). In Iran, the percentage of polymorphism between populations of *G. pratense* is relatively high at 11.83% (Esfandani-Bozchaloyi et al., 2018).

Geranium pratense is native to Britain and Ireland, being largely confined to the lowlands where it is characteristic of dry or moist neutral grasslands.

1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

Geranium pratense is found in England, Wales and Scotland but is uncommon in Ireland and, in the latter, is only considered native in County Antrim (Preston et al., 2002; Stroh, Walker, et al., 2023; Section 10, Figure 1). In England, native populations are largely absent from the south-west and East Anglia. The absence of native populations in the south-west and south-east of England but presence in central southern areas is anomalous. There is no obvious explanation for this distribution based on environmental factors (soil, geology or climate) except perhaps for Cornwall and parts of Devon where acid soils may be unsuitable for the species. It is unlikely to be a recorder effect as it is a conspicuous plant, except in winter, when few botanical surveys take place. Although it is more usual for a combination of factors to impact plant distribution, in this case, it may be that past anthropogenic factors such as habitat loss or degradation are the reason for the absence of *G. pratense* from some of these English regions. In Wales, it occurs largely in the east as a native species but has been widely introduced in the west. In Scotland, naturally occurring populations of *G. pratense* are confined to areas south of a line between Elgin and the northern tip of Jura and it is entirely absent as a native from the Scottish islands. In Ireland, the native plant is confined to a stretch of the coast between Dunluce Castle in the west and approaching Ballycastle in the east and on Rathlin Island (Beesley, 2006; Hackney, 1992). In the remainder of Ireland, non-native populations are widely and sparsely scattered, apart from concentrations around the coasts in the counties of Antrim, Derry, Donegal and Wexford and in both coastal and inland localities in County Sligo.
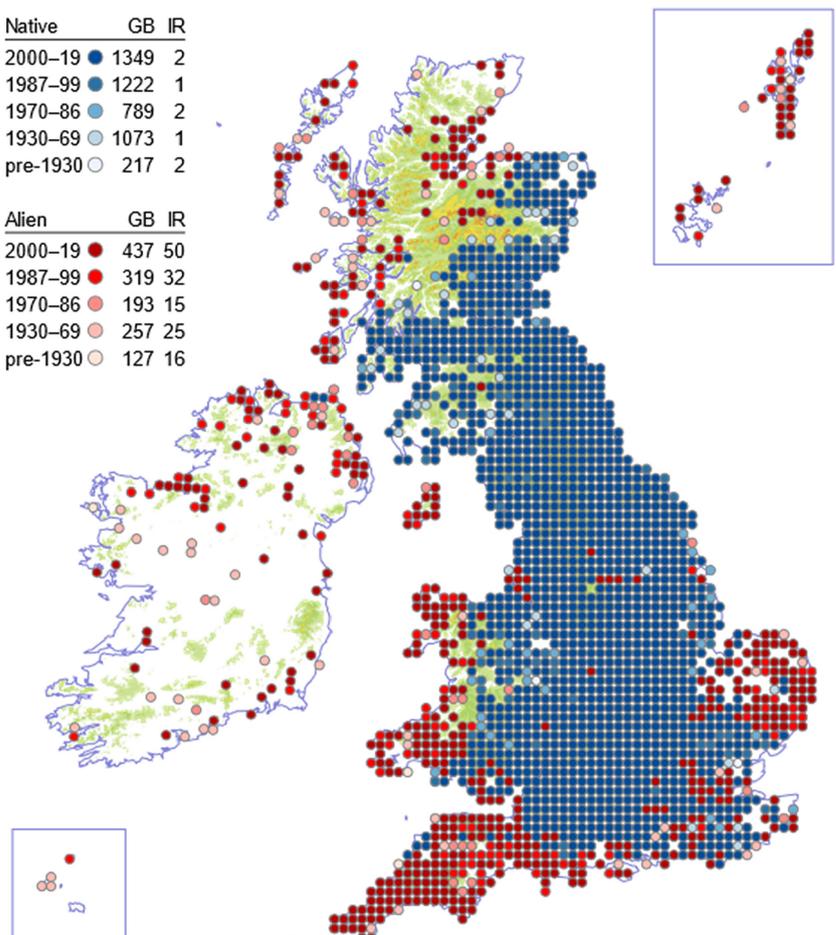
FIGURE 1 The distribution of *Geranium pratense* in the British Isles. Each dot represents at least one record in a 10 km square of the National Grid. Colour distinguishes native versus alien status, and shade indicates the date range of the most recent record. Figures for Great Britain (GB) and Ireland (IR) indicate total numbers of squares in each category. Source: Stroh, Humphrey, et al. (2023).

In Britain and Ireland, both outside and within its native range described above, *G. pratense* has become established through introduction in seed mixtures and from escape via self-seeding from gardens (Crawley, 2005; Preston et al., 2002; Stroh, Walker, et al., 2023).

In the period 2000–2019, natural populations of *G. pratense* were recorded from 1351 10 km squares in Britain and Ireland (35% of the total number of 10 km squares) and a further 487 10 km squares as an alien totalling 1838 10 km squares overall (48% of the total). In Ireland, for the period 2000–2019, there are two 10 km square native records (Northern Ireland) and 50 10 km squares where it is recorded as alien (Stroh, Walker, et al., 2023).

The species is largely confined to the lowlands in Britain and Ireland. It reaches 375 m at Alston (Cumbria), and exceptionally 845 m on Great Dun Fell (Cumbria) (Preston et al., 2002; Stroh, Walker, et al., 2023). In other parts of its European range, it reaches subalpine zones with altitudinal limit ranging from 800 m in Norway, in Bavaria (Germany) to 1100 m, in the Alps in South Tyrol (Italy) and Carinthia (Austria) to 1600 m, in Styria (Austria) to 1900 m, in the Tatra mountains (Poland) to 1125 m, in Transylvania (Romania) to 1300 m and in Russia to 2100 m (Gams, 1924; Krasnoborov in Sugorkina, 1995). In the western Himalayas of Pakistan, *G. pratense* is one of the dominant species of alpine vegetation occurring between 3500 and 4200 m (Awan et al., 2021). In Xinjiang Province, China, *G. pratense* grows in grassland and alpine habitats between 1400 and 4000 m (Abdusalam et al., 2021). *Geranium pratense* has an extensive range in Europe and Asia. It is found throughout most of Europe but is rare in the Mediterranean region and in the far north (Figure 2). It extends eastwards to Russia, north-western China and Mongolia. In continental Europe, it has extensively naturalised, often from gardens, both within and outside its native range (Gams, 1924; Wahlstrøm, 1978). *Geranium pratense* has been introduced to Canada, Greenland, New Zealand and the United States where it has been reported to form self-sustaining populations in the wild (van Kleunen et al., 2019).

2 | HABITAT

2.1 | Climatic and topographical limitations

Of the 13 European climate zones identified by Metzger et al. (2005), *G. pratense* is absent or largely absent from the Mediterranean North, Mediterranean South, Anatolian and Alpine North zones, with its core range within the Continental, Atlantic Central, Boreal and Nemoral zones.

Average mean January temperature, average mean July temperature and average mean annual rainfall for British hectads (10 km × 10 km squares) with recorded *G. pratense* populations are 3.0°C, 14.9°C and 922 mm, respectively (Hill et al., 2004). *Geranium pratense* does not encounter any climatic limits in Britain and Ireland as it is known from the boreal zone to the north and occurs as far south as northern Spain. Its absence from northern Scotland (Figure 1) thus does not appear to be mediated by climate.

Table 1 shows climate parameter values from the world distributional range of *G. pratense* (Vangansbeke et al., 2021). These indicate
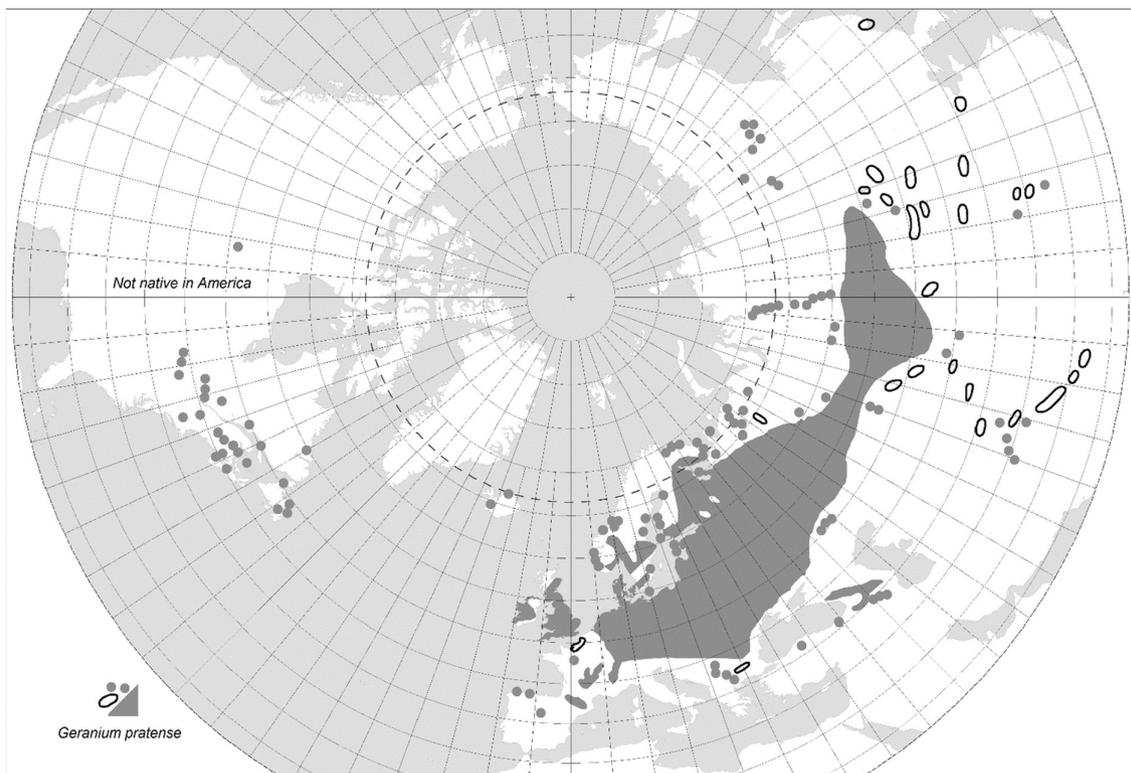

FIGURE 2 Global distribution of *Geranium pratense*. Reproduced, with modifications, from Hultén and Fries (1986), by permission of Koeltz Scientific Books, Koenigstein, Germany.

TABLE 1 Average mean temperature parameters and average mean annual precipitation for the distributional range of *G. pratense* (after Vangansbeke et al., 2021).

Climate parameter	Median (mean)	5th percentile	95th percentile
Mean annual temperature (°C)	5.3 (5.0)	−0.4	9.4
Minimum annual temperature (°C)	1.1 (0.8)	−4.6	5.4
Maximum annual temperature (°C)	9.1 (8.9)	3.8	13.4
Annual precipitation (mm)	610 (652)	506	1025

that UK populations tend to grow towards the warmer and wetter end of its range of climatic conditions.

Geranium pratense belongs to the Eurasian Boreo-temperate floristic element (Preston & Hill, 1997) and as such is widespread in both the boreal and temperate zones.

2.2 | Substratum

The underlying geology of extant populations of *G. pratense* usually includes non-acidic superficial deposits resulting from glacial, aeolian, riverine or other mass movement processes and sedimentary rocks such as limestones, shales and clays.

The major soil groups on which *G. pratense* occurs in Britain and Ireland (using the soil classification of Avery (1990) with soil groups in parentheses), are brown soils (brown calcareous earths, brown calcareous alluvial soils, brown earths, brown alluvial soils, argillic brown earths, paleo-argillic brown earths), lithomorphic soils (rendzinas), ground-water gley soils (alluvial gley soils, orthic gley soils), ground-water gley soils (alluvial gley soils, humic –alluvial gley soils, humic gley soils), surface-water gley soils (stagnohumic gley soils) and man-made soils (Crawley, 2005; Rodwell, 1992). In populations on road verges and riverbanks, soils may have been modified by engineering operations and the importation of materials whereas meadow populations may be subject to agricultural practices including the periodic application of organic fertilisers and lime.

On the active river plain of the Northern Dvina (Arkhangelsk, Russia), on the islands in the river delta, soils experience strong accumulative and erosion impacts. There, *G. pratense* occurs on poor, sandy alluvial soils with a high ground water table (Parinova et al., 2013) as well as on alluvial sandy-clay-loam soils in microelevated areas (Parinova et al., 2018).

The species is accorded an Ellenberg value of 6 for moisture by Hill et al. (2004) and thus is most abundant on moderately damp soils of intermediate moisture but absent from very dry or permanently wet soils. On the Ramensky scale (Ramensky et al., 1956), the species has an index value of 64–74 (Sugorkina, 1995), which equates to a value of 5 on the original Central European Ellenberg scale (Ellenberg et al., 1991). This value was re-calibrated to 6 for Great Britain by Hill et al. (2004). Tyler et al. (2020) categorise *G. pratense* as occurring on substrates that are mesic–moist. Chytrý et al. (2021) give a moisture indicator value of 5—indicative of fresh soils, focus on soils of average moisture, absent from wet soils and from those that frequently dry out. In a recent analysis of Ellenberg-type

indicator values from 13 European data sets (Tichý et al., 2023), the harmonised indicator value for *G. pratense* for moisture was 5.6.

In soil samples from 13 *G. pratense* populations from sites in northern England taken from late July through to the end of August 2020, percentage soil organic content determined using the loss-on-ignition method ranged from 2.8% to 37% with a mean of 16.7%. Three trowel samples of upper-level soil were collected at random locations at each site and samples were subsequently amassed into one single sample per site for analysis (Paul Ashton, unpublished data).

Hundt (1983) gives values of 5.5% and 5.9% for organic matter content for soils of the Agropyro-Alopecuretum *Geranium pratense* variant and Arrhenatheretum elatioris plant communities, respectively, in Germany. Both plant communities typically contain *G. pratense*.

Geranium pratense is a mesophyte with an Ellenberg value for reaction of 7 occurring on soils that range from weakly acid to weakly alkaline (Hill et al., 2004). The harmonised European Ellenberg-type indicator value from Tichý et al. (2023) is very similar at 6.8.

In a sample of 13 *G. pratense* populations from sites in northern England from 2020, soil pH ranged from 6.3 to 7.0 with a mean of 6.7 (Paul Ashton, unpublished data). For the Central European flora, *G. pratense* has been assigned an Ellenberg value for reaction of 8 (Ellenberg et al., 1991). In a recent compilation of indicator and trait values for Swedish vascular plants, Tyler et al. (2020) categorise *G. pratense* as occurring on soils that are subneutral to circumneutral with pH ranging from 5.5 to 7.5. Similarly, a Czech database of plant traits (Chytrý et al., 2021) give a reaction indicator value of 7 for *G. pratense*, indicative of slightly acidic to slightly basic conditions, never occurring in very acidic conditions.

Hundt (1983) gives pH values of 5.5 and 5.3, respectively, for soils of the Agropyro-Alopecuretum *Geranium pratense* variant and Arrhenatheretum elatioris plant communities in Germany.

Hill et al. (2004) assign *G. pratense* an Ellenberg nitrogen value of 7, characterising it as a plant species often found in richly fertile places. It is important to note, however, that while Hill et al. (2004) refer to Ellenberg N values as nitrogen values, such values are now considered indicators of site productivity, rather than of soil nitrogen content or nitrogen availability (Hill & Carey, 1997; Wagner et al., 2007). For the Central European flora, *G. pratense* has also been assigned an Ellenberg nitrogen value of 7 (Ellenberg et al., 1991). The harmonised European Ellenberg-type indicator value from Tichý et al. (2023) is very similar at 6.7. Indicator values for *G. pratense* for soil nitrogen and phosphorus in Tyler

et al. (2020), equate to 'moderately rich' for nitrogen and 'high availability' for phosphorus. The Pladias database for the Czech flora and vegetation (Chytrý et al., 2021) give a nutrient indicator value of 7, occurring at nutrient-rich sites more often than at average sites and only exceptionally at poor sites.

Data on the nutrient content of soils where *G. pratense* is a component of the vegetation are sparse. Hundt (1983) gives values of 10 mg/100 g P_2O_5 and 23 mg/100 g K_2O and 4 mg/100 g P_2O_5 and 25 mg/100 g K_2O for soils of the Agropyro-Alopecuretum *Geranium pratense* variant and Arrhenatheretum elatioris plant communities, respectively, in Germany.

Critchley et al. (2002) sampled the topsoils from a range of lowland grassland types in Environmentally Sensitive Areas (ESAs) in England, UK. They were analysed for pH, extractable phosphorus (P), potassium (K) and magnesium (Mg), total nitrogen (N), organic matter (OM), and estimated available water capacity. The MG1 *Arrhenatherum elatius* National Vegetation Classification (NVC) grassland community, the type in which *G. pratense* is most frequently encountered (Section 3), was sampled at 23 sites. Means and standard deviations for soil properties for MG1 grassland were 11.07 (7.05) (Olsen extractable P mgl^{-1}), 133 (51.9) (extractable K mgl^{-1}), 101 (42.7) (extractable Mg mgl^{-1}) & 0.84 (0.284) (total N). The extractable P levels are low to moderate by agricultural standards but exceed those of more species-rich, less modified neutral and calcareous grassland types sampled in the study. However, caution should be exercised due the small sample size, the uncertainty as to whether any of the samples were from MG1 supporting G.

pratense, and any bias in sampling towards more species-rich subcommunities of MG1.

According to Hill et al. (2004) and Tyler et al. (2020), *G. pratense* is salt intolerant and is absent from saline sites. However, Chytrý et al. (2021) state that *G. pratense* has some salt tolerance, occurring mostly on low-salt to salt-free soils, but occasionally on slightly salty soils, such as in inland saline meadows.

3 | COMMUNITIES

In Britain and Ireland, *G. pratense* is a perennial herb of rough grassland on road verges, railway embankments, woodland rides and stream sides, ditch margins and in damp hay meadows and lightly grazed pastures. It also occurs in shady places such as willow carr, damp thickets, open scrub and osier holts (Crawley, 2005; Davis, 1973; Preston et al., 2002). *Geranium pratense* is a photophilous plant and tolerates little shade (Sugorkina, 1995; Tyler et al., 2020). However, indicator values for light derived from Hill et al. (2004) and Chytrý et al. (2021) imply a plant generally of well-lit places, but also occurring in partial shade up to about 30% of diffuse radiation incident in an open area.

Geranium pratense is largely confined to neutral or mesotrophic grasslands (Table 2). It is frequent in grasslands dominated by *Arrhenatherum elatius*, especially those conforming to the NVC type MG1 *Arrhenatherum elatius* grassland (Rodwell, 1992; Paul Ashton, unpublished data). Rodwell (1992) describes a variant of the *Festuca rubra* subcommunity of MG1 known as the *Geranium pratense*

TABLE 2 Plant communities in which *Geranium pratense* has been recorded in Britain and Ireland and their relationship to European vegetation classifications. Annex 1 habitats of Directive 92/43/EEC are based on a hierarchical classification of European habitats developed by the CORINE (coordination of information on the environment) biotopes project. Phytosociological alliance denotes the basic phytosociological unit of the European Vegetation Checklist that serves as the lowest rank in broad-scale vegetation surveys. The EUNIS (European University Information System) is a hierarchical pan-European habitat classification system.

British plant community (National Vegetation Classification) types	Annex 1 habitats & species directive	Phytosociological alliance	EUNIS
Neutral or mesotrophic grasslands			
MG1 *Arrhenatherum elatius* grassland	—	Arrhenatherion elatioris	E2.2 low and medium altitude hay meadows
MG2 *Arrhenatherum elatius–Filipendula ulmaria* tall-herb grassland	—	Arrhenatherion elatioris	E5.4 Moist or wet tall-herb and fern fringes of the lowlands
MG3 *Anthoxanthum odoratum-Geranium sylvaticum* grassland	6520 Mountain hay meadows	Triseto-Polygonion bistortae	E2.3 Mountain hay meadow
MG5 *Cynosurus cristatus-Centaurea nigra* grassland	—	Cynosurion cristati	E2.1a Mesic permanent pastures of lowlands and mountains
MG6 *Lolium perenne- Cynosurus cristatus* grassland	—	Cynosurion cristati	E2.1a Mesic permanent pastures of lowlands and mountains
MG8 *Cynosurus cristatus-Caltha palustris* grassland	—	Calthion	E3.4a moist or wet mesotrophic to eutrophic hay meadow
Open vegetation			
OV27 *Epilobium angustifolium* community	—	Carici piluliferae- Epilobion angustifolii	E5.1 Anthropogenic herb stands

variant, often with *Lathyrus pratensis*, *Centaurea nigra*, *Vicia sepium* and *Cruciata laevipes*.

