Biological Flora of the British Isles: *Salvia pratensis* 

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

2. *Salvia pratensis* is an erect, rosette-forming, perennial herb with a broad native distribution covering much of Europe—from the British Isles, Spain and Morocco in the west, across Europe into Asia, as far east as the Urals. In the British Isles, the species is nationally scarce, confined to a few south- to west-facing sites with calcareous soils in Southern England and one site in Wales. It is predominately found in unimproved pasture, hay meadows and grassy verges, but can occur on the fringes of scrub or woodland. Although the species is abundant in central Europe, changes to land management since the mid-20th century have resulted in fragmented and threatened populations in several European countries. It is cultivated as an ornamental, as is *S. × sylvestris*, the hybrid with *S. nemorosa*.

3. Populations are typically gynodioecious, having both female (male-sterile) and hermaphrodite individuals at variable proportions. The species has a mixed mating system and is self-compatible via insect pollination, but predominantly outcrosses. Honeybees and bumblebees are abundant pollinators, but a diverse range of bee species and other insect species visit *S. pratensis* flowers. Inbreeding depression has been documented, presenting a conservation concern for small, fragmented populations.

4. The species is the focus of conservation efforts and has been reintroduced to sites where it had become locally extinct in Britain. To sustain favourable habitat, site management should maintain low soil nutrient levels, and prevent scrub encroachment and the dominance of coarse grasses. The removal of sward by hay cutting or grazing after plants have flowered and set seed is advised, in addition
Meadow Clary (Meadow Sage, Saets y Waun). Lamiaceae, subfamily Nepetoideae, tribe Mentheae, subgenus Scarea, sect. Plethiosphace. Salvia pratensis L. (S. bertolonii Vis.) is an erect, gynodioecious perennial herb with a basal rosette and persistent deep tap root. Basal leaves simple, 7–15 cm long, ovate or ovate-oblong, apex obtuse, base cordate; margins crenate or doubly dentate, 25–35 obtuse teeth per side. Petiole to 15 cm, hairy, flat, narrowly winged. Lamina rugose with reticulate venation; dark green above with a pale midrib, glabrous to minutely hairy; paler beneath with sparse long hairs on veins. Flowering stems usually 1–5, rarely up to 50, erect, 30–100 cm tall, quadrangular, pale green, with long retrorse hairs, glandular on upper parts and simple eglandular lower down. Stem leaves in opposite pairs, sessile, up to 15–cm long lower down, reducing in size up the stem. Leaves weakly scented when rubbed. Inflorescence a terminal verticillaster, spicate or 1-branched, lax and sticky. Verticils 2–50 per inflorescence, each with four to six strongly zygomorphic flowers with c. 2 mm glandular-hairy pedicels. Each verticil subtended by two ovate bracts, tip acuminate, often reflexed, shorter than or similar length to the calyx, green often with hints of violet. Calyx 7–11 mm, green, crimson-tipped, campanulate, upper lip three-lobed, lower lip two-lobed, with long glandular and short eglandular hairs. Corolla bright blue-violet, rarely white or pink, three times the calyx length. Hermaphrodite (male-fertile) flowers 15–30 mm, female (male-sterile) flowers c. 10 mm. The relative proportions of the two flower types vary among populations (see Section 8.1). Corolla fused, upper lip hood-shaped (semi-circular and laterally compressed) and arching, lower lip three-lobed with glandular hairs on the outer surface. Each flower with a single, long-exserted, shortly branched style, following the curve of the upper corolla lip. Hermaphrodite flowers with two stamens, each with two thecae separated by an elongate connective. The thecae are held beneath the upper lip of the corolla, connected by a filament that acts as a lever mechanism in pollination. Fruit a schizocarp, each with four nutlets at the base of a persistent calyx. Nutlets brown, obovoid, smooth, c. 2 mm.

Salvia pratensis is an extremely variable species, most notably in corolla dimensions (Hedge, 1972). Four subspecies are accepted by The World Checklist of Vascular Plants database (WCVP, 2020): Salvia pratensis subsp. haematodes (L.) Arcang. (native to Italy and Crete); Salvia pratensis subsp. laciniosa (Jord.) Briq. (native to France); Salvia pratensis subsp. pozeugensis (Watzl) Diklic (native to the N.W. Balkan Peninsula); and Salvia pratensis subsp. pratensis (spanning the whole native range of the species; POWO, 2019). However, no infraspecific taxa are accepted by Flora Europaea (Hedge, 1972), nor by Stace (2019).

Wide intraspecific variation, including flower polymorphism due to gynodioecy, has contributed to many taxonomic inconsistencies for S. pratensis and related taxa. These inconsistencies have been compounded by hybridisation between some species of Salvia sect. Plethiosphace (Hedge, 1972; Scheel, 1930), Salvia bertolonii Vis. has been recognised at species level, and by others, at subspecies rank within S. pratensis (subsp. bertolonii (Vis.) Soó); however, many others consider it synonymous with typical S. pratensis (Balant et al., 2019; Hedge, 1972; WCVP, 2020). Salvia dumentorum Andrz. ex Besser is often recognised as a distinct species (WCVP, 2020), having narrower, oblong or cordate-oblong leaves and smaller corollas on hermaphrodite flowers than S. pratensis (Nachychko et al., 2017), but some believe it to be better placed within S. pratensis (Hedge, 1972). Salvia dumentorum, which has a native range spanning Central Europe to Central Asia (Nachychko et al., 2017), is not covered within this account.