MG1 with populations of *G. pratense* occurs abundantly on roadside verges (Figure 3) and railway embankments but also more locally along the less intensively managed margins of lowland meadows, along the sides of streams, canals and in woodland rides and glades. In upland regions of the north Pennines, Cumbria and Lancashire, it may occur on ungrazed road verges that conform to the *Arrhenatherum elatius* subcommunity of MG3 *Anthoxanthum odoratum—Geranium sylvaticum* grassland of which *G. pratense* is a preferential (Rodwell, 1992; Rodwell et al., 2000; Elizabeth Sullivan, unpublished data).

Peterken (2008) described *Geranium pratense* as being abundant on roadside verges in the Cotswolds, but infrequent in the verges of the lower Wye Valley, both in Gloucestershire, UK. For Cambridgeshire, Leslie (2019) pointed out that while the species is now found most frequently on the verges of paths, tracks and roads, in older floras, it had been described as a plant typically of moist pastures and meadows. For Cornwall, French (2020) suggested that the seeding of road verges may play a role regarding its frequent occurrence in such habitats, but nitrogen deposition in combination with a comparatively high tolerance of the species to such deposition may also play a role regarding its frequent occurrence along suitable road verges (see Section 4, below).

In the Derbyshire Dales, *G. pratense* occurs in ungrazed or episodically grazed tall-herb communities conforming to MG1 *Arrhenatherum elatius* grassland, *Centaurea nigra* subcommunity and MG2 *Filipendula ulmaria-Arrhenatherum elatius* tall-herb grassland, *Filipendula ulmaria* subcommunity (Heather Robertson & Richard Jefferson, unpublished data).

It also occasionally occurs in four types of neutral grassland managed as hay meadows, usually at low frequency: MG3 *Anthoxanthum odoratum—Geranium sylvaticum* grassland; MG5 *Cynosurus cristatus—Centaurea nigra* grassland; MG8 *Cynosurus cristatus—Caltha palustris* grassland and more species-rich stands of MG6 *Lolium perenne—Cynosurus cristatus* grassland, *Anthoxanthum odoratum* sub-community (Wallace & Prosser, 2017; John O'Reilly, unpublished data; Stuart Smith, unpublished data).

Its rarity in neutral grasslands other than MG1 is illustrated by the fact that the Lowland Grassland Survey of Wales did not record *G. pratense* in any of the over 10,000 quadrats sampled (Stevens et al., 2010). According to Sugorkina (1995), *G. pratense* is grazing intolerant and this may explain its general absence from grasslands which are grazed for all or part of the year (see Section 4). In many counties across its native British and Irish range, road verges are an important stronghold for populations of *G. pratense* (see for example Killick et al., 1998).

Tyler et al. (2020) consider the species as being able to endure regular grazing/mowing while having a preference for unmanaged habitats. On Clifton Ings (York, UK), the species forms tall and dense stands along a narrow strip of woodland, where it is fenced off from the mown and grazed floodplain meadows (Irina Tatarenko, personal observation).

Geranium pratense may occasionally occur in more disturbed, species-poor plant communities such as the OV27 *Epilobium angustifolium* (*Chamaenerion angustifolium*) community (Paul Ashton, unpublished data; Rodwell, 2000). Salisbury (1952) mentions that *G. pratense* can occur rarely as a late fixed dune species where the soils are calcareous. In Northern Ireland, it has been recorded from this habitat (Hackney, 1992).

Typical associates (all habitats) include *Alopecurus pratensis*, *Arrhenatherum elatius*, *Bromus hordeaceus*, *Centaurea nigra*, *Cerastium fontanum*, *Chamaenerion angustifolium*, *Dactylis glomerata*, *Epilobium hirsutum*, *Festuca rubra*, *Filipendula ulmaria*, *Heracleum sphondylium*, *Holcus lanatus*, *Lathyrus pratensis*, *Leucanthemum vulgare*, *Lolium perenne*, *Plantago lanceolata*, *Poa pratensis s.l.*, *Poa trivialis*, *Ranunculus*

FIGURE 3 Typical roadside verge habitat conforming to MG1 *Arrhenatherum elatius* grassland. Near Swayfield, Lincolnshire, UK.

acris, *Ranunculus repens*, *Rhinanthus minor*, *Rumex acetosa*, *Trifolium pratense*, *Veronica chamaedrys*, *Vicia cracca* and *Vicia sepium* (Rodwell, 1992; Sinker et al., 1991; John O'Reilly, unpublished data; Richard Jefferson, unpublished data; Elizabeth Sullivan, unpublished data).

In continental Europe, *Geranium pratense* occurs in a range of mesic lowland hay meadows and pastures in western and central Europe. In an analysis and classification of vegetation plots of mesic grasslands from across Europe (Rodríguez-Rojo et al., 2017), *G. pratense* was considered a diagnostic species for the Pastinaco sativae—Arrhenatheretum elatioris Passarge 1964 (Central European mesic and mesotrophic hay meadows) and the Potentillo albae—Festucetum rubrae Blažková 1979 (hay meadows on river terraces with seasonally wet soils from western and central Bohemia). It has also been associated with a number of other mesic grassland types, especially the Ranunculo repentis—Alopecuretum Ellmauer 1993 (Central European meadows on light wet and fertilised loamy-clayey soils on valley floors and river sides) and the Tanaceto vulgaris—Arrhenatheretum elatioris Fischer ex Ellmauer 1993 (Western and Central European meadows in sunny artificial habitats, in settlement areas and at industrial sites, rich in ruderal species).

Geranium pratense occurs in lowland to submontane False Oat-grass meadows of the Arrhenatherion in Central Europe (Ellenberg, 1988). Typical associated species include *Trisetum flavescens*, *Galium mollugo*, *Heracleum sphondylium*, *Leucanthemum vulgare*, *Crepis biennis*, *Campanula patula*, *Dactylis glomerata*, *Tragopogon pratensis*, *Veronica chamaedrys*, *Knautia arvensis* and *Avenula pubescens* (Dierschke, 1999; Ellenberg, 1988). Hundt (1983) states that in eastern Germany, it occurs as a character species in the Arrhenatheretum elatioris and the *Geranium pratense* variant of the Agropyro-Alopecuretum.

The species may also occur in suboceanic meadows of the Deschampsion cespitosae alliance in Central Europe (Botta-Dukát et al., 2005). These meadows occur on low terraces of river floodplains and in depressions that may periodically flood for short periods but generally seldom dry out even in the summer. These meadows are dominated by *Alopecurus pratensis*, and less frequently by *Holcus lanatus*, *Poa pratensis*, *Festuca pratensis*, *Sanguisorba officinalis* and *Cirsium canum*. A few species more typical of wetter meadows of the Calthion and Molinion may occur as associates at moderate frequency, such as *Cardamine pratensis*, *Silene flos-cuculi* and *Filipendula ulmaria* (Botta-Dukát et al., 2005).

In a study of temperate European roadside vegetation (Ullman & Heindl, 1989), *G. pratense* was found to be a characteristic dominant of the widespread *Heracleum sphondylium—Anthriscus sylvestris* Arrhenatherion/Agropyretalia plant community.

The Czech flora and vegetation database (Chytrý et al., 2021) lists *G. pratense* as occurring frequently in the following broad vegetation types: (i) wetland and riverine herbaceous vegetation—nitrophilous herbaceous fringes of lowland rivers, (ii) meadows and mesic pastures (Class: Molinio-Arrhenatheretea Tüxen 1937)—mesic *Arrhenatherum* meadows and alluvial meadows of lowland rivers

and (iii) anthropogenic vegetation (Class: Galio-Urticetea Passarge ex Kopecky 1969)—perennial nitrophilous herbaceous vegetation of mesic sites.

For Central Europe, it has been suggested by Görs and Müller (1969) that the natural occurrence of *G. pratense* is in fringe vegetation dominated by tall herbs at the edge of forests, rivers and streams (i.e. in the so-called 'saum' communities). Müller (1974) specifically mentions natural Artemisietea fringe vegetation communities as a primary habitat of the species, from which it may have subsequently spread into anthropogenic habitats such as analogue nitrophilic saum communities and semi-natural Molinio-Arrhenatheretea grassland communities.

Accordingly, in south-west Poland, *G. pratense* has been recorded in similarly nitrophilic fringe vegetation of the Geranio phaei-Urticetum dioicae association found along river or stream banks on alluvial soils or in forest glades or margins (Świerkosz et al., 2002).

In the north of European Russia, *G. pratense* grows in floodplain meadows of the river Northern Dvina in association with *Alopecurus pratensis*, *Lathyrus pratensis*, *Anthriscus sylvestris*, *Festuca pratensis*, *Elytrigia repens*, *Agrostis capillaris* and *Veronica chamaedrys* (Parinova et al., 2013).

Geranium pratense may also occur in environments with a lower light flux and it occurs as a forest understorey species in herb-rich mixed coniferous forest in Estonia (Moora et al., 2007) where *Picea abies* is the predominant tree species together with *Fraxinus excelsior* and *Acer platanoides* growing in old stands and *Betula pendula* and *Tilia cordata* in young stands. *Corylus avellana* predominates in the shrub layer of old stands. Given the indicator values for light cited above, this suggests that its occurrence in forests must be limited to higher light flux environments in habitats such as glades.

In Asia, *G. pratense* often grows in floodplain meadows, dry grasslands and steppe vegetation. At low altitudes in the Altai-Sayan mountains, it occurs as a diagnostic species of the Filipendulo vulgaris–Dactyletum glomeratae ass. carumetosum carvi subass. prov. together with *Pulmonaria mollis* and *Rubus saxatilis* (Makunina & Maltseva, 2008). It is also a diagnostic species of Molinio-Arrhenatheretea in forest meadows in Western Siberia (Korolyuk et al., 2016). Troshkina (2018) also describes its occurrence in vegetation rich in ruderal species in the Altai Mountains.

Although speculative, it is conceivable that nitrophilic fringe vegetation as described above may also have originally been the main habitat for *G. pratense* in Britain and Ireland. Such vegetation may have resembled the MG2 *Arrhenatherum elatius—Filipendula ulmaria* tall-herb grassland that is now largely confined to limestones of the Derbyshire and Yorkshire Dales, UK (Rodwell, 1992; see also Table 2).

With the presumed near total loss of near-natural fringe vegetation in the landscape, *G. pratense* has subsequently been able to exploit similar anthropogenic habitats such as, for example, road verges.

Pierce et al. (2017) classified its ecological strategy as competitive/competitive–stress tolerant–ruderal (C/CSR), which is consistent with its occurrence in productive tall herb and grassland communities, but also sometimes in vegetation rich in ruderal species.

4 | RESPONSE TO BIOTIC FACTORS

Geranium pratense populations growing in Central European Arrhenatheretum hay meadows were found to be reasonably tolerant of fertiliser application (Kornaś & Dubiel, 1991a, 1991b).

In some cases, fertiliser application in such meadows results in increased abundance of the species, and there is a possibility that its frequent occurrence in MG1 grassland along roadside verges, as mentioned above, might benefit from elevated nitrogen deposition along roads through vehicle emissions. Such elevated deposition has been well-documented (Cape et al., 2004), as have been its effects on plant species composition of roadsides (Truscott et al., 2005), and as observed for Hertfordshire by James (2009: 268), the species thrives 'in rather rank calcareous roadside verges'. In a study of the impacts of fertilisation and cutting date on the flora of previously unfertilised mountain hay meadows in southern Germany, Boob et al. (2019) found that experimental application of NPK fertiliser of the order of 35 kg N, 35 kg P_2O_5 and 120 kg K_2O ha^{-1} a^{-1} had a positive impact on the abundance of *G. pratense*. They describe this species as a high nutrient indicator species, reflecting its mostly competitive ecological strategy as outlined above. *Geranium pratense* is thus able to successfully compete for light, and hence persist to a degree in denser and taller growing herbaceous vegetation resulting from fertiliser application. However, note that the level of fertiliser application cited above is low by agricultural standards but higher than that at which a decline in overall species richness for European species-rich meadows might be predicted (Tallowin, 1996).

However, due to its late phenology, the occurrence of *G. pratense* in meadows may be incompatible with annual hay cutting early enough to prevent it from setting seed. In the North Pennines and the Yorkshire Dales, *G. pratense* is frequently restricted to road verges, compared with the related *G. sylvaticum* that characteristically occurs in the traditionally managed 'northern' meadows in the same localities (Smith & Jones, 1991). The susceptibility of *G. pratense* to early cutting is particularly pronounced due to its very limited capacity for lateral spread (see Sections 5.1 and 6.3) and the transient nature of its soil seed bank (see Section 8.4), resulting in a reliance of seedling regeneration on seed production in the preceding year. Mowing of a site in July or early August, before the majority of seed capsules can ripen, can largely prevent seed production in that year (Davis, 1973). In contrast, an earlier cut in May or June can still allow some late flowering due to a second 'generation' of reproductive shoots being formed (see Section 7), and consequently, some seeds still being produced (Davis, 1973). Results by Kornaś and Dubiel (1991b) indicate that cutting without hay removal may exert a negative effect on *G. pratense*.

Geranium pratense is considered susceptible to both grazing and trampling (Dierschke & Briemle, 2002). In accordance with this, a botanical survey in the Forest of Bowland, Lancashire, found *G. pratense* to be absent from grassland managed as permanent pasture, whereas its presence was compatible with light autumn and winter grazing in North Yorkshire (Elizabeth Sullivan unpublished data). In Mongolia, a field experiment in which several patches of a *G. pratense* population were fenced off from grazing over a five-year period revealed that young plants were not tolerant of grazing, while adult individuals could survive being grazed (Narantuya, 2016). The species was characterised by its absence from ungrazed burned plots of tall-herb vegetation in a study by Lloyd (1972), but information on its response to burning otherwise appears to be absent. *Geranium pratense* appears to be reasonably tolerant of management abandonment in former hay meadows, and able to persist locally for some years after cessation of management (Kornaś & Dubiel, 1991b).

5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

Geranium pratense was found to occur sparsely, often as solitary individuals in meadows in surveys of grassland communities including hay meadows, permanent pasture and roadside verges in the Forest of Bowland, an upland area in northwest England, where semi-natural grasslands are located in the valleys (Sullivan, 2018). No records were found in surveys of sites managed as permanent pasture though individual plants were observed in pastures with light autumn and winter grazing in North Yorkshire (Elizabeth Sullivan, unpublished data).

When grown in experimental seed mixes typical of Arrhenatherion communities, occurrences of *G. pratense* were described as clearly defined individuals (Lorentzen et al., 2008). However, *G. pratense* does have short rhizomes (see Section 6) and limited clonal growth has been recorded (Chytrý et al., 2021; Fitter & Peat, 1994). Duchoslavová and Herben (2020) reported mean clonal growth of 1.0 cm per year over a 10-year period but found that the clonal rhizomes only persisted for 4 years.

The species is considered to be potentially dominant but lacking traits associated with a high degree of ability to compete for light or nitrogen (Clark et al., 2020). Cover of *G. pratense* was found to decrease with increasing richness of other species in an investigation comparing monocultures with different numbers of species in seed mixes. In the same experiment, cumulative cover of *Arrhenatherum elatius* increased on a per-individual sown basis. Maximum and mean heights of *G. pratense* also decreased as species richness in the seed mixes increased (Lorentzen et al., 2008).

5.2 | Performance in various habitats

Geranium pratense is more often found in open habitats, with shade tolerance decreasing as the plant develops (Sugorkina, 1995). Mature plants have an Ellenberg light value of 7 (Hill et al., 2004), although Tichý et al. (2023) calculated a higher harmonised value of 7.6.

In dense, unmanaged vegetation on riversides and roadsides plants can grow taller, and Sugorkina (1995) reported that in areas

with higher nutrient levels, such as sites of former haystacks, individuals could reach 100–120 cm in height. Sugorkina (1995) also found that there was a correlation between the length of the petioles of rosette leaves and the height of the vegetation stand and reported that biological productivity of *G. pratense* varied according to fluctuations in climatic conditions and land-use: above-ground dry biomass in a floodplain meadow habitat in Kaluga Oblast in Russia, measured over several years, ranged from 160.7 to 880.2 g/m^2.

In a sample of 11 northern English populations sampled in late July and August 2020 (Paul Ashton, unpublished data), plant height means ± standard deviations ranged from 38.2 ± 28.1 cm for Tatham, Lancashire ($n = 8$) to 78.5 ± 11.9 cm for Paddington Meadows, Warrington, Cheshire ($n = 35$). Length of stem leaves ranged from 4.8 ± 0.9 cm for Tynemouth, Tyne & Wear ($n = 30$) to 7.7 ± 1.5 cm for Settle, North Yorkshire ($n = 15$). Width of stem leaves ranged from 9.3 ± 1.9 cm (Tynemouth; $n = 30$) to 14.6 ± 2.5 cm (Settle; $n = 15$). For all three parameters, the means from the sites at the two extremes of the ranges were significantly different ($p < 0.05$) from each other, thus demonstrating some measure of differing performance across populations within habitats broadly similar in their vegetation composition. All sites except Tatham, Lancashire, UK consisted of species-poor grassland dominated by *Arrhenatherum elatius*. The Tatham site supported closely related tall-herb vegetation with frequent *Chamaenerion angustifolium*. This site had the lowest mean values for plant height, length of stipules and bract length across the sites sampled. The sites had similar levels of soil moisture and pH. However, no soil nutrient data for the sites is available and this may be an important explanatory variable for the differing plant performance measures.

Plant height and the size of the leaf blade are highly dependent on soil moisture availability. In the wet climate at the bottom of the Tigritskiy Range in the Altai Mountains, Siberia, Russia, plants reach heights of 1–1.2 m, and produce leaf laminas as much as 20–22 cm in diameter, with the typical size being 5–12 cm (Troshkina, 2018). In the UK, *Geranium pratense* is present on periodically inundated riverbanks in North Yorkshire and Lancashire (Elizabeth Sullivan, unpublished data), and has been recorded in floodplain meadow habitats (Lousley, 1969; Peterken, 2008). Adaptions to damp conditions include mesomorphic and hygromorphic leaves (Chytrý et al., 2021).

5.3 | Effect of frost, drought, etc.

In line with the geographical distribution and altitudinal ranges of *Geranium pratense*, described in Sections 1 and 2, that suggest this species to be highly frost tolerant, the 'Plants for a Future' database (Fern, 1997) lists the species as typically occurring in USDA hardiness zones 5 to 9. The coldest of these, USDA hardiness zone 5, is characterised by average annual minimum temperatures of between −23.3°C and −28.9°C (Cathey, 1990).

Jentsch et al. (2011) studied the effect of drought over a five-year period on experimental grassland communities that included

Geranium pratense. Drought did not lead to any significant change in abundance in *G. pratense* in any of the 5 years. Kreyling, Wenigmann, et al. (2008) conducted a weather manipulation experiment on a similar grassland community consisting of *Arrhenatherum elatius*, *Holcus lanatus*, *Plantago lanceolata* and *G. pratense*. Their results showed that extreme drought increased above-ground net primary productivity in *G. pratense*. The same authors did suggest in another paper (Grant et al., 2014) that under experimental drought conditions, *G. pratense* benefited from competitive release, compared with nondrought control conditions, indicating that this increased productivity is a 'realised niche' effect that appears to be due to the relatively high drought tolerance of this species, compared to that of companion species such as more shallow-rooted grasses that had also been planted in the experiment, rather than reflecting an innate benefit of drought on the growth of *G. pratense*. In line with this interpretation, the authors did not observe an effect of drought on above-ground biomass in single-species plots of *G. pratense* (Grant et al., 2014).

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

Geranium *pratense* has adventitious, polycyclic roots with a sympodial branching pattern, and its short, epigeogenous (i.e., formed at the soil surface) rhizomes (Klimešová, 2018; Klimešová & Klimeš, 2019) are in line with the previously mentioned limited capacity for lateral spread. Root length typically ranges from 8 to 12(15) cm, and the main root typically persists for 10(12) years (Sugorkina, 1995).

The shoots develop as rosette leaves and flowering stems. The rosette leaves have a hairy petiole of around 10–30 cm with blades 6–15(20) cm in diameter. The lobes have sharply pointed teeth three or four times longer than they are wide (Gams, 1924; Poland & Clement, 2020; Sugorkina, 1995; Yeo, 2001). A study undertaken in Estonia estimated the densities and types of trichomes on both upper and lower leaf surfaces of several species including *G. pratense*. Mean ± standard error densities of the number of trichomes per mm^2 for *G. pratense* were as follows: nonglandular trichomes 20 ± 7; peltate glandular trichomes 58 ± 10; nonglandular capitate trichomes 6.35 ± 0.35 (Li et al., 2018). The relative hairiness of the plant may contribute to it being avoided by grazing livestock and slugs, as described in Section 9.1.

The stem leaves are opposite, with lower leaves stalked and upper leaves ± sessile. Stipules are ovate to lanceolate and red brown in colour. The flowering stem bifurcates at the first or second node (Chytrý et al., 2021; Gams, 1924; Sugorkina, 1995).

The branches of the inflorescence and pedicels have glandular hairs. The inflorescence is dense and dichasially branched, with flowers being formed on the 2nd- to 12th-order axes (Sugorkina, 1995). The floral axis is horizontal (Gams, 1924; Sugorkina, 1995; Yeo, 2001).

The pollen grains have been described by Gams (1924) as black in colour, spherical and verrucous in shape and measuring *c.* 100 μm. According to the detailed morphological study of Troshkina (2018), the pollen grains of *G. pratense* are large or very large (97.6) 102.0–111.0 μm, tricolpate, and the furrows are short (27.53 μm) and wide (18.87 μm). The exine surface is continuous, obscurely cellular and clavate. The heads are roundish and variable in size, ranging from 0.77 to 1.8 μm. The heads have 3, 4 or 5 tips connected by obscure furrows or not connected (Figure 4., adapted from Troshkina, 2018).

The fruits of *G. pratense* are yellowish-brown. The rostrum length is 21–30 mm and the fruit length is 32–36 mm. The mericarp ornamentation is characterised by reticulate, smooth surface covered with both nonglandular and glandular hair (Moghadam et al., 2015). A cluster of bristles is situated on a callus at the base of the mericarp, preventing the seeds from falling out prematurely (Yeo, 1984).

The seeds of *G. pratense* are punctate or flat, with an oblique base, dark brown to black, and 2.8–3.3 mm in length. The chalazal (i.e. located at the seed end opposite from the micropylar opening through which fertilisation did occur during flowering, and through which the seedling root will emerge during seed germination) disc has a horseshoe-shaped fringe. The cells of the external testa layer are up to 170 μm long (Tokarski, 1972). Plants studied in Iran had larger seeds, 3.8–4.3 mm long and 2–3 mm wide; the seed surface is glabrous, reticulate-rugulate; testa cells are square and square-polygonal, with thick anticlinal walls; position of the hilum is lateral (Moghadam et al., 2015).

G. pratense is hypostomatous, that is, stomata are present only on the lower leaf surface, at a density of 273 stomata/mm^2 (Fitter & Peat, 1994; Peat & Fitter, 1994).

6.2 | Mycorrhiza

Arbuscular mycorrhizal association was first reported by Harley and Harley (1987) and subsequently by Davison et al. (2011) who recovered 17 arbuscular mycorrhizal fungal sequence groups (= virtual taxa VT) from *G. pratense*, 16 species in the genus *Glomus* (Glomeraceae) and one species of *Acaulospora* (Acaulosporaceae).

In this research by Davison et al. (2011) in Estonia, 11 temperate forest understorey species had been selected for study and

G. pratense was one of six species classified as a habitat generalist, the remaining five species being forest specialists. Arbuscular mycorrhizal fungi (AMF) communities were generally not characteristic of individual plant species but those associated with ecological groups of plant species. A comparison with an online global database (Öpik et al., 2010) showed that generalist plants tend to associate with generalist AMF. Thus, in the study by Davison et al. (2011), the habitat range of the host and a possible interaction with season played a role in the assembly of AMF communities in individual plant root systems.

Uibopuu et al. (2012) tested the effects of two AMF communities originating from early successional and old forest stands on eight forest plant species including *G. pratense*. In a glasshouse experiment, they found that a positive growth response of *G. pratense* was greater with soil inoculum from old forest than with inoculum from young forest. The naturally growing individuals of *G. pratense* also had significantly higher biomass in old stands than in young stands.

6.3 | Perennation: Reproduction

Geranium pratense is a long-lived, herbaceous, polycarpic perennial hemicryptophyte (Hill et al., 2004). Plants overwinter belowground, with overwintering adult plants characterised by a short epigeogenous rhizome with closed overwintering buds made of up 3–5 leaf scales containing the primordia of true leaves (Sugorkina, 1995), and a root system consisting of a main root with adventitious polycyclic roots serving as storage organs (Sugorkina, 1995; see also Section 6.1). Ramets regenerate annually in spring from wintering buds at the soil surface. In 2021, visible growth from the base was observed at the end of February for a *G. pratense* plant grown from native seed material in a garden in south Lincolnshire, UK (Richard Jefferson, personal observation).

Reproduction of *G. pratense* is principally by seed. Plants grown in gardens often begin to flower and set seed from the second year onward, whereas in natural habitats, they typically require several years to reach flowering size (Irmisch, 1874). As shown in a study following the fate and performance of transplanted individuals of *G. pratense* in a grassland restoration experiment, once individuals have
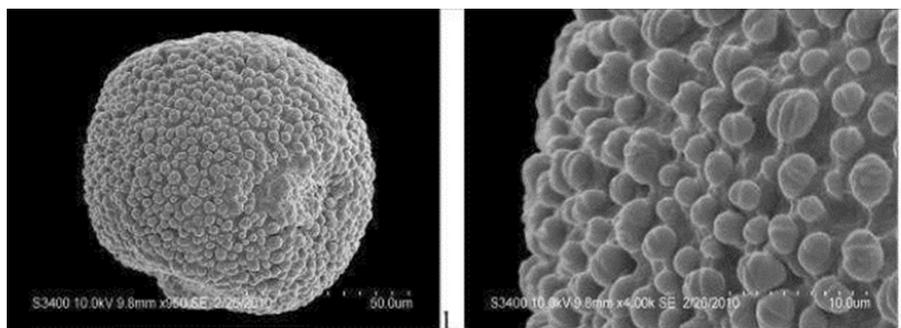

FIGURE 4 Pollen grain of *Geranium pratense*. Left: general view (scale 50 μm); right: sculpture of the exine surface (scale 10 μm). Adapted from Troshkina (2018).

first reached flowering size, they subsequently usually flower and set seed annually (Davies, 2002).

The capacity of *G. pratense* for lateral spread is very limited (see also Section 5.1). Hill et al. (2004) consider *G. pratense* a species with 'little or no vegetative spread'. Grime et al. (2007) have classified it as 'perennial with compact unbranched rhizomes or forming small tussocks ≤100 mm in diameter', which in their categorization of lateral spread represents those perennial species least capable of lateral spread. Nonetheless, the rhizomes of old generative plants can fragment, resulting in clumps of genetically identical but physiologically independent individuals (Sugorkina, 1995). According to Sugorkina (1995), whole genets can live for up to 15–30 years (or longer), whereas individual shortened epigeogenic rhizomes can persist for about 8 to 10 years. A characterisation of 66 individuals of *G. pratense* in a 12-year grassland biodiversity experiment in Germany found rhizomes to be shorter-lived, with an average age of 2.7 years and a maximum age of 5 years (Roeder et al., 2017).

6.4 | Chromosomes

Geranium pratense exhibits intraspecific euploidy (exact multiple of the haploid number (n) of chromosomes; Khan et al., 2020), aneuploidy (having an abnormal number of chromosomes in a haploid set), and polyploidy (possessing more than two complete sets of chromosomes; Kumar & Singhal, 2013; Martin et al., 2022). In a recent monograph of the genus *Geranium*, Aedo (2023) has listed the results of 45 chromosome counts for *G. pratense* across its distribution range, of which 42 did find $2n = 28$, including five counts that analysed material from British populations. The following deviating chromosome numbers have been recorded from other parts of its distribution range: $n = 12$ (Tischler, 1935; Tjebbes, 1928), $2n = 26$ (Martin et al., 2022), and $2n = 56$ (i.e. tetraploid plants; Khan et al., 2020; Kumar & Singhal, 2013). No origin was reported for the material analysed by Tjebbes (1928) and by Tischler (1935). *Geranium pratense* plants with $2n = 26$ were recorded in samples from Kars (northeast Turkey), at an altitude of 2139 m (Martin et al., 2022). Tetraploid plants with $2n = 56$ were recorded in the Himalayan region of India both by Kumar and Singhal (2013) and by Khan et al. (2020). Kumar and Singhal (2013) found tetraploid plants in a cold desert environment in the Lahaul and Spiti district (Himachal Pradesh, India), in subalpine and alpine meadows at altitudes between 3000 and 4500 m. Khan et al. (2020) found plants of the tetraploid cytotype ($2n = 56$) along with plants of the diploid cytotype ($2n = 28$) in the cold deserts of Ladakh (India) on mountain slopes between 3000 and 3500 m altitudes. The latter authors observed that tetraploid plants tended to grow much taller than diploid plants and possessed larger pubescent leaves (Khan et al., 2020). It has been suggested that polyploidy in plants may relate to cold tolerance as an adaptation to conditions at high elevations (Schinkel et al., 2016). Accordingly, the reported occurrence of tetraploid plants of *G. pratense* in Himalayan high-altitude environments may represent an example of such adaptation.

6.5 | Physiological data

Geranium pratense is classified as a C3 photosynthetic plant (Kattge et al., 2011). CAM photosynthesis has also been suggested (Thomas & Beevers, 1949), based on a previously reported high level of diurnal fluctuation of organic acids (overnight increase by 700%) in leaves of the species (Kraus, 1884 cited erroneously in Bennet-Clark, 1933, as being from 1883). Such nocturnal accumulation could indeed be characteristic of plants performing CAM photosynthesis (Winter & Smith, 2022). However, upon closer examination of the original source paper by Kraus (1884) we found that for *G. pratense*, in the text of the paper, the author had referred to only a small increase of the measured acidity value from 0.7 units measured in the afternoon to 0.8 units measured in the early morning, whereas in his Table 4 a value of 5.8 had been given instead of 0.8 (Kraus, 1884). The table would indeed have represented a 700% increase in acid content. However, this stands in stark contrast with Kraus's own interpretation of only a small increase, which may have been lost in translation from the German. Hence later interpretations of *G. pratense* as being able to perform CAM photosynthesis, based on data reported in this table, are almost certainly incorrect. It is also noted that for other species investigated by Kraus (1884), reported values were identical in the text and in the table, providing further indication that one of the two different values reported for *G. pratense* was due to a typographical error. Furthermore, all other British and Irish native *Geranium* species are considered C3 plants (Fitter & Peat, 1994).

The transpiration and CO_2 assimilation rates of *G. pratense* growing in two habitats under different water regimes were studied near Voronezh, Russia (Iljin, 1916). The ratio between transpiration rates (gram/hour/gram of dry weight) and CO_2 assimilation (cm^3/hour/gram of dry weight) was 12.16/10.16 in dry steppe, in contrast to 3.08/10.16 in wet meadow (Iljin, 1916). The measurements in these natural habitats demonstrated a negative response of this mesophytic species to environmental stress in the dry and hot steppe habitat (Iljin, 1916). Holohan et al. (2019) measured leaf gas exchange in *G. pratense* grown in a free-air carbon dioxide enrichment (FACE) field experiment in a floodplain meadow near Giessen in Germany (Jäger et al., 2003). Plants grown at ambient (400 ppm) and elevated (480 ppm) levels of CO_2 for 17 years reacted differently to the experimental step increase in CO_2 concentration from 200 to 2000 ppm. The intrinsic water-use efficiency (WUEi) ($mmol_{CO_2} \, mol_{H_2O}^{-1}$) was significantly higher ($p < 0.05$) in plants grown under elevated CO_2. This unique physiological response was persistent among offspring and was irreversible in at least a single generation even when returned to growth at 400 ppm [CO_2] in growth chambers. However, the ability to increase WUEi does not necessarily translate into an ecological advantage for the species (Holohan et al., 2019).

Irm-LC/MS technology enables the on-line coupling of a liquid chromatograph to a stable isotope ratio mass spectrometer (Hettmann et al., 2005). These methods were applied to study malic and citric acids, which are involved in the Krebs cycle, in several

meadow plants. *G. pratense* exhibits more negative δ13C values (‰) of malic (−23.96‰) and citric (−26.02‰) acid in spring than in autumn (−21.2‰ and −24.27‰, respectively), reflecting increased energy use by plants for spring growth (Hettmann et al., 2005).

6.6 | Biochemical data

The flowers contain anthocyanins: malvidin 3-O-glucoside-5-O-(6-O-acetylglucoside) and a minor fraction of malvidin 3-O-(6-O-acetyl glucoside; Markham et al., 1997). The expression of blue colour is controlled by high concentrations of flavonol co-pigments kaempferol and myricetin 3-O-glucoside and 3-O-sophoroside (Yoshida et al., 2009). The ratio of anthocyanin to flavonol in the petals of *G. pratense* is 1: 4 (Houghton et al., 2021). These chemical interactions (co-pigmentation) work towards the stabilisation of the colours in plant species.

The amino acid composition in the leaves and stems of *Geranium pratense* was studied by detecting amino acids *derivatized* with *phenyl isothiocyanate*, using reverse phase high-performance liquid chromatography. The amounts are given in mg/g of dry biomass: asparagine (1.17), glutamine (0.93), *o*-proline (0.43), serine (1.1), glycine (0.16), histidine (0.08), arginine (1.6), threonine (0.31), alanine (0.11), proline (0.87), tyrosine (0.12), valine (0.06), iso-lecithin (0.16), lecithin (0.22), phenylalanine (0.09), lysine (0.3), cystine plus cysteine (0.84), methionine (0.19), tryptophan (0.016) (Razarenova et al., 2012). In comparison with above-ground organs, rhizomes and roots were found to contain much higher concentrations of alanine (1.46), proline (3.37), lysine (3.02) and methionine (3.15), whereas no asparagine, histidine, threonine and phenylalanine was detected in these underground organs (Razarenova, 2013).

Venjakob et al. (2022) examined the nectar nutrient content of 34 grassland species including *G. pratense* in Germany. They found that carbohydrate to amino acid ratios (C: AA) were generally carbohydrate-biased but ranged from equal mean ratios of C: AA = 1 to mean ratios largely dominated by carbohydrates. *Geranium pratense* was one of three species with mean ratios of C:AA >20:1). The nectar of *G. pratense* contains only four amino acids (alanine, aspartic acid, lysine and histidine) in small amounts (Venjakob et al., 2022).

Gallic acid (3.57 mg/g), ellagic acid (5.14 mg/g), hyperoside (1.69 mg/g) and isoquercetin (0.24 mg/g) were measured in dry aboveground parts of *G. pratense* (Razarenova, 2013). The latter was shown to have a high antiviral effect and has been suggested as an anti-COVID-19 medication (Mbikay & Chrétien, 2022).

Tannins were measured in aboveground and belowground parts of *G. pratense* using the potassium permanganate titration method. Tannins in the dry matter of stems and leaves were found to increase from 21.62% to 23.9% through the growing season, while in roots and rhizomes they decreased from 38.82% to 34.07% (Razarenova, 2013).

The biochemical composition of *G. pratense* has been widely studied for medicinal use of the plant (see Section 10, below).

7 | PHENOLOGY

Plant growth from overwintering rhizome buds starts in spring, first with the formation of a rosette of leaves, and subsequent formation of peduncles, that is, shoots carrying additional leaves and the inflorescence with flowering buds (Sugorkina, 1995). After growth has been initiated, cover of the species seasonally increases until the plants die back again. This has for example been documented by Shevyrnogov et al. (2021) who found that cover of *G. pratense* in a meadow plant community in Khakassia, Russia increased from 1% of ground surface in June to 5% in August. For the British flora, Clapham et al. (1987) and Sell and Murrell (2009) specify flowering of *G. pratense* to occur from June to September. After fruiting or mowing, existing reproductive shoots die back to the renewal zone of the rhizome (Sugorkina, 1995).

Notably, several individual plants of *G. pratense* occurring in grassland adjacent to the Lancaster Canal, Lancashire, UK, were in flower in early October in 2021 and in early November in 2022 (Richard Jefferson, personal observation). At this location, such later flowering dates may be driven either by a warmer autumn microclimate created by the water in the nearby canal and/or by climate warming (see Section 11). *G. pratense* was also recorded in recent years by volunteer recorders as flowering during the Botanical Society of Britain and Ireland's (BSBI) New Year Plant Hunt from 1 to 2 January 2019 and from 1 to 3 January 2021 (2019: VC3—South Devon and VC27—East Norfolk; 2021: VC23—Oxfordshire and VC67—South Northumberland; BSBI Distribution Database; BSBI, 2023). In two of these four instances (VC3 in 2019 and VC23 in 2021), observations were made in a more urban habitat context which could have resulted in a warmer microclimate.

The precise seasonal timing of phenological events depends on the climate, as indicated below by a comparison of British populations with Russian populations. In the continental climate of Russia's Moscow region, vegetative growth of adult plants is typically observed from early May onwards (Sugorkina, 1995). In this climate, rosettes produce shoots in early to mid-June, and then the plants start to flower. Flowering typically extends until September, which according to Sugorkina (1995) is due to the formation of a second 'generation' of reproductive shoots.

In contrast, under milder oceanic British climatic conditions, vegetative growth tends to start earlier. For example, in an experiment carried out along a length of road verge near Spaldwick, about 11 km west of Huntingdon, England, Davis (1973) observed the first appearance of leaves as early as mid-March and the first flowering on 24 May. Flowering in uncut control plots of this author's verge management experiment peaked on 19 July and had largely finished by mid-August, with occasional flowers observed right until the end of experimental recording in mid-September. The first ripe seed capsules were recorded on 26 July, with numbers steadily increasing until the end of recording in mid-September (Davis, 1973). Davis (1973) also found that established plants might still reach the flowering stage again after mowing, even if reproductive shoots are mown as late as in early June. The reason for this appears to

be the already mentioned potential for formation of a second 'generation' of reproductive shoots in the same vegetation period (Sugorkina, 1995). However, a cut in August prevented further flowering in the same year (Davis, 1973).

Another phenological study of a population of *G. pratense* in England was carried out by Smith and Jones (1991), who between 1 June 1988 and 21 August 1988 collected data on the reproductive phenology of the species at a verge near Ravenstonedale, Cumbria. They found that both flowering and the formation of unripe fruit followed a Gaussian curve, with a peak in flowering on 28 July, and a peak in the occurrence of unripe fruit 2 weeks later on 11 August (Smith & Jones, 1991). Ripe fruits dispersing seeds were observed from early August (Smith & Jones, 1991).

Similar phenological delays under Russian continental climate conditions compared to British oceanic climate conditions have also been observed with respect to the timing of seedling establishment. Seedling establishment in Russia's Moscow Region typically occurs in early May, although occasionally seedlings can already be found in autumn, soon after seed dispersal (Sugorkina, 1995). In contrast, in a sowing experiment carried out under field conditions in Warwickshire, Roberts and Boddrell (1985) observed substantial seed germination of *G. pratense* from January onwards, with almost complete germination by May.

Timing of seedling establishment is also affected by the existence of suitable gaps in the vegetation, as indicated by the results of a Polish study (Kostrakiewicz-Gieralt, 2015). This author found that after gap creation in meadow vegetation, more seedlings emerged when gaps were created in spring, but some seedling emergence was also stimulated by gap creation in early July or in mid-September.

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

Geranium pratense is usually insect pollinated and British and European floras classify the reproduction type of this species as facultative allogamy, that is, outcrossing prevails but selfing is possible (Bundesamt für Naturschutz, 2020; Chytrý et al., 2021; Fitter & Peat, 1994). There is agreement that *G. pratense* is gynodioecious, that is, female and hermaphroditic plants coexist within a population, but it is also noted that individuals may be gynomonoecious, that is, have both female and hermaphrodite flowers, or synoecious (hermaphroditic) (Chytrý et al., 2021; Fitter & Peat, 1994; Gams, 1924). In a study by Correns (1907), the average diameter of flowers of hermaphrodite plants (40 mm) was larger than that of the female flowers of gynomonoecious plants (30 mm). The overall percentage of pistillate (female only) flowers in European population and in the Urals was low, with only 1.47% among 946 plants studied (Demiyanova, 2013).

Geranium pratense is protandrous (Bundesamt für Naturschutz, 2020; Fitter & Peat, 1994; Hildebrand, 1865). The stamens reach maturity well before the stigmas (Figure 5), with the

FIGURE 5 Close up of the flower showing the arrangement of the stamens, anthers, and a non-receptive stigma.

two sets of five stamens becoming erect, shedding pollen and then lying adjacent to the petals, after which the stigmas become receptive (Hildebrand, 1865; Proctor et al., 1996). Abdusalam et al. (2021) found in their study that the average length of the male flowering phase was 8.05 h, made up of an 'inner male stage' with an average length of 4.25 h, and an 'outer male stage' with an average length of 3.8 h. The female flowering stage was comparatively shorter, with an average of 5.21 h. Proctor et al. (1996) did point out that pollinators such as bees land on the central organs of the flower, and hence it is important that the stamens are erect to facilitate bees getting into contact with them.

Abdusalam et al. (2021) investigated the role of slow stamen (group-by-group) movement in male–female sexual function, and the effect of stamen movement on pollen removal, male–male and male–female interference, and mating patterns in *G. pratense* as a plant exhibiting temporal floral closure. The study used natural populations in Xinjiang Province, China. *Geranium pratense* is known to use stamen group-by-group movement to facilitate anther-stigma spatial–temporal separation but this has not previously been experimentally determined. Spatial separation (two whorls of five stamens and pistil length) was shown to be stronger than temporal separation (via sequential stamen maturation and pollen presentation). Abdusalam et al. (2021) found that stamen movements to the centre of the flower, where nectar rewards are located in an inner space serving as a nectar holder (Jeiter et al., 2017), increase pollen removal. The most common pollinators visited more frequently and for longer durations during the male floral stage than during the female floral stage (Abdusalam et al., 2021). Floral closure on the first day of flowering may reduce stamen-stamen and pistil-stamen

interference. In a pollination experiment involving 20 randomly assigned flowers per pollination treatment, the seed set of naturally and outcrossed pollinated flowers was found to be more prolific than that of self-pollinated flowers, with averages of seed set of 55% for hand cross-pollinated flowers, 23% for naturally pollinated flowers, 8% each for hand-self-pollinated flowers, and for flowers covered with a paper bag after all stamens were tied together with the style, and 0% for automatically self-pollinated flowers, with the latter indicating the absence of spontaneous autogamy (Abdusalam et al., 2021). Similarly, Hildebrand (1865) noted that while immature stigmas often receive pollen from stamens within the same flower, experimental self-pollination only very rarely resulted in actual seed formation. Both these sets of results fit well with Proctor et al.'s (1996: 332) statement of the species being 'mainly or entirely cross-pollinated'. Prior to floral temporal closure in *G. pratense*, group-by-group stamen movement, dehiscence of stamens, pistil movement, and male–female spatial–temporal functional separation may prevent male–female and stamen-stamen interference and pollen discounting, and may increase pollen removal and cross-pollination.

Geranium pratense flowers are visited by honeybees (*Apis mellifera* L.) and by a range of bumblebees (Figure 6), solitary bees, wasps, hoverflies, beetles, moths and butterflies to access pollen and nectar resources within the flower (Abdusalam et al., 2021; Dlussky et al., 2000; Foster et al., 2017; Kirk & Howes, 2012; Martinková et al., 2015; Nichols et al., 2019; Proctor et al., 1996; Redhead et al., 2018). Table 3 lists the insect species known to visit the flowers of *G. pratense* in Britain and Ireland but is likely to be incomplete. Most of the species listed in Table 3 visit the flowers of a wide range of species from several different plant families. The exceptions are *Chelostoma campanularum* Kirby and *Melitta haemorrhoidalis* Fabricius which both specialise in collecting pollen from species within the Campanulaceae, especially *Campanula* species (Falk &

Lewington, 2016). However, both species may visit the flowers of other species in addition to those of the Campanulaceae to collect nectar (Falk & Lewington, 2016) which explains the records for these bees visiting *G. pratense* flowers in the plant-pollinator interactions database (Redhead et al., 2018).

Tyler et al. (2020) presented an index for nectar production values based on Baude et al. (2016) who used a seven-point scale. *Geranium pratense* was listed as Index 3, meaning that nectar production was small (0.2–5.0 g/m^2/year), but there are copious amounts of collectable pollen. On average, total nectar production of *G. pratense* was measured as 0.8 mg per flower, 174 mg per plant, and 52 kg per hectare. The nectar contains 45.4% of sugar. Pollen production has been measured as 0.7 mg per flower and 79 mg per plant. A honeybee collects up to 19.9 mg nectar from 81 flowers of *G. pratense* in one trip (Anonymous, 2022). When compared to other meadow species, *G. pratense* produces a modest amount of nectar (Gubanov et al., 1990; Venjakob et al., 2022).

In a study of flora preferences of bumblebees in British gardens and allotments, *G. pratense* was found to be of particular importance as a nectar source for the most common species of bumblebees (Foster et al., 2017). *Bombus pratorum* L., *B. lapidarius* L. and *B. pascorum* L. were recorded as the most frequent visitors, which was notable since these species are short-, medium- and long-tongued, respectively. The open flowers of *G. pratense* are accessible for bees with varying morphologies to access pollen and nectar (Kirk & Howes, 2012).

Foster et al. (2017) undertook their study using data from gardens and allotments but similar findings about the importance of *G. pratense* as a nectar source for bees were reported in an investigation of visits by bees to native species of plants farmed for commercial wildflower seed mixes (Nichols et al., 2019). Species of wild bees recorded as visitors to *G. pratense* in the study were: *Bombus hortorum* L., *B. hypnorum* L., *B. lapidarius* L., *B. pascuorum* L., *B. terrestris*

FIGURE 6 *Bombus pratorum* worker visiting a *Geranium pratense* flower to access nectar. The nectar glands are located in a nectar holder at the base of the inner whorl of stamens.

TABLE 3 Insect species recorded as visiting the flowers of *Geranium pratense* in Britain and Ireland. Sources: 1, Redhead et al. (2018); 2, Hutchinson et al. (2020); 3, Foster et al. (2017); 4, Nichols et al. (2019).

Order/family/species	Source
Hymenoptera	
Andrenidae	
Andrena bicolor Fabricius, 1775	1
Andrena dorsata (Kirby, 1802)	1
Andrena wilkella (Kirby, 1802)	1
Apidae	
Anthophora furcata (Panzer, 1798)	1
Apis mellifera Linnaeus, 1758	1
Bombus distinguendus Morawitz, 1869	1
Bombus hortorum (Linnaeus, 1761)	1, 3, 4
Bombus hypnorum (Linnaeus, 1758)	1, 3, 4
Bombus lapidarius (Linnaeus, 1758)	1, 3, 4
Bombus lucorum s.l. (Linnaeus, 1761)	1, 3
Bombus muscorum (Linnaeus, 1758)	1
Bombus pascuorum (Scopoli, 1763)	1, 3, 4
Bombus pratorum (Linnaeus, 1761)	1, 3
Bombus terrestris (Linnaeus, 1758)	1, 3, 4
Bombus vestalis (Geoffroy, 1785)	4
Colletidae	
Hylaeus hyalinatus Smith, 1842	1
Megachilidae	
Chelostoma campanularum (Kirby, 1802)	1
Megachile centuncularis (Linnaeus, 1758)	1
Megachile maritima (Kirby, 1802)	1
Megachile versicolor Smith, F., 1844	1
Megachile willughbiella (Kirby, 1802)	1
Osmia bicornis (Linnaeus, 1758)	1, 4
Halictidae	
Lasioglossum calceatum (Scopoli, 1763)	4
Lasioglossum malachurum (Kirby, 1802)	4
Melittidae	
Melitta haemorrhoidalis (Fabricius, 1775)	1
Diptera	
Syrphidae	
Dasysyrphus tricinctus (Fallén, 1817)	1
Episyrphus balteatus (De Geer, 1776)	1, 2
Eriozona syrphoides (Fallén, 1817)	1
Platycheirus manicatus (Meigen, 1822)	1, 2
Rhingia campestris (Meigen, 1822)	1
Sphegina verecunda Collin, 1937	1
Lepidoptera	
Hesperiidae	
Ochlodes sylvanus (Esper, 1777)	1
Thymelicus sylvestris (Poda, 1761)	1, 2

TABLE 3 (Continued)

Order/family/species	Source
Lycaenidae	
Lycaena phlaeas (Linnaeus, 1761)	1
Polyommatus icarus (Rottemburg, 1775)	1
Nymphalidae	
Aglais urticae (Linnaeus, 1758)	1
Lasiommata megera (Linnaeus, 1767)	1
Maniola jurtina (Linnaeus, 1758)	1
Pararge aegeria (Linnaeus, 1758)	1
Pyronia tithonus (Linnaeus, 1771)	1
Vanessa atalanta (Linnaeus, 1758)	1
Pieridae	
Anthocharis cardamines (Linnaeus, 1758)	1
Gonepteryx rhamni (Linnaeus, 1758)	1
Pieris brassicae (Linnaeus, 1758)	1, 2
Pieris napi (Linnaeus, 1758)	1
Pieris rapae (Linnaeus, 1758)	1

agg. L., *B. vestalis* L., *Lasioglossum calceatum* Scopoli., *L. malachurum* Kirby and *Osmia bicornis* L. *Geranium pratense* was ranked third in the top 14 wildflower species (of a total of 45) visited by 37 out of the 40 wild bee species recorded in their study area, and these 14 plant species collectively received 99.7% of all visits and 92.5% of bee species. However, when solitary bees and bumblebees were compared, richness of the latter was highest on *G. pratense*, but the species was not in the top 10 ranked wildflower species for solitary bee richness (Nichols et al., 2019).

Hutchinson et al. (2020) studied the pollinating insect visitors of two contrasting habitats, a wildflower meadow sown in the late 1990s and an amenity grassland. They used belt transects and surveyed both habitats four times a month in 2017 from April to July, recording bees, butterflies and hoverflies deemed to be collecting pollen or feeding from nectar. Over the course of the study, they made 412 observations of 60 species of pollinating insects visiting 45 species of flowering plants across both habitats. *Geranium pratense*, a constituent of the wildflower meadow, had 39 visits and was ranked 6 out of the top 25 plant species that were visited across both habitats. Fourteen species of insects visited the species, including representatives of all four taxonomic groups—bumblebees, solitary bees, hoverflies and butterflies, although social bees were the dominant visitors.

Martinková et al. (2015) sampled the endophagous insects feeding on the pollen and nectar of flowers of 12 herbaceous plant species at a single site in the Czech Republic over a period of 5 days. During each daily sampling session, 10–200 randomly selected flowers of each species were collected along with the associated fauna. Fifteen insect species consisting of 217 individuals of four insect families (Coleoptera, Diptera, Hemiptera and Hymenoptera) were found within the flowers of *G. pratense*. Of the total number of individuals, 72% were from just two beetle species, *Dasytes plumbeus* Müller (Coleoptera: Melyridae) and *Meligethes aeneus* F. (Coleoptera:

Nitidulidae). The insect fauna of *G. pratense* was the second most species-rich among the 12 species sampled in the research.

In Russia, inflorescences of *G. pratense* were also confirmed as very attractive for foraging social insects. Here the main pollinators of *G. pratense* recorded were honeybees, bumblebees and wasps (Dlussky et al., 2000; Sugorkina, 1995). Sugorkina (1995) reports that *G. pratense* is an important 'honey plant' and a 'bee bread plant' as it provides copious nectar and produces a significant amount of pollen, respectively (Dolgoshev, 1948).

Geranium pratense is also listed as a nectar plant for the European high-altitude butterfly species *Eumedonia eumedon* Esper (Bundesamt für Naturschutz, 2020).

8.2 | Hybrids

There are numerous cultivated hybrids of *G. pratense* and perhaps the most popular is 'Johnson's Blue', which is a sterile hybrid of *G. pratense* and the non-native *G. himalayense* Klotzsch (Yeo, 2001). It has been described as *Geranium* x *johnsonii* P.D. Sell, and this hybrid cultivar is widely grown in gardens (Stace, 2019; Stace et al., 2015). There are a few records of the hybrid as a garden escape in grassy places and on tipped soil but the reliability of these records is unknown (Stace et al., 2015).

In cultivation, *G. pratense* has spontaneously formed fertile hybrids with *G. collinum* Stephan ex Willd. and *G. dahuricum* DC., and sterile ones with *G. sylvaticum* L., *G. swatense* Schönb.-Tem., *G. psilostemon* Lebed., *G. transbaicalicum* Serg., *G. regelii* Nevski and *G. saxatile* Karelin & Kirilow (Yeo, 2001).

8.3 | Seed production and dispersal

Only the upper one of the two ovules per carpel (see Section 6.1) develops into a seed, that is, each carpel typically produces only a single seed. This means that the whole fruit, which consists of five carpels, typically produces five seeds (Boesewinkel & Been, 1979; Sugorkina, 1995). Primary seed dispersal is ballistic, that is, through an explosive mechanism (Ridley, 1930). At maturity, the tissue of the beak dries, with the succulent outer layer drying faster that the inner layer of thick-walled cells. This causes the dried fruit to fall apart into five mericarps (Boesewinkel & Been, 1979). As a result, the carpellary beak coils up, and the seed which was previously held back by a cluster of stiff hairs at the lower end of the carpel orifice, is thrown into the air (Ridley, 1930). The central column of the fruit, with the tops of the carpellary beaks still attached, is left behind (Ridley, 1930). The seed dispersal mechanism of *G. pratense* differs in some details from that of other *Geranium* species (Yeo, 1984). One notable characteristic of the species is that during the pre-explosive interval, the seeds of *G. pratense* are prevented from dropping from the divergent mericarp by setae. Only in the second stage of discharge do these then yield to the centrifugal momentum of the seed, allowing it to escape (Yeo, 1984). According

to Sugorkina (1995), through this ballistic seed dispersal, the seeds of *G. pratense* can be flung across distances of up to 2.2m.

Secondary anthropochorous seed dispersal has also been discussed in the literature. An analysis by Hundt (1975) of local occurrence or absence thereof of populations in fields in the Düben Heath landscape in eastern Germany suggests that transport of seeds with hay was an important means by which *G. pratense* was able to spread in that landscape. He noted that within that region, the occurrence of *G. pratense* in Arrhenatheretum grassland was somewhat irregular, but notably limited to parishes where farmers lived who had also owned meadows in the floodplain of the river Elbe, where *G. pratense* was common. At the same time, Arrhenatheretum grasslands with *G. pratense* in them did not meaningfully differ from grasslands from which the species was absent, both in terms of other aspects of taxonomic composition and in terms of soil conditions (Hundt, 1975). Another way in which *G. pratense* has colonised new locations is by escaping from ornamental gardens (Gams, 1924; Slavík, 1996). Spreading of *G. pratense* has also been observed along roads and railway lines, indicating the importance of such linear transport infrastructure for dispersal (Slavík, 1996).

Davis (1973) found that in unmown control plots, individual peduncles bore an average of 30 capsules, but he recorded up to 129 capsules on a single plant with two peduncles. In this study, the mean number of capsules produced in unmown control equalled about $300/m^2$ (Davis, 1973). If each capsule produced all five seeds, these figures would equate to an average of 150 seeds produced per peduncle, and an average of $1500 seeds/m^2$. During work carried out in Russian floodplain meadows along the river Ugra in Kaluga Oblast, Sugorkina (1995) found that seed production in stands of *G. pratense* ranged from 330 to $4880 seeds/m^2$. Seed production of an individual peduncle ranged from 40 to 150 seeds, and annual seed production of multistemmed whole plants ranged from 40 to 480 seeds (Sugorkina, 1995).

Mean seed mass recorded in the literature ranges from 3.50mg (Sugorkina, 1995) to 9.90mg (Dallmann, 1933 cited in Salisbury, 1942), with intermediate values of 6.37mg, 7.40 and 7.48mg reported in other studies (Grime et al., 1981; Van Assche & Vandelook, 2006; Ziron, 2000). Interannual variation in seed mass can be large, with one study reporting a mean seed mass of 5.85 and of 9.30mg, respectively, for the same source population in consecutive years, based on measurements from four replicate seed lots of 100 seeds each per year (Janicka et al., 2021). The seeds are oval, about 2.4 to 3.5mm long and about 1.5–2mm wide, reticulate, and of a dark-brown colour (Boesewinkel & Been, 1979; Janicka et al., 2021; Sugorkina, 1995). The seed coat is formed by both the inner and outer integument (Boesewinkel & Been, 1979), and made up of multiple layers including both a lignified subpalisade layer and a water-impermeable palisade layer (Meisert, 2002). The seed coat also contains stomata that have been hypothesised to facilitate the intake of water during germination, rather than playing a part in the process of gas exchange (Boesewinkel & Been, 1979). A gap at the chalazal end of the seed is sealed by a suberised stopper formed from remnant nucellus (Boesewinkel & Been, 1979), and this closed chalazal slit and the palisade later have

been assumed to represent the structural basis of the water impermeability of fresh seeds (Meisert, 2002; Meisert et al., 1999) in Geraniaceae. More recently, research in other *Geranium* species has indicated that the water gap function enabling seed germination is not fulfilled by this chalazal gap, but instead by 'hinged valve' palisade cells adjacent to the micropyle of the seed (Gama-Arachchige et al., 2010). However, it remains to be demonstrated whether the same is the case for the seeds of *G. pratense*.

8.4 | Viability of seeds: Germination

Fresh mature seeds of *G. pratense* are characterised by physical seed dormancy (Baskin & Baskin, 2014). In a 10-day test of water permeability on moist filter paper, Meisert (2002) found that 96% of such seeds from German populations did not imbibe any water. Accordingly, germination of fresh seeds is very low, with 0.8% germination observed in a Czech study by Martinková et al. (1997), 4.3% in a study by Van Assche and Vandelook (2006) using seeds from a Belgian population, and 8% in a study by Grime et al. (1981) using freshly collected seeds in the region around Sheffield. In two seed burial experiments carried out by Roberts and Boddrell (1985) using freshly collected seed from South Warwickshire populations, almost complete seed germination of *G. pratense* occurred under field conditions over a 5-month period from January to May. Similarly, Van Assche and Vandelook (2006) found in another burial experiment that most of the fresh seeds of *G. pratense* they had buried in early August had germinated in the soil during the autumn and winter after burial, with only 1% of seeds recovered intact 9 months later at the beginning of May. Moreover, intact ungerminated seeds were swollen when recovered, indicating that they had become permeable, but that radicle emergence had been prevented by low soil temperatures (Van Assche & Vandelook, 2006). Results from these various studies indicate that physical seed dormancy in *G. pratense* mainly serves to ensure optimal seasonal timing of germination in the winter and spring after the seeds have been produced, rather than to facilitate the build-up of a persistent soil seed bank (Van Assche & Vandelook, 2006). In agreement with this interpretation, Švamberková et al. (2017) found in an outdoor sowing experiment under field conditions that seedling establishment was high in the first spring after autumn-sowing, but comparatively low in the spring straight after spring sowing, while being absent in the second spring after spring sowing. A lack of seed bank formation on sites where the species is present in the vegetation has also been indicated by studies of natural seed banks of *G. pratense* in Russia (Rabotnov, 1951, 1958, both cited in Sugorkina, 1995), Germany (Poschlod & Jordan, 1992) and Estonia (Wagner et al., 2003).

An extended period of several months of seed germination, as described both by Roberts and Boddrell (1985) and by Van Assche and Vandelook (2006), could help ensure that some seedlings establish successfully even if conditions temporarily turn unfavourable. In line with these studies, a study investigating seedling establishment in gaps created in meadow vegetation at different times of the growing season (Kostrakiewicz-Gieralt, 2015) found that although numbers of establishing *G. pratense* seedlings were highest in gaps created on 15 April, there was also some seedling establishment after gaps were created on 1 July or on 15 September.

Alleviation of the physical seed dormancy of *G. pratense* can be instantly achieved by mechanical scarification of the seed coat, that is, by perforating the testa, for example with a scalpel (Grime et al., 1981; Van Assche & Vandelook, 2006). Scarified seeds can achieve rapid and near-complete germination (Grime et al., 1981; Van Assche & Vandelook, 2006). Grime et al. (1981) applied scarification after dry storage, resulting in 75% germination using a 15-h photoperiod at 20°C and a night temperature of 15°C, with half of this germination having occurred within 5 days. Van Assche and Vandelook (2006) scarified both fresh seeds and seeds that had been stored dry for 3 months, recording 89% germination and over 95% germination, respectively, using a 12-h photoperiod and a constant temperature of 23°C for incubation. Thus, unlike several annual *Geranium* species that achieved only 70%–75% germination of scarified fresh seed, *G. pratense* appears to be characterised by possessing mainly physical seed dormancy, rather than a combination of both physical dormancy and physiological dormancy (Van Assche & Vandelook, 2006).

Unlike scarification, dry storage of seeds at room temperature, regardless of length of storage, appears to have only limited or no effects on germination ability. Van Assche and Vandelook (2006) found no increase in the germination ability of seeds stored dry at room temperature for periods ranging from 3 months to 2 years compared to that of fresh seeds, and dry-stored seeds remained impermeable for the entire 2 years. Similarly, Meisert (2002) found that seeds remained impermeable for an even longer period of 5 years. However, while in Van Assche and Vandelook's (2006) study, some germination was observed after 2 years of dry storage, it is unknown whether the seeds used by Meisert (2002) were still viable after 5 years. In contrast to Van Assche and Vandelook (2006), Grime et al. (1981) reported somewhat higher levels of 20% germination after 5 weeks of dry storage at 20°C. Similar levels of germination were found by Janicka et al. (2021) after 5 months of dry storage at 15°C, with 17% germination from material collected in the first year of their study, and 23% of germination from material collected the following year. Interestingly, Grime et al. (1981) described *G. pratense* as a species with an unusual response to dry storage, as dry storage in air at 5°C for periods ranging from 3 months to 12 months resulted in much higher germination of between 86% and 96%, compared to the 20% observed after dry storage at 20°C. However, unlike the fast germination they observed after scarification, germination after dry storage at 5°C was much slower. After seed scarification, 50% of observed germination occurred after just 2 to 5 days, whereas in unscarified seeds that had been stored dry at 5°C, 27 to 43 days were required for half of the observed germination to occur (Grime et al., 1981). Sugorkina (1995), testing the germination of seed of Russian provenance, similarly found that in laboratory germination trials carried out in the same year as when seeds were collected, germination took place over a period of 2 to 3 months. The same mechanism mentioned above as causing gradual cumulative germination under field

conditions (Roberts & Boddrell, 1985) may be responsible for the observed gradual germination under laboratory conditions.

The inability of *G. pratense* to form a persistent soil seed bank fits with the fact that its germination appears to be hardly affected by light levels and by degree of temperature fluctuation. Van Assche and Vandelook (2006) reported that percentage germination during 10-day germination tests was similar for a constant temperature regime of 23°C and for an alternating temperature regime of 12 h at 20°C and 12 h at 10°C, thus indicating that diurnal temperature fluctuation is not required for germination. Furthermore, according to Grime et al. (1981), relatively high levels of germination occur across a relatively wide range of constant temperatures. In their study, at least 50% of maximum germination was observed for constant temperatures ranging from 6°C to 33°C. However, these results stand in contrast to those of Van Assche and Vandelook (2006) who found that a constant temperature of 23°C resulted in much more rapid and complete germination of scarified fresh seeds and of seeds scarified after 3 months of dry storage, compared with lower constant temperatures of 10°C or 5°C.

When investigating the moisture requirement of seeds for germination, Ziron (2000) used seed that had been stored cold and dry at room temperature for a few weeks. In this study, replacement of water as a germination medium with a polyethylene glycol (PEG)-6000 solution with nominal osmotic potential of −0.4 MPa resulted in in average reduction of germination by about 60% to 70% germination across a range of light and temperature regimes (Ziron, 2000). This indicates that even under moderate drought stress, some germination is possible.

To explore the light requirement for seed germination, Grime et al. (1981) also compared germination at different light fluxes, using seeds that had been allowed to after-ripen during dry storage at 20°C. They found that over an extended period, complete germination of 99% to 100% took place both in light and shade treatments, with 83% germination in darkness (Grime et al., 1981). Similar observations were made by Ziron (2000), who also found somewhat reduced but still substantial germination in darkness, compared with levels observed in light and shade conditions. More recently, Górski et al. (2013), using seeds that had been stored cold and dry for an unspecified period, have found that germination of *G. pratense* is moderately inhibited under a leaf canopy lowering the red: far red ratio of incoming light. Initial seedling establishment under field conditions after sowing in autumn was higher when sowing was carried out in vegetation-free gaps, compared to when sowing in undisturbed grassland vegetation (Švamberková et al., 2017).

8.5 | Seedling morphology

Figure 7 illustrates the developmental stages of *G. pratense* seedlings from initial germination to the mature seedling stage. The following
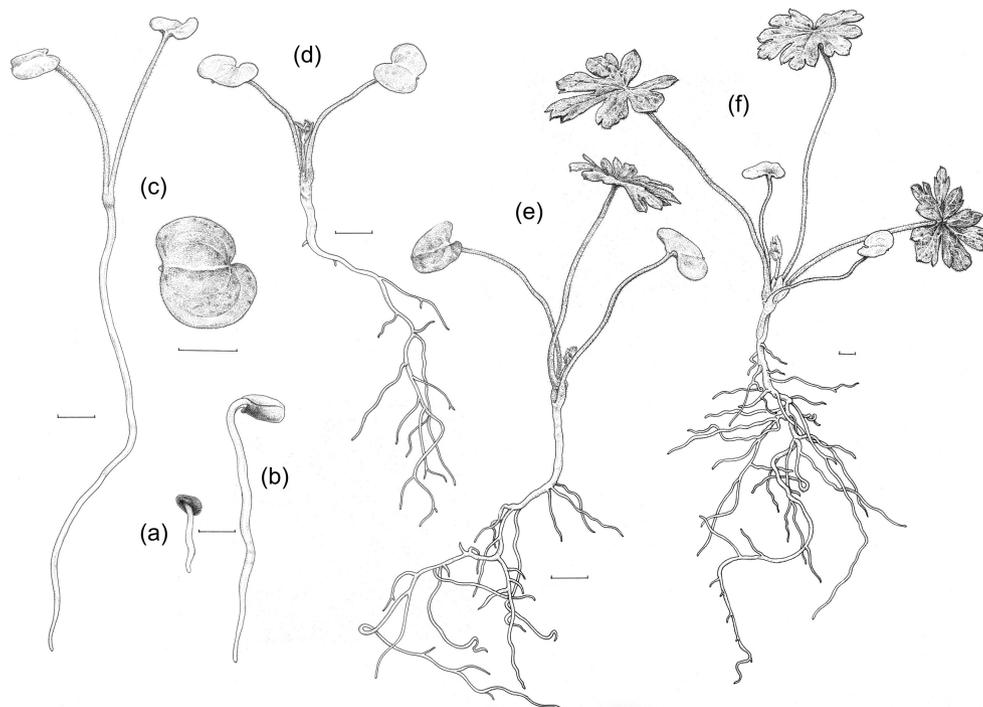
FIGURE 7 The development of *Geranium pratense* seedlings from germination. Seeds were scarified and sown on 29 March 2020. All seedlings were grown from seed obtained from Emorsgate Seeds, King's Lynn, UK. Stages shown include the following stages: (a) emergent radicle on 8 April 2020, (b) larger seedling root on 10 April 2020, (c) seedling with cotyledon and top view of a cotyledon on 14 April 2020, (d) appearance of first true leaf on 19 April 2020, (e) seedling with one fully grown true leaf on 27 April 2020, and (f) seedling at the four-leaf stage on 16 May 2020. The seedlings were grown and drawn by Lucy Hulmes ©. As plantlets were uprooted, the age sequence is represented by different specimens. All scale bars indicate 5 mm.

description has been assembled from direct observation of the seedlings and the descriptions in Muller (1978) and Sugorkina (1995). The hypocotyl is 10–15 mm long, reddish, with short ordinary unicellular hairs towards the top, and ± herbaceous. The two herbaceous cotyledons are asymmetrically wider than long (mean length/width = 0.77), with a cordate base that is 11–14 mm wide and wider than long, and with short glandular and ordinary unicellular hairs. The cotyledon tip is emarginate cuspidate. The cotyledons have petioles of 5–6 cm with partly glandular unicellular hairs. An epicotyl is absent. True seedling leaves are 1.5 to 3 cm in diameter, alternate, have a 6–10 cm long petiole with glandular and ordinary unicellular hairs and adnate membranous stipules, and are palmatipartite with lobed segments. Their base is strongly emarginate. These leaves have only ordinary unicellular hairs, and acuminate lobe tips.

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

In spite of its relative intolerance of grazing (see Sections 3 and 4), *G. pratense* can occur in grasslands grazed by domestic herbivores including sheep, cattle and equines. Sugorkina (1995) summarises the limited information available on its feed value for livestock in Russia. It is consumed by cattle and other domestic livestock in hay but is not a preferred forage species in pasture.

In Russia, it is consumed by a range of wild herbivores including *Lepus europaeus* Pallas, *Marmota monax* L., and species of pika (*Ochotona* sp.), whilst black grouse *Tetrao tetrix* L., readily eat the seeds (Larin et al., 1951 in Sugorkina, 1995). In eastern Europe, *G. pratense* features on a list of plants consumed by the European bison (*Bison bonasus* L.) (Borowski et al., 1967).

Various phytophagous insect taxa have been recorded as feeding on *G. pratense* in Britain and Ireland (Table 4). Eleven insect species have been recorded as feeding on *G. pratense*, including three beetles, four micromoths and one species each of butterfly, sawfly, gall midge and aphid. Furthermore, 46% are monophagous and 54% are polyphagous. Overall, the phytophagous insect and mite fauna of *G. pratense* is depauperate when compared to many other British perennial herbs that have a comparable or even lower area of occupancy (as measured by 10 km squares) (Lawton & Schroder, 1977). For example, the grassland plant *Centaurea scabiosa*, a tall perennial plant has an area of occupancy of 1106 10 km squares in Britain and Ireland, fewer than *G. pratense* (1838), supports around five times the number of phytophagous species (DBIF, 2020). Another grassland perennial, *Sanguisorba officinalis* with an even lower area of occupancy (825 10 km squares), has around 60% more associated species than *G. pratense* (DBIF, 2020).

The British native species of the Geraniaceae in the genera *Erodium* and *Geranium* have been documented to support at least 62 species of phytophagous insects and mites (DBIF, 2020). The family does not appear in the group of plant families with the highest total numbers of phytophagous insects in Britain (Ward & Spalding, 1993). The restricted number of native plant species and genera per family (13 and 2 respectively) may partly explain the relative paucity of the insect/mite fauna of the family as these parameters are significantly correlated with phytophagous insect/mite richness (Ward & Spalding, 1993).

In a laboratory experiment quantifying the grazing activity of the slug *Arion lusitanicus* Mabille on a range of seven herbaceous species, Honek and Martinkova (2007) found that *G. pratense* was one of two species avoided by slugs. This is consistent with research by Kozłowski and Kozłowski (2004) showing that leaves of *G. pratense* are unattractive to slugs. On the other hand, field-based experiments by Dudenhöffer et al. (2016) in Germany demonstrated that the seeds of the species are predated by a range of generalist arthropods and slugs.

FIGURE 8 Close up of the flower showing a pair of the weevil *Zacladus geranii* that is confined to feeding on larger species of *Geranium* in Britain and Ireland (Morris, 2008).

TABLE 4 Insect species recorded as feeding on *Geranium pratense* (larva unless otherwise specified) and excluding nectar and generalist pollen-feeding species (Table 3). Sources: 1, Asher et al. (2001); 2, DBIF (2020); 3, Bradley et al. (1973); 4, Emmet (1988); 5, Sinclair and Hutchins (2009); 6, Webb et al. (2018); 7, Davis (1973); 8, Morris (2008); 9, Morris (2002); 10, Benson (1952); 11, Redfern and Shirley (2011); 12, Blackman (2019). Key: E—England, W—Wales, S—Scotland, I—Ireland.

Order/family/species	Plant part and feeding habit	Source	Distribution/status
Lepidoptera			
Lycaenidae			
Aricia agestis (Denis & Schiffermüller, 1775).	Leaves. On *Helianthemum nummularium* and *Geranium* spp.	1, 2	Widespread (E), Local (W), Rare (S)
Tortricidae			
Cnephasia stephensiana (Doubleday, 1849)	Leaves. 1st instar mine then later instars live externally in spun leaves. Widely polyphagous on herbaceous plants	2, 3	Widespread (E, W, S), Rare (I)
Cnephasia asseclana (Denis & Schiffermüller, 1775)	Leaves. 1st instar mine then later externally in spun leaves. Widely polyphagous on herbaceous plants	2, 3	Widespread (E, W, S, I)
Pterophoridae			
Amblyptilia acanthadactyla (Hübner, 1813)	Flowers, maturing seeds and young leaves. Widely polyphagous on herbaceous plants	4	Widespread (E, W, S, I)
Amblyptilia punctidactyla (Haworth, 1811)	Flowers and maturing seeds. Polyphagous on herbaceous plants	4	Widespread (E, W, S, I)
Coleoptera			
Chrysomelidae			
Aphthona pallida (Bach, 1856).	Leaves (adults) Monophagous	5	Scarce (E, S)
Curculionidae			
Zacladus geranii (Paykull, 1800) (Figure 8)	Larva—seeds/fruits Adult—flowers, leaves Monophagous—on larger *Geranium* spp.	2, 7, 8	Widespread (E, W), Rare (S)
Limobius borealis (Paykull, 1792)	On *Geranium* spp. Monophagous.	2, 6, 9	Scarce (E, W)
Hymenoptera			
Tenthredinidae			
Ametastegia carpini (Hartig, 1837)	Leaves. Monophagous	2, 10	Local (E, W, S)
Diptera			
Cecidomyiidae			
Dasineura geranii (Kiefer, 1907)	Flowers (gall). Monophagous.	2, 11	No data
Hemiptera			
Aphididae			
Acyrthosiphon malvae (Mosley, 1841).	Flowers, leaves. Polyphagous.	2, 12	Local to widespread (E–southern)

9.2 | Plant parasites

Plasmopara pusilla (de Bary) Schröter is a downy mildew found on the leaves of *G. pratense* (British Mycological Society, 2022; Ellis & Ellis, 1997). It causes brown blotches on the adaxial surface of the leaf and a white down on the abaxial side. Another Eurasian species, *Uromyces geranii* (DC.) Fr. Is an oligophagous rust fungus that occurs on the abaxial surface of the leaves of various *Geranium* species including *G. pratense* (British Mycological Society, 2022; Ellis & Ellis, 1997). The uredinia are cinnamon brown and the aecia are orange and up to 2 cm in length. Two other oligophagous species that occur on *G. pratense* are *Ramulina geranii* Fuckel, that forms dark-brown blotches on living leaves and *Pirottaea paupercula* Nannf. On stems (British Mycological Society, 2022; Ellis & Ellis, 1997).

Plasmopara geranii-sylvatici Săvul. & O.Săvul. has been recorded on *G. pratense* in Poland and Slovakia although *Geranium sylvaticum* is its main host (Mułenko et al., 2008).

The Fungal Records Database of Britain and Ireland (British Mycological Society, 2022) also lists the oligophagous powdery mildew *Podosphaera fugax* (Penz. & Sacc.) U. Braun & S. Takam as forming hypophyllous colonies on the leaves of *G. pratense*.

A range of plurivorous species have also been recorded on mostly dead stems and leaves of *G. pratense* (Fitter & Peat, 1994).

9.3 | Plant diseases

None known.

10 | HISTORY

There is no specific reference to material for *G. pratense* in Godwin (1975), although for *Geranium* sp. there is a pollen record from the Middle or Late Weichselian, and a seed record from zone viii. A pollen grain suggested to be either *G. pratense* or *G. sylvaticum* was recorded from Colney Heath (St Albans) dated to 13,560 B.P. However, based on current distribution maps it was suggested to most likely be *G. sylvaticum* (Godwin, 1975). The first record of *G. pratense* in Britain and Ireland documented in the literature is from 1571 (L'Obel in Pearman, 2017).

10.1 | Medicinal uses

Several *Geranium* species are used in traditional medicines. The roots of *G. pratense* are used in traditional Tibetan medicine for the treatment of fever, coughs and body ache (Pandey, 2007). In India, *G. pratense* roots are applied as a poultice to relieve inflammation associated with bruising; the whole plant is also made into a powder to treat coughs, jaundice and gastric disorders (Sood et al., 2001, cited in Kumar & Singhal, 2013). In traditional Chinese medicine, the consumption of aerial parts of *G. pratense* is recommended to 'dispel wind-damp, free channels and network vessels, check dysentery and diarrhoea' (Zhou et al., 2011). *Geranium pratense* subsp. *finitimum* has also been used in Turkey to treat stomach ache (Öz Aydın et al., 2006). It was stated by Loudon (1832: 506) that 'The most common property of European *Geraniums* is to be astringent', for which *G. pratense* was included, and that they 'have been recommended for various purposes, and among others for removing calculous [urinary] disorders.'

Geranium species contain the essential oil geraniol and geraniin, a hydrolysable tannin. Geraniol has been shown to have antimicrobial properties (Pattnaik et al., 1997) and can inhibit tumour growth (Burke et al., 1997). Geraniin can also inhibit tumour activity (Li et al., 2013), and has antioxidant (Lin et al., 2008), antiviral (Yang et al., 2007), antibacterial, antifungal (Goahr et al., 2003) and anti-inflammatory (Jiang et al., 2016; Küpeli et al., 2007) properties. The aqueous extract of *G. pratense* subsp. *finitimum* has been shown to have anti-inflammatory activity (Küpeli et al., 2007), and the extracted polyphenolic compounds (quercetin 3-*O*-β-D-glucopyranoside, quercetin 3-*O*-β-D-galactopyranoside, quercetin 3-*O*-(2"-*O*-galloyl)-β-D-glucopyranoside and quercetin 3-O-(2"-*O*-galloyl)-β-D-galact opyranoside) from aerial parts of *G. pratense* subsp. *finitimum* have been shown to provide protection against endothelial injury of rat aorta caused by free radicals (Akdemir et al., 2001).

When investigating the use of medicinal plants to reduce the incidence of soil-borne plant diseases, an aqueous root extract of *G. pratense* was shown to inhibit the growth of mycelial suspensions of *Streptomyces scabies*, *Phytophthora megasperna*, V*erticillium dahliae*, and *Pythium ultimum* (Ushiki et al., 2011). An aqueous root extract also suppressed the growth of *Escherichia coli*, *Pseudomonas aeruginosa*, *Staphylococcus aureus* and *Bacillus cereus* (Razarenova, 2013).

10.2 | Cultivation

Historically, species of medicinal value are more likely to be cultivated, especially if combined with showy flowers as seen in *G. pratense*. The first record of a *Geranium* being introduced for cultivation is for *Geranium macrorrhizum* from Italy in 1576 (Loudon, 1832).

Loudon (1832) recorded 'ornamental' variants of *G. pratense* growing in gardens. This includes white flowered cranesbill, variegated flowered cranesbill (straw-coloured flowers), double flowered cranesbill (blue flowers) recorded in Scotland (mountains), and the Daurian cranesbill (blue flowered), introduced from Dauria in 1818. All were reported to grow on 'common garden soil', while *G. pratense* was recorded from meadows and pastures on sandy loam soils. However, it was noted that all could be propagated by 'division', perhaps indicating that all types of *G. pratense* were being cultivated. More recently, *G. pratense* has been recommended for growing in garden soils over limestone, especially if dry (Yeo, 2001).

11 | CONSERVATION

11.1 | Status

Geranium pratense has been classified as of Least Concern under IUCN criteria in the GB vascular plant Red List (Cheffings et al., 2005) and more recently in the Wales Red Data List (Dines, 2008) and in the England Red List (Stroh et al., 2014). It is listed as Vulnerable in the Irish Red List (Wyse Jackson et al., 2016). There was no significant change in its distribution over the period between the first two British vascular plant hectad distribution atlases (Perring & Walters, 1962; Preston et al., 2002) although there had been a small increase due to introductions (see below). The change index reflected this with a value of +0.15 (Preston et al., 2002). In support of this assessment, *G. pratense* belonged to a group of species that showed no significant change over the period 1987–2004 in a re-survey of a sample of tetrads in 2003–2004 previously surveyed in 1987–1988 (Braithwaite et al., 2006).

In the most recent vascular plant hectad Atlas for Britain and Ireland (Stroh, Walker, et al., 2023), Hill's (2012) Frescalo modelling approach was used to adjust trend estimates for differences in recorder effort across different time periods. The results indicated a stable long-term trend in occurrence for the period 1930–2019 and a stable to increasing more recent short-term trend for the period 1987–2019, with 54 slope estimates from a random selection of 100 linear trend lines falling into the 'stable' trend class, and 46 slope estimates falling into the 'moderate increase' trend class. The indicated partial short-term increase is due to a range expansion since 2000, probably due to introductions, especially in northern and western Scotland, west Wales and in Ireland (Stroh, Walker, et al., 2023).

However, the limitations of the Atlas data and analyses may mask the true state of change (see e.g. Rich & Karran, 2006) because change statistics based on occupancy within hectads are unlikely to detect declines at much smaller scales, for example, in the

population density or abundance of the species within habitats or at a specific location.

Preston et al. (2002) and Stroh, Walker, et al. (2023) state that *G. pratense* was formerly frequent in hay meadows but has become increasingly restricted to roadsides due to changes in agricultural practices. Although there is strong evidence for the loss of semi-natural grasslands during the second half of the twentieth century (including hay meadows; Blackstock et al., 1999; Fuller, 1987; Stroh et al., 2019) there are no data on the former presence or frequency of *G. pratense* in such grasslands, so it is not possible to verify this contention. However, its intolerance of grazing (Sections 3 and 4) indicates that the meadow habitat may be more unsuitable, as many such sites receive a period of grazing during the year.

In Northern Ireland, *G. pratense* is very rare and native localities are confined to County Antrim (see Section 1) where the first record was from 1821. It is listed as a Northern Ireland priority species and a Northern Ireland Species Action Plan has been developed for it (Department of Agriculture, Environment & Rural Affairs, 2005). One stronghold, White Park Bay, is an Area of Special Scientific Interest under the *Nature Conservation and Amenity Lands (Northern Ireland) Order* 1985.

The status of the species in Britain and Ireland is made more complex by the marked increase in alien sites since the 1962 *Atlas* (Perring & Walters, 1962; Preston et al., 2002; Stroh, Walker, et al., 2023), and separating native and alien plants within its native range can be difficult or impossible. The increase in alien localities is probably largely down to its frequent inclusion in conservation wildflower meadow seed mixtures (for neutral soils) or in butterfly and pollinator seed mixes (Crawley, 2005; Nichols et al., 2019). Other alien sites may have established from garden escapes or from the disposal of garden waste as several cultivars of the species are widely grown in gardens (Miller, 2002). Cultivation and breeding of *G. pratense* apparently dates back many hundreds of years (Yeo, 2001) and it is used as a garden plant over large parts of Europe (Gams, 1924).

Hundt (1975) reported that in the mid-1970s, *G. pratense* was extending its distribution area in continental Europe due to human-mediated dispersal, such as transport on farm machinery (agestochory). However, the same author also predicted that in future, the intensification of semi-natural grassland by the addition of fertilisers and intensive grazing would lead to losses of populations of *G. pratense* and concomitant decline in its range (Hundt, 1975).

Geranium pratense is identified as an indicator of high-value habitat. Walker (2018), for example, identified *G. pratense* as an axiophyte (a species indicative of high habitat quality) in 8 out of 20 (40%) counties that have produced lists of axiophytes in Great Britain. Of the 20 counties, *G.pratense* is present in 18 (90%) as a native plant. Similarly, the Nature Conservancy Council's England Field Unit drew up lists of unimproved mesotrophic grassland indicator species and allocated *G. pratense* to the category of a species not entirely restricted to unimproved mesotrophic grassland but nonetheless usually confined to low nutrient status grasslands (Rowell & Robertson, 1994). The grassland indicators were allotted numerical scores depending on their level of affinity for high-value semi-natural

grassland. The numerical values are on a 4-point scale (1, 2, 4 & 8) with *G. pratense* assigned a value of 2. On this scale, plant species tolerant of higher nutrient status soils and that also occur widely in semi-improved grasslands scored 1, whereas species virtually confined to semi-natural mesotrophic grassland scored 8. The total scores for individual indicator species for grassland sites surveyed during the 1980s and 1990s were used as an aid to site evaluation for conservation.

11.2 | Conservation

The conservation of this species in Britain and Ireland is reliant on ensuring low-intensity management, usually involving cutting and light or episodic grazing, of its various grassland habitats (see Sections 3 and 4). An amplified fragment length polymorphism (AFLP)-based study of *G. pratense* populations in Germany with potential relevance for conservation was carried out by Michalski and Durka (2012). The study included 26 natural populations, with spatial distances between populations varying from 0.8 to 116 km. Among others, it found that expected heterozygosity within populations was lower ($He = 0.15$) than would be expected for this outcrossing species. Genetic differentiation was high among populations within each of three German provenances studied (mean pairwise $F_{ST} = 0.20$), and even higher among provenances ($F_{ST} = 0.48$). Overall, an increase of genetic differentiation between populations with increasing distance was observed. Gene flow distances were estimated indirectly first on a regional scale and second for the local scale in populations. It was found that isolation by distance due to gene flow is responsible for the genetic differentiation observed between populations at distances of up to 10 km, whereas genetic drift was mostly responsible for observed pattern at larger distances. Spatial genetic structure was estimated by the Sp statistic measuring pairwise coefficients of relationship between different geographical populations (Vekemans & Hardy, 2004). The mean Sp = 0.064 value obtained for the three populations of *G. pratense* in the lowlands and downs of central Germany was almost three times higher than is known for other outcrossing species. This observation suggests a small genetic patch size in *G. pratense* and restrictions on effective gene dispersal (Michalski & Durka, 2012). This study found little evidence for adaptive population differentiation in *G. pratense* caused by climatic selection or geographical barriers. Further studies are required to test an effect of historical land use or environmental gradients on the population genetic structure of *G. pratense*.

Michalski and Durka (2012) did also suggest that there may be negative impacts associated with introducing nonadapted gene pools into the vicinity of local native populations of *G. pratense* such as from plants derived from seed mixes or from garden escapes. Possible harmful effects include intraspecific hybridisation between alien and local genotypes leading to outbreeding depression and subsequent lower fitness of progenitors and the risk that alien genotypes may become invasive if superior to local ecotypes. While

hypothetically, effects such as hybrid effects or genetic rescue may sometimes be beneficial in the context of garden escapes, however, in our view, *Geranium pratense* may not require genetic rescue quite yet. Also, due to the great numbers of cultivars around, a loss of native genotypes appears to be the most likely consequence.

11.3 | Climate change

The most recent climate change predictions for the UK—UKCP18 (Met Office, 2018) provide detailed predictions for how the British climate might change over the next 50 years. In general terms, these predict over land a move towards warmer, wetter winters and hotter, drier summers. *G. pratense* is a widespread species with a wide latitudinal distribution in the temperate and boreal zones and, given the climate parameters for the species distribution provided in Section 2.1, its range, distribution, and abundance in the UK may not be radically changed under the predicted climate change scenarios.

Section 7 refers to records of flowering of individuals of *G. pratense* in flower in early October 2021 and early November 2022 in northern England. A clearly documented effect of recent climate change are shifts in the phenology of species and ecosystems. While it is well documented that many plants in the UK now flower a month earlier under recent climate warming (Büntgen et al., 2022), little attention has been paid to the finish dates of flowering. While the biology of temperate flowering phenology is complex, and more years of phenological data from a range of locations would be needed as evidence, it is conceivable that extension of the flowering period of *G. pratense* may be driven by climate warming.

Data from the Meteorological Office for 2021 show that in 2021, in every month apart from January and May, the average UK temperature was above average compared with the period 1981–2010. In 2022, up to and including October, in every month the average temperature was above average compared to the period 1991–2020 (Met Office, 2022).

Kreyling and colleagues (Kreyling, Beierkuhnlein, et al., 2008); Kreyling et al., 2010, 2011) examined the impact of five winter soil freeze–thaw cycles (FTCs), including a control, on experimental synthetic temperate grassland and dwarf-shrub communities in Bayreuth, Germany over a period of 3 years. The frequency of soil FTCs is predicted to increase with climate change (Henry, 2008). This may have implications for the structure of ecosystems including plant community composition as FTCs are known to cause nitrogen flushes and to temporally increase N availability and nitrate leaching.

Geranium pratense was included in one of the three synthetic grassland communities under investigation, which also contained two grasses and one other forb (Kreyling, Beierkuhnlein, et al., 2008). The above ground cover (%) of *G. pratense* in the vegetation decreased markedly over the period of the experiment in the FTC manipulations, from *c.* 4% cover at the outset to less than 1% cover at the end of the experiment (Kreyling et al., 2011). However, the authors observed a similar reduction throughout the experiment also in the control treatment.

There are limitations to the conclusions that can be drawn from this experiment on the impact of FTCs on *G. pratense* and its habitats due to the short duration of the experiment and the artificial nature of the grassland. However, an increase in the frequency of FTCs has the potential to impact on the species and the structure of its semi-natural grassland habitats in the longer term. There is therefore a need for long term experiments in semi-natural plant communities plus process-orientated laboratory studies to gain a better understanding of the causal processes involved in the changes observed (Kreyling et al., 2011). The potential impacts of extreme climate events, especially of drought, on the distribution and abundance of *G. pratense* also needs to be considered, although there is some evidence of drought tolerance (see Section 5.3, Kreyling, Wenigmann, et al., 2008).

CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14205.

DATA AVAILABILITY STATEMENT

No data were used in this article.

ORCID

Markus Wagner https://orcid.org/0000-0002-2263-304X
Elizabeth Sullivan https://orcid.org/0000-0002-3477-7681
Irina Tatarenko https://orcid.org/0000-0001-6835-2465
Duncan B. Westbury https://orcid.org/0000-0001-7094-0362
Paul Ashton https://orcid.org/0000-0001-8715-574X

REFERENCES

Abdusalam, A., Maimaitituerxun, R., Hashan, H., & Abdukirim, G. (2021). Pollination adaptations of group-by-group stamen movement in a meadow plant with temporal floral closure. *Plant Diversity, 43*, 308–316. https://doi.org/10.1016/j.pld.2021.04.001

Adenegha, T. (2022). *Multi-scale patterns of genetic differentiation and isolation by distance across the North of England in the grassland species Geranium pratense L. (Meadow Crane's-bill, MRes thesis).* Edge Hill University.

Aedo, C. (2023). *A monograph of the genus Geranium L. (Geraniaceae).* Consejo Superior de Investigaciones Cientficas.

Akdemir, Z. S., Tatli, I. I., Saracoglu, I., Ismailoglu, U. B., Sahin-Erdemli, I., & Calis, I. (2001). Polyphenolic compounds from *Geranium pratense* and their free radical scavenging activities. *Phytochemistry, 56*, 189–193. https://doi.org/10.1016/S0031-9422(00)00367-8

Anonymous. (2022). *Geranium pratense—honey production.* https://ylejbees.com/medonosy/818-geran-lugovaya-medonos?ysclid=l7cxa6sd117933327

Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G., & Jeffcoate, S. (2001). *The millennium atlas of butterflies in Britain and Ireland.* Oxford University Press.

Avery, B. W. (1990). *Soils of the British Isles*. CABI.

Awan, M. S., Shaheen, M. D. H., Khan, R. W. A., Aziz, S., & Habib, T. (2021). Diversity and distribution pattern of alpine vegetation communities from Ratti Gali Lake and its adjacent areas, Kashmir Himalayas, Pakistan. *Pakistan Journal of Botany, 53*, 665–672. https://doi.org/10.30848/PJB2021-2(45)

Baskin, C. C., & Baskin, J. M. (2014). *Seeds: Ecology, biogeography, and evolution of dormancy and germination* (2nd ed.). Academic Press.

Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A. K., Morton, R. D., Smart, S. M., & Memmott, J. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature, 530*, 85–88. https://doi.org/10.1038/nature16532

Beesley, S. (2006). *County Antrim scarce, rare & extinct vascular plant register and checklist of species.* MAGNI publication no. 19. National Museums & Galleries of Northern Ireland.

Bennet-Clark, T. A. (1933). The role of the organic acids in plant metabolism. Part I. *New Phytologist, 32*, 37–71. https://doi.org/10.1111/j.1469-8137.1933.tb06998.x

Benson, R. B. (1952). *Hymenoptera: Symphyta. Handbooks for the Identification of British Insects Vol. 6, Part 2(b).* Royal Entomological Society of London.

Blackman, R. L. (2019). *Aphids on world plants: An online identification and. information guide .* http://www.aphidsonworldsplants.info/

Blackstock, T. H., Rimes, C. A., Stevens, D. P., Jefferson, R. G., Robertson, H. J., Mackintosh, J., & Hopkins, J. J. (1999). The extent of semi-natural grassland communities in lowland England and Wales: A review of conservation surveys 1978–96. *Grass and Forage Science, 54*, 1–18. https://doi.org/10.1046/j.1365-2494.1999.00157.x

Boesewinkel, F. D., & Been, W. (1979). Development of ovule and testa of *Geranium pratense* L. and some other representative of the Geraniaceae. *Acta Botanica Neerlandica, 28*, 335–348. https://doi.org/10.1111/j.1438-8677.1979.tb00357.x

Boob, M., Trucksess, B., Seither, M., Elsäßer, M., Thumm, U., & Lewandowski, I. (2019). Management effects on botanical composition of species-rich meadows within the Natura 2000 network. *Biodiversity and Conservation, 28*, 29–750. https://doi.org/10.1007/s10531-018-01689-1

Borowski, S., Krasiński, Z., & Miłkowski, L. (1967). Food and role of the European bison in forest ecosystems. *Acta Theriologica, 12*, 367–376.

Botta-Dukát, Z., Chytrý, M., Hájková, P., & Havlová, M. (2005). Vegetation of lowland wet meadows along a climatic continentality gradient in Central Europe. *Preslia, 77*, 89–111.

Bradley, J. D., Tremewan, W. G., & Smith, A. (1973). *British Tortricoid moths. Cochlidae and Tortricidae: Tortricinae.* The Ray Society.

Braithwaite, M. E., Ellis, R. W., & Preston, C. D. (2006). *Change in the British flora 1987–2004.* Botanical Society of the British Isles.

British Mycological Society. (2022). Fungal records database of Britain and Ireland. http://frdbi.info/

BSBI. (2023). BSBI distribution database. https://database.bsbi.org

Bundesamt für Naturschutz. (2020). *FloraWeb: Data and information on wild plants and vegetation in Germany.* Species profile–Geranium pratense L.

Büntgen, U., Piermattei, A., Krusic, P. J., Esper, J., Sparks, T., & Crivellaro, A. (2022). Plants in the UK flower a month earlier under recent warming. *Proceedings of the Royal Society Series B: Biological Sciences, 289*, 20212456 . https://doi.org/10.1098/rspb.2021.2456

Burke, Y. D., Stark, M. J., Roach, S. L., Sen, S. E., & Crowell, P. L. (1997). Inhibition of pancreatic cancer growth by the dietary isoprenoids farnesol and geraniol. *Lipids, 32*, 151–156. https://doi.org/10.1007/s11745-997-0019-y

Cape, J. N., Tang, Y. S., van Dijk, N., Love, L., Sutton, M. A., & Palmer, S. C. F. (2004). Concentrations of ammonia and nitrogen dioxide at roadside verges, and their contribution to nitrogen deposition. *Environmental Pollution, 132*, 469–478. https://doi.org/10.1016/j.envpol.2004.05.009

Cathey, H. M. (1990). *USDA plant hardiness zone map.* Miscellaneous publication 1475. U.S. National Arboretum.

Cheffings, C. M., Farrell, L., Dines, T. D., Jones, R. A., Leach, S. J., McKean, D. R., Pearman, D. A., Preston, C. D., Rumsey, F. J., & Taylor, I. (2005). *The vascular plant red data list for Great Britain.* Joint Nature Conservation Committee.

Chytrý, M., Danihelka, J., Kaplan, Z., Wild, J., Holubová, D., Novotný, P., Řezníčková, M., Rohn, M., Dřevojan, P., Grulich, V., Klimešová, J., Lepš, J., Lososová, Z., Pergl, J., Sádlo, J., Šmarda, P., Štěpánková, P., Tichý, L., Axmanová, I., ... Pyšek, P. (2021). Pladias database of the Czech flora and vegetation. *Preslia, 93*, 1–87. https://doi.org/10.23855/preslia.2021.001

Clapham, A. R., Tutin, T. G., & Moore, D. M. (1987). *Flora of the British Isles* (3rd ed.). Cambridge University Press.

Clark, A. T., Turnbull, L. A., Tredennick, A., Allan, E., Harpole, W. S., Mayfield, M. M., Soliveres, S., Barry, K., Eisenhauer, N., de Kroon, H., Rosenbaum, B., Wagg, C., Weigelt, A., Feng, Y., Roscher, C., & Schmid, B. (2020). Predicting species abundances in a grassland biodiversity experiment: Trade-offs between model complexity and generality. *Journal of Ecology, 108*, 774–787. https://doi.org/10.1111/1365-2745.13316

Correns, C. (1907). Zur Kenntnis der Geschlechtsformen polygamer Blütenpflanzen und ihrer Beeinflussbarkeit. *Jahrbücher für Wissenschaftliche Botanik, 44*, 124–173.

Crawley, M. J. (2005). *Flora of Berkshire.* Brambleby Books.

Critchley, C. N. R., Chambers, B. J., Fowbert, J. A., Sanderson, R. A., Bhogal, A., & Rose, S. C. (2002). Association between lowland grassland plant communities and soil properties. *Biological Conservation, 105*, 199–215. https://doi.org/10.1016/S0006-3207(01)00183-5

Cullen, J., Knees, S. G., & Cubey, H. S. (Eds.). (2011). *The European garden flora: A manual for the identification of plants cultivated in Europe, both out-of-doors and under glass. Vol. 3: Angiospemae—Dicotyledons: Resedaceae to Cyrillaceae* (2nd ed.). Cambridge University Press.

Dallmann, A. A. (1933). Quantitative attributes of seeds and fruits. *The North Western Naturalist, 8*, 202–211.

Davies, A. (2002). *The floristic restoration of agriculturally improved grassland* (PhD thesis). University of Sheffield.

Davis, B. N. K. (1973). The effects of mowing on the meadow cranes-bill *Geranium pratense* L., and on the weevil *Zacladus geranii* (Payk.). *Journal of Applied Ecology, 10*, 747–759. https://doi.org/10.2307/2401867

Davison, J., Öpik, M., Daniell, T. J., Moora, M., & Zobel, M. (2011). Arbuscular mycorrhizal fungal communities in plant roots are not random assemblages. *FEMS Microbiology Ecology*, *78*, 103–115. https://doi.org/10.1111/j.1574-6941.2011.01103.x

DBIF. (2020). *Database of nsects and their food plants.* http://dbif.brc.ac.uk/hosts.aspx

Demiyanova, E. I. (2013). The sexual structure of native populations of some dioecious and gynodioecious plants of Okskiy reserve. *Bulletin of Perm University*, *2*, 19–22.

Department of Agriculture, Environment & Rural Affairs. (2005). Northern Ireland species action plan—Meadow cranesbill. https://www.daera-ni.gov.uk/publications/northern-ireland-species-action-plan-meadow-cranesbill

Dierschke, H. (1999). Short survey of Arrhenatheretalia grassland in Germany. *Annali di Botanica*, *57*, 7–14.

Dierschke, H., & Briemle, G. (2002). *Kulturgrasland: Wiesen, Weiden und verwandte Staudenfluren.* Ulmer.

Dines, T. D. (2008). *A vascular plant red data list for Wales.* Plantlife.

Dlussky, G. M., Lavrova, N. V., & Erofeeva, E. A. (2000). Mechanisms of restriction of pollinator range in *Chamaenerion angustifolium* and two *Geranium* species (*G. palustre* and *G. pratense*). *Zhurnal Obshcheĭ Biologii*, *61*, 181–197.

Dolgoshev, V. M. (1948). Flowering calendar of the most important honey plants in the Moscow region . In *Calendar of Russian nature* (Vol. *1*, pp. 136–198). Moscow Society of Naturalists.

Duchoslavová, J., & Herben, T. (2020). Effect of clonal growth form on the relative performance of species in experimental communities over time. *Perspectives in Plant Ecology, Evolution and Systematics*, *44*, 125532 . https://doi.org/10.1016/j.ppees.2020.125532

Dudenhöffer, J., Pufal, G., Roscher, C., & Klein, A. (2016). Plant density can increase invertebrate post dispersal seed predation in an experimental grassland community. *Ecology and Evolution*, *6*, 3796–3807. https://doi.org/10.1002/ece3.2039

Edwards, D., Konyves, K., Lancaster, N., & Dee, R. (2023). *RHS Plant Finder 2023*. Royal Horticultural Society.

Ellenberg, H. (1988). *Vegetation ecology of Central Europe* (4th ed.). Cambridge University Press.

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., & Paulissen, D. (1991). Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, *18*, 1–248.

Ellis, M. B., & Ellis, J. P. (1997). *Microfungi on land plants: An identification handbook* (2nd ed.). Richmond.

Emmet, A. M. (1988). *A field guide to the smaller British Lepidoptera* (2nd ed.). The British Entomological and Natural History Society.

Esfandani-Bozchaloyi, S., Sheidai, M., Keshavarzi, M., & Noormohammadi, Z. (2018). Species identification and population structure analysis in *Geranium* subg. *Geranium* (Geraniaceae). *Hacquetia*, *17*, 235–246. https://doi.org/10.1515/hacq-2017-0007

Falk, S., & Lewington, R. (2016). *Field guide to the bees of Great Britain and Ireland*. Bloomsbury.

Fern, K. (1997). *Plants for a future: Edible and useful plants for a healthier world*. Permanent Publications.

Fitter, A. H., & Peat, H. J. (1994). The ecological flora database. *Journal of Ecology*, *82*, 415–425. https://doi.org/10.2307/2261309

Foster, G., Bennett, J., & Sparks, T. (2017). An assessment of bumblebee (*Bombus* spp) land use and floral preference in UK gardens and allotments cultivated for food. *Urban Ecosystems*, *20*, 425–434. https://doi.org/10.1007/s11252-016-0604-7

French, C. (2020). *A flora of Cornwall*. Wheal Seton Press.

Fuller, R. M. (1987). The changing extent and conservation interest of lowland grasslands in England and Wales: A review of grassland surveys 1930–84. *Biological Conservation*, *40*, 281–300. https://doi.org/10.1016/0006-3207(87)90121-2

Gama-Arachchige, N. S., Baskin, J. M., Geneve, R. L., & Baskin, C. C. (2010). Identification and characterization of the water gap in physically dormant seeds of Geraniaceae, with special reference to *Geranium carolinianum. Annals of Botany*, *105*, 977–990. https://doi.org/10.1093/aob/mcq078

Gams, H. (1924). *Geranium pratense* . In G. Hegi (Ed.), *Illustrierte Flora von Mittel-Europa* (Vol. *4/3*, pp. 1688–1690). J.F. Lehmanns.

Goahr, A. A., Lahloub, M. F., & Niwa, M. (2003). Antibacterial polyphenol from *Erodium glaucophyllum*. *Zeitschrift für Naturforschung C*, *58*, 670–674. https://doi.org/10.1515/znc-2003-9-1013

Godwin, H. (1975). *History of the British flora* (2nd ed.). Cambridge University Press.

Görs, S., & Müller, T. (1969). Beitrag zur Kenntnis der nitrophilen Saumgesellschaften Südwestdeutschlands. *Mitteilungen der Floristisch-Soziologischen Arbeitsgemeinschaft N. F.*, *14*, 153–168.

Górski, T., Górska, K., & Stasiak, H. (2013). Inhibition of seed germination by far red radiation transmitted through leaf canopies. *Polish Journal of Agronomy*, *13*, 10–38.

Grant, K., Kreyling, J., Heilmeir, H., Beierkuhnlein, C., & Jentsch, A. (2014). Extreme weather events and plant–plant interactions: Shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall. *Ecological Research*, *29*, 991–1001. https://doi.org/10.1007/s11284-014-1187-5

Grime, J. P., Hodgson, J., & Hunt, R. (2007). *Comparative plant ecology: A functional approach to common British species* (2nd ed.). Castlepoint Press.

Grime, J. P., Mason, G., Curtis, A. V., Rodman, J., Band, S. R., Mowford, M. A. G., Neal, A. M., & Shaw, S. (1981). A comparative study of germination characteristics in a local flora. *Journal of Ecology*, *69*, 1017–1059. https://doi.org/10.2307/2259651

Gubanov, I. A., Kiseleva, K. V., Novikov, V. S., & Tikhomirov, V. N. (1990). *Meadow herbaceous plants. Biology and conservation*. Agropromizdat.

Hackney, P. (Ed.) (Ed.). (1992). *Stewart & Corry's Flora of the north-east of Ireland* (3rd ed.). Institute of Irish Studies, Queens's University of Belfast.

Harley, J. L., & Harley, E. L. (1987). A check-list of mycorrhiza in the British flora. *New Phytologist (Supplement)*, *105*, 1–102. https://doi.org/10.1111/j.1469-8137.1987.tb00912.x

Henry, H. A. L. (2008). Climate change and soil freezing dynamics: Historical trends and projected changes. *Climatic Change*, *87*, 421–434. https://doi.org/10.1007/s10584-007-9322-8

Hettmann, E., Gleixner, G., & Juchelka, D. (2005). *irm-LC/MS: δ13C analysis of organic acids in plants*. Application Note 30075. Thermo Fisher Scientific.

Hildebrand, F. (1865). Experimente zur Dichogamie und zum Dimorphismus. 1. Dichogamie von *Geranium pratense*. *Botanische Zeitung*, *23*, 1–6.

Hill, M. O. (2012). Local frequency as a key to interpreting species occurrence data when recording effort is not known. *Methods in Ecology and Evolution*, *3*, 195–205. https://doi.org/10.1111/j.2041-210X.2011.00146.x

Hill, M. O., & Carey, P. D. (1997). Prediction of yield in the Rothamsted Park Grass Experiment by Ellenberg indicator values. *Journal of Vegetation Science*, *8*, 579–586. https://doi.org/10.2307/3237210

Hill, M. O., Preston, C. D., & Roy, D. B. (2004). *PLANTATT—Attributes of British and Irish plants: Status, size, life history, geography and habitats*. Centre for Ecology and Hydrology.

Holohan, A. D., Müller, C., & McElwain, J. (2019). Heritable changes in physiological gas exchange traits in response to long-term, moderate free-air carbon dioxide enrichment. *Frontiers in Plant Science*, *10*, 1210 . https://doi.org/10.3389/fpls.2019.01210

Honek, A., & Martinkova, Z. (2007). A field method for quantifying the grazing activity of slugs, with particular reference to *Arion lusitanicus* (Mollusca). *Malacologia*, *49*, 273–281. https://doi.org/10.4002/0076-2997-49.2.273

Houghton, A., Appelhagen, I., & Martin, C. (2021). Natural blues: Structure meets function in anthocyanins. *Plants*, *10*, 726 . https://doi.org/10.3390/plants10040726

Hultén, E., & Fries, M. (1986). *Atlas of North European vascular plants north of the tropic of cancer* (Vol. *II*). Koeltz Scientific Books.

Hundt, R. (1975). Zur anthropogenen Verbreitung und Vergesellschaftung von *Geranium pratense* L. *Vegetatio*, *31*, 23–32. https://doi.org/10.1007/BF00127872

Hundt, R. (1983). Zur Eutrophierung der Wiesenvegetation unter soziologischen, ökologischen, pflanzengeographischen und landwirtschaftlichen Aspekten. *Verhandlungen der Gesellschaft für Ökologie*, *11*, 195–206.

Hutchinson, L., Norrey, J., Lockton, A., & Coulthard, E. (2020). Small areas of wildflower grassland in urban areas support significant species richness and abundance of pollinating insects. *Entomologist's Gazette*, *71*, 103–119. https://doi.org/10.31184/G00138894.712.1724

Iljin, V. S. (1916). Relation of transpiration to assimilation in steppe plants. *Journal of Ecology*, *4*, 65–82. https://doi.org/10.2307/2255326

Irmisch, T. (1874). Beitrag zur Morphologie einiger europäischen *Geranium*-Arten, insbesondere des G. *sanguineum* und G. *tuberosum*. *Botanische Zeitung*, *32*, 545–553.

Jäger, H. J., Schmidt, S. W., Kammann, C., Grunhage, L., Muller, C., & Hanewald, K. (2003). The University of Giessen free-air carbon dioxide enrichment study: Description of the experimental site and of a new enrichment system. *Journal of Applied Botany*, *77*, 117–127.

James, T. J. (2009). *Flora of Hertfordshire*. Hertfordshire Natural History Society.

Janicka, M., Pawluśkiewicz, B., Małuszyńska, E., & Gnatowski, T. (2021). Diversity of the seed material of selected plant species of naturally valuable grassland habitats in terms of the prognosis of introduction success. *Sustainability*, *13*, 13979 . https://doi.org/10.3390/su132413979

Jeiter, J., Hilger, H. H., Smets, E. F., & Weigend, M. (2017). The relationship between nectaries and floral architecture: A case study in Geraniaceae and Hypseocharitaceae. *Annals of Botany*, *120*, 791–803. https://doi.org/10.1093/aob/mcx101

Jentsch, A., Kreyling, J., Elmer, M., Gellesch, E., Glaser, B., Grant, K., Hein, R., Lara, M., Mirzae, H., Nadler, S. E., Nagy, L., Otieno, D., Pritsch, K., Rascher, U., Schädler, M., Schloter, M., Singh, B. K., Stadler, J., Walter, J., … Beierkuhnlein, C. (2011). Climate extremes initiate ecosystem-regulating functions while maintaining productivity. *Journal of Ecology*, *99*, 689–702. https://doi.org/10.1111/j.1365-2745.2011.01817.x

Jiang, L., Liu, Y., He, P. C., Chen, J. Y., Liu, S. X., & Tan, N. (2016). Geraniin ameliorates cisplatin-induced nephrotoxicity in mice. *Free Radical Research*, *50*, 813–819. https://doi.org/10.3109/10715762.2016.1173206

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., van Bodegom, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., … Wirth, C. (2011). TRY—A global database of plant traits. *Global Change Biology*, *17*, 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Khan, N. A., Singhal, V. K., Tantray, Y., Jaryal, R. K., & Gupta, R. C. (2020). A case of intraspecific euploidy (2x, 4x) and secondary chromosomal associations in wild accessions of *Geranium pratense* L. from cold deserts of Ladakh (India). *Nucleus*, *63*, 143–149. https://doi.org/10.1007/s13237-019-00299-8

Killick, J., Perry, R., & Woodell, S. (1998). *The Flora of Oxfordshire*. Pisces.

Kirk, W. D. J., & Howes, F. N. (2012). *Plants for bees. A guide to the plants that benefit the bees of the British Isles*. International Bee Research Association.

Klimešová, J. (2018). *Temperate herbs: An architectural analysis*. Academia.

Klimešová, J., & Klimeš, L. (2019). L. Clo-Pla3—database of clonal growth of plants from Central Europe . http://clopla.butbn.cas.cz

Kornaś, J., & Dubiel, E. (1991a). Land use and vegetation changes in the hay meadows of the Ojcow National Park during the last thirty years . *Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel, Zürich*, *106*, 208–231. Białowieża Geobotanical Station, University of Warsaw.

Kornaś, J., & Dubiel, E. (1991b). Changes of vegetation of the hay-meadows in the Ojców National Park (S. Poland) during the last 30 years . In J. B. Faliński (Ed.), *Vegetation processes as subject of geobotanical maps. Proceedings of XXXIII Symposium of IAVS, Warsaw, April 8–12, 1990. Phytocoenosis 3 (N.S.), Supplementum Cartographiae Geobotanicae* (Vol. *2*, pp. 135–144).

Korolyuk, A. Y., Tishchenko, M. P., & Yamalov, S. (2016). Forest meadows of the west Siberian plain and revision of the order *Carici macrourae–Crepidetalia sibiricae*. *Vegetation of Russia*, *29*, 67–88. https://doi.org/10.31111/vegrus/2016.29.67

Kostrakiewicz-Gieralt, K. (2015). The impact of time of gap origin on microsite conditions and seedling recruitment in Molinetum caeruleae meadows. *International Journal of Conservation Science*, *6*, 111–124.

Kozłowski, J., & Kozłowski, M. (2004). Food preferences of *Deroceras reticulatum*, *Arion lusitanicus* and *Arion rufus* for various medicinal herbs and oilseed rape. *Journal of Plant Protection Research*, *44*, 239–249.

Kraus, G. (1884). Ueber die Wasservertheilung in der Pflanze. *IV. Die Acidität des Zellsaftes*. *Abhandlungen der Naturforschenden Gesellschaft zu Halle*, *16*, 141–205.

Kreyling, J., Beierkuhnlein, C., & Jentsch, A. (2010). Effects of soil freeze–thaw cycles differ between experimental plant communities. *Basic and Applied Ecology*, *11*, 65–75. https://doi.org/10.1016/j.baae.2009.07.008

Kreyling, J., Beierkuhnlein, C., Pritsch, K., Schloter, M., & Jentsch, A. (2008). Recurrent soil freeze–thaw cycles enhance grassland productivity. *New Phytologist*, *177*, 938–945. https://doi.org/10.1111/j.1469-8137.2007.02309.x

Kreyling, J., Jurasinski, G., Grant, K., Retzer, V., Jentsch, A., & Beierkuhnlein, C. (2011). Winter warming pulses affect the development of planted temperate grassland and dwarf-shrub heath communities. *Plant Ecology & Diversity*, *4*, 13–21. https://doi.org/10.1080/17550874.2011.558125

Kreyling, J., Wenigmann, M., Beierkuhnlein, C., & Jentsch, A. (2008). Effects of extreme weather events on plant productivity and tissue die-back are modified by community composition. *Ecosystems*, *11*, 752–763. https://doi.org/10.1007/s10021-008-9157-9

Kumar, P., & Singhal, V. K. (2013). Chromosome number and secondary chromosomal associations in wild populations of *Geranium pratense* L. from the cold deserts of Lahaul-Spiti (India). *Cytology and Genetics*, *47*, 107–114. https://doi.org/10.3103/S0095452713020084

Küpeli, E., Tatli, I. I., Akdemir, Z. S., & Yesilada, E. (2007). Estimation of antinociceptive and anti-inflammatory activity on *Geranium pratense* subsp. *finitimum* and its phenolic compounds. *Journal of Ethnopharmacology*, *114*, 234–240. https://doi.org/10.1016/j.jep.2007.08.005

Larin, M. V., Agababyan, S. M., Rabotnov, T. A., Lyubskaya, A. F., Larina, V. K., & Kasimenko, M. A. (1951). *Forage plants of hayfields and pastures of the USSR* (Vol. *2*). State Publishing House of Agricultural Literature.

Lawton, J. H., & Schroder, D. (1977). Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. *Nature*, *265*, 137–140. https://doi.org/10.1038/265137a0

Leslie, A. C. (2019). *Flora of Cambridgeshire*. RHS Media.

Li, J., Wang, S. R., Yin, J. M., & Pan, L. N. (2013). Geraniin induces apoptotic cell death in human lung adenocarcinoma A549 cells in vitro and in vivo. *Canadian Journal of Physiology and Pharmacology*, *91*, 1016–1024. https://doi.org/10.1139/cjpp-2013-0140

Li, S., Tosens, T., Harley, P. C., Jiang, Y., Kanagendran, A., Grosberg, M., Jaamets, K., & Niinemets, U. (2018). Glandular trichomes as a barrier against atmospheric oxidative stress: Relationships with ozone

uptake, leaf damage and emission of LOX products across a diverse set of species. *Plant, Cell and Environment*, 41, 1263–1277. https://doi.org/10.1111/pce.13128

Lin, S. Y., Wang, C. C., Lu, Y. L., Wu, W. C., & Hou, W. C. (2008). Antioxidant, anti-semicarbazide-sensitive amine oxidase, and anti-hypertensive activities of geraniin isolated from *Phyllanthus urinaria*. *Food and Chemical Toxicology*, 46, 2485–2492. https://doi.org/10.1016/j.fct.2008.04.007

Lloyd, P. S. (1972). The ecological significance of fire in limestone grassland communities of the Derbyshire Dales. *Journal of Ecology*, 56, 811–826. https://doi.org/10.2307/2258108

Lorentzen, S., Roscher, C., Schumacher, J., Schulze, E.-D., & Schmid, B. (2008). Species richness and identity affect the use of aboveground space in experimental grasslands. *Perspectives in Plant Ecology, Evolution and Systematics*, 10, 73–87. https://doi.org/10.1016/j.ppees.2007.12.001

Loudon, J. C. (Ed.) (Ed.). (1832). *Hortus Britannicus—A catalogue of all the plants indigenous, cultivated in, or introduced to Britain*. Longman Rees Orme Brown Green and Longman.

Lousley, J. E. (1969). *Wild flowers of chalk and limestone*. Collins.

Makunina, N. I., & Maltseva, T. V. (2008). Dry valley steppified meadows of the foothills of the Altai-Sayan mountain region . In V. I. Vasilevich, E. P. Gnatyuk, V. V. Gorshkov, V. S. Ipatov, V. Y. Neshataev, I. N. Safronova, V. V. Timofeeva, & T. Yurkovskaya (Eds.), *Fundamental and applied problems of botany at the beginning of the 21st century. Proceedings of the all-Russian conference September 22–27, 2008. Part 5: Geobotany* (pp. 189–194). Russian Botanical Society.

Markham, K. R., Mitchell, K. A., & Boase, M. R. (1997). Malvidin-3-O-glucoside-5-O-(6-acetylglucoside) and its colour manifestation in "Johnson's blue" and other "blue" geraniums. *Phytochemistry*, 45, 417–423. https://doi.org/10.1016/S0031-9422(96)00831-X

Martin, E., Kahraman, A., Dirmenci, T., Bozkurt, H., & Eroglu, H. E. (2022). New chromosomal data and karyological relationships in *Geranium*: Basic number alterations, dysploidy, polyploidy, and karyotype asymmetry. *Brazilian Archives of Biology and Technology*, 65, 1–16. https://doi.org/10.1590/1678-4324-2022210354

Martinková, Z., Honěk, A., & Štolková, J. (1997). The incidence of primary seed dormancy in weed species of The Czech Republic. *Ochrana Rostlin*, 33, 265–279.

Martinková, Z., Skuhrovec, J., Barták, M., Bezděc, J., Bogusch, P., Hadrava, J., Hájek, J., Janšta, P., Jelínek, J., Kubáň, V., & Štys, P. (2015). Role of host plant in determining the insect community associated with the flowers of dicotyledoneous herbaceous plants. *Acta Societatis Zoologicae Bohemicae*, 79, 95–104.

Mbikay, M., & Chrétien, M. (2022). Isoquercetin as an anti-covid-19 medication: A potential to realize. *Frontiers in Pharmacology*, 13, 830205 . https://doi.org/10.3389/fphar.2022.830205

Meisert, A. (2002). Physical dormancy in Geraniaceae seeds. *Seed Science Research*, 12, 121–128. https://doi.org/10.1079/SSR2002104

Meisert, A., Schulz, D., & Lehmann, H. (1999). Structural features underlying hardseededness in Geraniaceae. *Plant Biology*, 1, 311–314. https://doi.org/10.1111/j.1438-8677.1999.tb00257.x

Met Office. (2018). *UK climate projections 2018 (UKCP18)*. https://www.metoffice.gov.uk/research/approach/collaboration/ukcp/index

Met Office. (2022). *UK climate maps and data*. https://www.metoffice.gov.uk/research/climate/maps-and-data

Metzger, M. J., Bunce, R. G. H., Jongman, R. H. G., Mücher, C. A., & Watkins, J. W. (2005). A climatic stratification of the environment of Europe. *Global Ecology and Biogeography*, 14, 549–563. https://doi.org/10.1111/j.1466-822X.2005.00190.x

Michalski, S. G., & Durka, W. (2012). Assessment of provenance delineation by genetic differentiation patterns and estimates of gene flow in the common grassland plant *Geranium pratense*. *Conservation Genetics*, 13, 581–592. https://doi.org/10.1007/s10592-011-0309-7

Miller, D. M. (2002). The taxonomy of *Geranium* species and cultivars, their origins and growth in the wild . In M. Lis-Balchin (Ed.), *Geranium and Pelargonium: The genera Geranium and Pelargonium* (pp. 11–19). Taylor & Francis.

Moghadam, N. S., Mehrvarz, S. S., Ahamadian, A., & Shavvon, R. S. (2015). Micromorphology of fruits and seeds of Iranian *Geranium* (Geraniaceae), and its systematic significance. *Nordic Journal of Botany*, 33, 673–683. https://doi.org/10.1111/njb.00859

Moora, M., Daniel, T., Kalle, H., Liira, J., Püssa, K., Roosaluste, E., Öpik, M., Wheatley, R., & Zobel, M. (2007). Spatial pattern and species richness of boreonemoral forest understorey and its determinants—A comparison of differently managed forests. *Forest Ecology & Management*, 250, 64–70. https://doi.org/10.1016/j.foreco.2007.03.010

Morris, M. G. (2002). *True weevils (part I) coleoptera: Curculionidae (subfamilies raymondionyminae to smicronychinae). Handbooks for the identification of British insects Vol. V part 17b*. Royal Entomological Society.

Morris, M. G. (2008). *True weevils (part II) coleoptera: Curculionidae, ceutorhynchinae. Handbooks for the identification of British insects Vol. V part 17c*. Royal Entomological Society.

Mułenko, W., Bacigálová, K., Wołczańska, A., Świderska, U., & Mamczarz, M. (2008). Parasitic microfungi of the Tatra Mountains: 5. Plasmopara representatives on the species of *Geranium*. *Biologia*, 63, 302–306. https://doi.org/10.2478/s11756-008-0049-4

Muller, F. M. (1978). *Seedlings of the north-western European lowland*. Dr W. Junk Publishers.

Müller, T. (1974). Einige Bemerkungen zu den Saumgesellschaften . In W. H. Sommer & R. Tüxen (Eds.), *Tatsachen und probleme der grenzen in der vegetation* (pp. 189–194). Cramer.

Narantuya, N. (2016). The natural and human impacts on coenopopulation structure of *Geranium pratense* L. in meadow community of Mongolia . In A. I. Shmakov & T. M. Kopitina (Eds.), *Problems of botany of southern Siberia and Mongolia. Proceedings of the 15th international Scientific and Practical Conference (Barnaul, May 23–26, 2016)* (pp. 75–77). Publishing House of Altai State University.

Nichols, R. N., Goulson, D., & Holland, J. M. (2019). The best wildflowers for wild bees. *Journal of Insect Conservation*, 23, 819–830. https://doi.org/10.1007/s10841-019-00180-8

Öpik, M., Vanatoa, A., Vanatoa, E., Moora, M., Davison, J., Kalwij, J. M., Reier, Ü., & Zobel, M. (2010). The online database MaarjAM reveals global and ecosystemic distribution patterns in arbuscular mycorrhizal fungi (Glomeromycota). *New Phytologist*, 188, 223–241. https://doi.org/10.1111/j.1469-8137.2010.03334.x

Öz Aydın, S., Dirmenci, T., Tümen, G., & Baser, K. H. C. (2006). Plants used as analgesic in folk medicine of Turkey . In S. F. Ertug (Ed.), *Proceedings of the IVth International Congress of Ethnobotany (ICEB 2005)* (pp. 167–171). Ege Yayinlari.

Pandey, M. R. (2007). Use of medicinal plants in traditional Tibetan therapy system in upper mustang, Nepal. *Our Nature*, 4, 69–82. https://doi.org/10.3126/on.v4i1.505

Parinova, T. A., Nakvasina, E. N., & Sidorova, O. V. (2013). *Meadows of the Island floodplain in the lower Northern Dvina*. Northern Arctic Federal University.

Parinova, T. A., Volkov, A. G., & Popova, A. A. (2018). Microscale heterogeneity of floodplain meadows (using the example of the delta of the Northern Dvina river). *Contemporary Problems of Ecology*, 11, 35–44.

Pattnaik, S., Subramanyam, V. R., Bapaji, M., & Kole, C. R. (1997). Antibacterial and antifungal activity of aromatic constituents of essential oils. *Microbios*, 89, 39–46.

Pearman, D. A. (2017). *The discovery of the native flora of Britain & Ireland*. Botanical Society of Britain & Ireland.

Peat, H. J., & Fitter, A. H. (1994). A comparative study of the distribution and density of stomata in the British flora. *Biological Journal*

of the Linnean Society, *52*, 377–393. https://doi.org/10.1111/j.1095-8312.1994.tb00999.x

Perring, F. H., & Walters, S. M. (Eds.) (Eds.). (1962). *Atlas of the British Flora*. Thomas Nelson & Sons.

Peterken, G. F. (2008). *Wye Valley*. Harper Collins.

Pierce, S., Negreiros, D., Cerabolini, B. E. L., Kattge, J., Diaz, S., Kleyer, M., Shipley, B., Wright, S. J., Soudzilovskaia, N. A., Onipchenko, V. G., van Bodegom, P. M., Frenette-Dussault, C., Weiher, E., Pinho, B. X., Cornellissen, J. H. C., Grime, J. P., Thompson, K., Hunt, R., Wilson, P. J., … Tampucci, D. (2017). A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology*, *31*, 444–457. https://doi.org/10.1111/1365-2435.12722

Poland, J., & Clement, E. (2020). *The vegetative key to the British flora* (2nd ed.). Hobbs the Printers Ltd.

Poschlod, P., & Jordan, S. (1992). Wiederbesiedlung eines aufgeforsteten Kalkmagerrasenstandortes nach Rodung. *Zeitschrift für Ökologe und Naturschutz*, *1*, 119–139.

Preston, C. D., & Hill, M. O. (1997). The geographical relationships of British and Irish vascular plants. *Botanical Journal of the Linnean Society*, *124*, 1–120. https://doi.org/10.1111/j.1095-8339.1997.tb01785.x

Preston, C. D., Pearman, D. A., & Dines, T. D. (2002). *New atlas of the British and Irish Flora*. Oxford University Press.

Proctor, M. C. F., Yeo, P., & Lack, A. (1996). *The natural history of pollination*. Collins New Naturalist Library No. 93. Harper Collins.

Rabotnov, T. A. (1951). Live seeds in the soils of the meadows of the Oka river floodplain (preliminary note). *Forage Production*, *3*, 111–119.

Rabotnov, T. A. (1958). On a methodology for studying germinating seeds in meadow soils. *Russian Botanical Journal*, *43*, 1572–1581.

Ramensky, L. G., Tsatsenkin, I. A., Chizhikov, O. N., & Antipin, N. A. (1956). *Ecological evaluation of pasture and fodder lands by the vegetation cover*. Selkhozgiz.

Razarenova, K. N. (2013). *Pharmacognostic study of some species of the genus Geranium L* (PhD thesis). Saint Petersburg State University.

Razarenova, K. N., Zakharova, A. M., Protasova, I. D., & Zhokhova, E. V. (2012). Amino acid composition of the aerial parts of *Geranium pratense* L., *Geranium sylvaticum* L., *Geranium palustre* L. *Butlerov Communications*, *31*, 73–78.

Redfern, M., & Shirley, P. (2011). *British plant galls: Identification of galls on plants and fungi* (2nd ed., Occasional Publication No. 125.). Field Studies Council.

Redhead, J. W., Coombes, C. F., Dean, H. J., Dyer, R., Oliver, T. H., Pocock, M. J. O., Rorke, S. L., Vanbergen, A. J., Woodcock, B. A., & Pywell, R. F. (2018). *Plant-pollinator interactions database for construction of potential networks*. NERC Environmental Information Data Centre. https://doi.org/10.5285/6d8d5cb5-bd54-4da7-903a-15bd4bbd531b

Rich, T. C. G., & Karran, A. B. (2006). Floristic changes in the British Isles: Comparison of techniques for assessing changes in frequency of plants with time. *Botanical Journal of the Linnean Society*, *152*, 279–301. https://doi.org/10.1111/j.1095-8339.2006.00574.x

Ridley, H. N. (1930). *The dispersal of plants throughout the world*. Reeve.

Roberts, H. A., & Boddrell, J. E. (1985). Seed survival and seasonal emergence in some species of *Geranium*, *Ranunculus* and *Rumex*. *Annals of Applied Biology*, *107*, 231–238. https://doi.org/10.1111/j.1744-7348.1985.tb01566.x

Rodríguez-Rojo, M. P., Jiménez-Alfaro, B., Jandt, U., Bruelheide, H., Rodwell, J. S., Schaminée, J. H. J., Perrin, P. M., Kacki, Z., Willner, W., Fernández-González, F., & Chytrý, M. (2017). Diversity of lowland hay meadows and pastures in Western and Central Europe. *Applied Vegetation Science*, *20*, 702–719. https://doi.org/10.1111/avsc.12326

Rodwell, J. S. (Ed.). (1992). *Grasslands and montane communities. British plant communities* (Vol. *3*). Cambridge University Press.

Rodwell, J. S. (Ed.). (2000). *Maritime communities and vegetation of open habitats. British plant vommunities* (Vol. *5*). Cambridge University Press.

Rodwell, J. S., Dring, J. C., Averis, A. B. G., Proctor, M. C. F., Malloch, A. J. C., Schaminee, J. H. J., & Dargie, T. C. D. (2000). *Review of coverage of the National Vegetation Classification*. JNCC report no. 302. Joint Nature Conservation Committee.

Roeder, A., Schweingruber, F. H., Fischer, M., & Roscher, C. (2017). Growth ring analysis of multiple dicotyledonous herb species—A novel community-wide approach. *Basic and Applied Ecology*, *21*, 23–33. https://doi.org/10.1016/j.baae.2017.05.001

Rowell, T. A., & Robertson, H. J. (1994). *The grassland database: VEGAN version 4.0 supplement to the version 3.0 manual*. English Nature Research Reports No 113. English Nature.

Salisbury, E. (1952). *Downs and dunes, their plant life and its environment*. Bell & Sons.

Salisbury, E. J. (1942). *The reproductive capacity of plants*. Bell & Sons.

Schinkel, C. C. F., Kirchheimer, B., Dellinger, A. S., Klatt, S., Winkler, M., Dullinger, S., & Hörandl, E. (2016). Correlations of polyploidy and apomixis with elevation and associated environmental gradients in an alpine plant. *AoB Plants*, *8*, plw064 . https://doi.org/10.1093/aobpla/plw064

Sell, P., & Murrell, G. (2009). *Flora of Great Britain and Ireland* (Vol. *3*). Cambridge University Press.

Sergievskaya, L. P. (1935). Family Geraniaceae . In P. N. Krylov (Ed.), *Flora of Western Siberia* (Vol. *5*, pp. 1819–1838). Krasnoye Znamya.

Shevyrnogov, A. P., Kononova, N. A., Volkova, A. I., Botvich, I. Y., & Pisman, T. I. (2021). A study of seasonal dynamics of herbaceous plant communities in Khakassia using ground-based and satellite data. *IOP Conference Series: Earth & Environmental Science*, *677*, 022072 . https://doi.org/10.1088/1755-1315/677/2/022072

Shi, B., Khayatnezhad, M., & Shakoor, A. (2021). The interacting effects of genetic variation in *Geranium* subg. *Geranium* (Geraniaceae) using scot molecular markers. *Caryologia*, *74*, 141–150. https://doi.org/10.36253/caryologia-1079

Sinclair, M., & Hutchins, D. (2009). *Aphthona pallida* (Bach, 1856) (Chrysomelidae) is a British species. *The Coleopterist*, *18*, 155–157.

Sinker, C. A., Packham, J. R., Trueman, I. C., Oswald, P. H., Perring, F. H., & Prestwood, W. V. (1991). *Ecological flora of the Shropshire region*. Shropshire Wildlife Trust.

Slavík, B. (1996). Verbreitung von *Geranium*-Arten (subgen. *Geranium*) in Tschechien. *Preslia*, *68*, 305–321.

Smith, R. S., & Jones, L. P. (1991). The phenology of mesotrophic grassland in the Pennine dales, Northern England: Historic hay cutting dates, vegetation variation and plant species phenologies. *Journal of Applied Ecology*, *28*, 42–59. https://doi.org/10.2307/2404112

Sood, S. K., Nath, R., & Kalia, D. C. (2001). *Ethnobotany of cold desert tribes of Lahaul-Spiti (north west Himalaya)*. Deep Publications.

Stace, C. (2019). *New Flora of the British Isles* (4th ed.). C&M Floristics.

Stace, C. A., Preston, C. D., & Pearman, D. A. (2015). *The hybrid flora of the British Isles*. Botanical Society of Britain & Ireland.

Stevens, D. P., Smith, S. L. N., Blackstock, T. H., Bosanquet, S. D. S., & Stevens, J. P. (2010). *Grasslands of Wales: A survey of lowland species-rich grasslands, 1987–2004*. University of Wales Press.

Stroh, P. A., Humphrey, T. A., Burkmar, R. J., Pescott, O. L., Roy, D. B., & Walker, K. J. (2023). BSBI online plant atlas 2020 . https://plantatlas2020.org/atlas

Stroh, P. A., Leach, S. J., August, T. A., Walker, K. J., Pearman, D. A., Rumsey, F. J., Harrower, C. A., Fay, M. F., Martin, J. P., Pankhurst, T., Preston, C. D., & Taylor, I. (2014). *A vascular plant Red List for England*. Botanical Society for Britain and Ireland.

Stroh, P. A., Walker, K. J., Humphrey, T. A., Pescott, O. L., & Burkmar, R. J. (2023). *Atlas 2020: Mapping changes in the distribution of the British and Irish flora*. Princeton University Press.

Stroh, P. A., Walker, K. J., Smith, S. L. N., Jefferson, R. G., Pinches, C. E., & Blackstock, T. H. (2019). *Grassland plants of the British and Irish lowlands. Ecology, threats and management*. Botanical Society for Britain and Ireland.

Sugorkina, N. S. (1995). *Geranium pratense* L. In V. N. Pavlov & V. N. Tikhomirov (Eds.), *Biological flora of the Moscow region* (Vol. 10, pp. 135–145). Poliex.

Sullivan, E. R. (2018). *Long-term change and genetic connectivity in the vegetation of mesotrophic semi-natural grasslands in the UK* (PhD thesis). Edge Hill University.

Švamberková, E., Vítová, A., & Lepš, J. (2017). The role of biotic interactions in plant community assembly: What is the community species pool? *Acta Oecologica*, *85*, 150–156. https://doi.org/10.1016/j.actao.2017.10.011

Świerkosz, K., Dajdok, Z., & Szczęśniak, E. (2002). The association *Geranio phaei-urticetum dioicae* in Southwest Poland. *Polish Botanical Journal*, *47*, 1–14. https://doi.org/10.6084/M9.FIGSHARE.92591

Tallowin, J. R. B. (1996). Effects of inorganic fertilisers on flower-rich hay meadows: A review using a case study on the Somerset Levels, UK. *Grassland and Forage Abstracts*, *66*, 147–152.

The World Flora Online. (2022). Geranium L. http://www.worldfloraonline.org/taxon/wfo-4000015557

Thomas, M., & Beevers, H. (1949). Physiological studies on acid metabolism in green plants. II. Evidence of CO_2 fixation in *Bryophyllum* and the study of diurnal variation of acidity in this genus. *New Phytologist*, *48*, 421–447. https://doi.org/10.1111/j.1469-8137.1949.tb05134.x

Tichý, L., Axmanová, I., Dengler, J., Guarino, R., Jansen, F., Midolo, G., Nobis, M. P., van Meerbek, K., Aćić, S., Attorre, F., Bergmeier, E., Biurrun, I., Bonari, G., Bruelheide, H., Campos, J. A., Čarni, A., Chiarucci, A., Ćuk, M., Ćušterevska, R., … Chytrý, M. (2023). Ellenberg-type indicator values for European vascular plant species. *Journal of Vegetation Science*, *34*, e13168. https://doi.org/10.1111/jvs.1316

Tischler, G. (1935). Die Bedeutung der Polyploidie für die Verbreitung der Angiospermen, erläutert an den Arten Schleswig-Holsteins, mit Ausblicken auf andere Flora-Gebiete. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, *67*, 1–36.

Tjebbes, K. (1928). The chromosome numbers of some flowering plants. *Hereditas*, *10*, 328–332. https://doi.org/10.1111/j.1601-5223.1928.tb02479.x

Tokarski, M. (1972). Morphological and taxonomical analysis of fruits and seeds of the European and Caucasian species of genus *Geranium* L. *Monographiae Botanicae*, *36*, 5–113. https://doi.org/10.5586/mb.1972.003

Troshkina, V. I. (2016). On the species status of *Geranium sergievskajae* (Peschkova) Troshkina (Geraniaceae). *Novitates Systematicae Plantarum Vascularium*, *47*, 31–39. https://doi.org/10.31111/novitates/2016.47.31

Troshkina, V. I. (2018). *The genus Geranium L. (Geraniaceae Juss.) in the flora of the Altai mountain country: Systematics, palynomorphology, chorology* (PhD thesis). Novosibirsk State University.

Truscott, A. M., Palmer, S. C. F., McGowan, G. M., Cape, J. N., & Smart, S. (2005). Vegetation composition of roadside verges in Scotland: The effects of nitrogen deposition, disturbance and management. *Environmental Pollution*, *136*, 109–118. https://doi.org/10.1016/j.envpol.2004.12.009

Tyler, T., Herbertsson, L., Olofsson, H., & Olsson, P. A. (2020). Ecological indicator and traits values for Swedish vascular plants. *Ecological Indicators*, *120*, 106923. https://doi.org/10.1016/j.ecolind.2020.106923

Uibopuu, A., Moora, M., Öpik, M., & Zobel, M. (2012). Temperate forest understory species performance is altered by local arbuscular mycorrhizal fungal communities from stands of different successional stages. *Plant and Soil*, *356*, 331–339. https://doi.org/10.1007/s11104-011-1116-0

Ullman, I., & Heindl, B. (1989). Geographical and ecological differentiation of roadside vegetation in temperate Europe. *Botanica Acta*, *102*, 261–269. https://doi.org/10.1111/j.1438-8677.1989.tb00103.x

Ushiki, J., Hayakawa, Y., & Tadano, T. (1996). Medicinal plants for suppressing soil-borne plant diseases. I. Screening for medicinal plants with antimicrobial activity in roots. *Soil Science and Plant Nutrition*, *42*, 423–426.

Van Assche, J. A., & Vandelook, F. E. A. (2006). Germination ecology of eleven species of Geraniaceae and Malvaceae, with special reference to the effects of drying seeds. *Seed Science Research*, *16*, 283–290. https://doi.org/10.1017/SSR2006255

van Kleunen, M., Pyšek, P., Dawson, W., Essl, F., Kreft, H., Pergl, J., Weigelt, P., Stein, A., Dullinger, S., König, C., Lenzner, B., Maurel, N., Moser, D., Seebens, H., Kartesz, J., Nishino, M., Aleksanyan, A., Ansong, M., Antonova, L. A., … Winter, M. (2019). The Global Naturalized Alien Flora (GloNAF) database. *Ecology*, *100*, 1–2. https://doi.org/10.1002/ecy.2542

Vangansbeke, P., Máliš, F., Hédl, R., Chudomelová, M., Vild, O., Wulf, M., Jahn, U., Welk, E., Rodríguez-Sánchez, F., & De Frenne, P. (2021). ClimPlant: Realized climatic niches of vascular plants in European forest understoreys. *Global Ecology and Biogeography*, *30*, 1183–1190. https://doi.org/10.1111/geb.13303

Vekemans, X., & Hardy, O. J. (2004). New insights from fine-scale spatial genetic structure analyses in plant populations. *Molecular Ecology*, *13*, 921–935. https://doi.org/10.1046/j.1365-294X.2004.02076.x

Venjakob, C., Ruedenauer, F. A., Klein, A. M., & Leonhardt, S. D. (2022). Variation in nectar quality across 34 grassland plant species. *Plant Biology*, *24*, 134–144. https://doi.org/10.1111/plb.13343

Wagner, M., Kahmen, A., Schlumprecht, H., Audorff, V., Perner, J., Buchmann, N., & Weisser, W. W. (2007). Prediction of herbage yield in grassland: How well do Ellenberg N-values perform? *Applied Vegetation Science*, *10*, 15–24. https://doi.org/10.1111/j.1654-109X.2007.tb00499.x

Wagner, M., Poschlod, P., & Setchfield, R. P. (2003). Soil seed banks in managed and abandoned semi-natural meadows in Soomaa National Park, Estonia. *Annales Botanici Fennici*, *40*, 87–100.

Wahlstrøm, R. (1978). *Geranium pratense* —A species new to northern Norway. *Blyttia*, *36*, 91–94.

Walker, K. J. (2018). *Vascular plant 'axiophyte' scores for Great Britain, derived from the assessments of the vice-county recorders of the Botanical Society of Britain and Ireland (May 2016)*. NERC Environmental Information Data Centre. (Dataset). https://doi.org/10.5285/af2ac4af-12c6-4152-8ed7-e886ed19622b

Wallace, H., & Prosser, M. (2017). *A review of the National Vegetation Classification for the Calthion group of plant communities in England and Wales*. Joint Publication JP021. Natural England.

Ward, L. K., & Spalding, D. F. (1993). Phytophagous British insects and mites and their food-plant families: Total numbers and polyphagy. *Biological Journal of the Linnean Society*, *49*, 257–276. https://doi.org/10.1111/j.1095-8312.1993.tb00905.x

Webb, J., Heaver, D., Lott, D., Dean, H. J., van Breda, J., Curson, J., Harvey, M. C., Gurney, M., Roy, D. B., van Breda, A., Drake, M., Alexander, K. N. A., & Foster, G. (2018). *Pantheon—Database version 3.7.6* . https://www.brc.ac.uk/pantheon/

Winter, K., & Smith, A. C. (2022). CAM photosynthesis: The acid test. *New Phytologist*, *233*, 599–609. https://doi.org/10.1111/nph.17790

Wyse Jackson, M., FitzPatrick, Ú., Cole, E., Jebb, M., McFerran, D., Sheehy Skeffington, M., & Wright, M. (2016). *Ireland red list No. 10: Vascular plants*. National Parks and Wildlife Service, Department of Arts, Heritage, Regional, Rural and Gaeltacht Affairs.

Yang, C. M., Cheng, H. Y., Lin, T. C., Chiang, L. C., & Lin, C. C. (2007). The in vitro activity of geraniin and 1,3,4,6-tetra-O-galloyl-beta-D-glucose isolated from *Phyllanthus urinaria* against herpes simplex virus type 1 and type 2 infection. *Journal of Ethnopharmacology*, *110*, 555–558. https://doi.org/10.1016/j.jep.2006.09.039

Yeo, P. F. (1984). Fruit-discharge-type in *Geranium* (Geraniaceae): Its use in classification and its evolutionary implications. *Botanical Journal of the Linnean Society*, *89*, 1–36. https://doi.org/10.1111/j.1095-8339.1984.tb00998.x

Yeo, P. F. (2001). *Hardy geraniums* (2nd ed.). B.T. Batsford.

Yoshida, K., Mori, M., & Kondo, T. (2009). Blue flower color development by anthocyanins: From chemical structure to cell physiology. *Natural Product Reports*, *26*, 884–915. https://doi.org/10.1039/b800165k

Zhou, J., Xie, G., & Yan, X. (2011). *Encyclopedia of traditional Chinese medicines—Molecular structures, pharmacological activities, natural sources and applications: Isolated compounds (T-Z), references, TCM plants and congeners* (Vol. 5). Springer.

Ziron, C. (2000). *Zum Keimverhalten ausgewählter Plantaginetea majoris- und Molinio-Arrhenatheretea-Arten* (PhD thesis). Justus Liebig University Giessen.