Salvia pratensis is cultivated widely as a garden ornamental and the species’ natural morphological variation has been exploited for horticultural selection and breeding. Fourteen cultivated taxon names are accepted or tentatively accepted by the Royal Horticultural Society’s Horticultural Database (Royal Horticultural Society, 2020). Of these, S. pratensis ‘Indigo’ is most widely available in the UK nursery trade (Cubey, 2020). Corolla colour is particularly variable within cultivated material, with some cultivars being known for their pink or white corollas (Compton, 2011).

Salvia pratensis is generally considered native to the British Isles (Rich et al., 1999; Sell & Murrell, 2009). However, its relatively late first recording in 1696 and the presence of many populations close to ancient roads and trackways do not exclude the possibility of it being an ancient introduction (King, 2004; Preston et al., 2002).

1 GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

Salvia pratensis has been historically recorded in 152 hectares throughout England and Wales (Preston et al., 2002). These records are only considered native where they occur on dry, calcareous, unimproved grasslands subject to at least some disturbance, and/or where the species has been long-recorded (Lousley, 1950; Rich et al., 1999; Scott, 1989). On this basis, a maximum of 37 hectares can be assumed native or probably native. This represents under 1% of all hectares in the British Isles, comprising 36 in Great Britain and one reputed in the Channel Islands in Alderney (Preston et al., 2002). However, the origin of several populations is disputed and Rich

| K E Y W O R D S |
|----------------|
| climatic limitation, communities, conservation, geographical and altitudinal distribution, germination, gynodioecious, management, reproductive biology |

to maintaining a degree of disturbance to provide bare patches of soil for seedling recruitment.
et al. (1999) suggest a lower value of 32 native hectads. Discrepancy between these figures is due to difficulty in ascertaining the true origin of the populations from records alone. All other hectad records (Figure 1) are naturalised sites resulting from the escape from garden cultivation, or introduction via grass seed contaminants (Rich et al., 1999). Rich et al. (1999) make particular reference to the late

**FIGURE 1** The distribution of *Salvia pratensis* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. Mapped by Colin Harrower, Biological Records Centre, Centre for Ecology and Hydrology, mainly from records collected by members of the Botanical Society of the British Isles, using Dr A. Morton’s DMAP software.
The species is considered native in 10 vice-counties across Central and Southern Britain (Table 1), including East and West Kent, Oxfordshire, West Gloucestershire, Buckinghamshire, South Wiltshire, Surrey and Berkshire (Druce, 1886, 1897, 1926; Grose, 1957; Hanbury & Marshall, 1899; Riddelsdell et al., 1948; Salmon, 1931). In addition to this, West Sussex and Monmouthshire contain populations which, based on the substrata, are most likely native (Rich et al., 1999; Wade, 1970), and possibly Middlesex from seeds washed down the Thames (Rich, 2000). The Cotswolds, particularly the vice-county of Oxfordshire, forms the stronghold for the species in Britain, where around 90% of British populations are found. In almost all of the vice-counties, at least one population was rerecorded up to 2003, with the exception of Berkshire where no populations have been recorded since 1955 (King, 2004; Rich et al., 1999).

Salvia pratensis belongs to the Temperate Element of the European flora (Preston & Hill, 1997). The species has a broad native distribution throughout Europe (Figure 2). The southern edge of the species’ native global distribution is Morocco, stretching across the Pyrenees to Turkey and across the Urals in Western Russia. The northern limit of the species’ native range is reached in the British Isles and the Netherlands in the west, across Germany and Poland, to the Baltic States and North Western Russia in the east (Hedge, 1972; Wigginton, 1999). Outlying and isolated occurrences are found in Sweden, Denmark and Finland where the species is naturalised (Gärdenfors, 2005). It has also been introduced to the United States of America, where it is naturalised in several states and included on noxious weed lists for 46 states (USDA National Plant Data Team, 2020).

In central and eastern Europe, S. pratensis can be found in abundance on roadside verges, in dry pastures and unimproved hay meadows (Hedge, 1972; Slavík, 2000). Ivanek (1984) describes S. pratensis forming over a quarter of the hay crop in Arrhenatherum elatius-associated grasslands in Poland.

The native distribution in Britain is limited to lowland hay meadows and chalk downland, and hence, the species is not commonly found at high altitudes, having a maximum altitude of around 300 m (Smith, 2019). In continental Europe, a maximum altitude of 1,920 m is recorded and, though it is not an alpine species, it is commonly found in abundance in alpine meadows (Hultén & Fries, 1986; Thompson, 1911).

2 | HABITAT

2.1 | Climatic and topographical limitations

Salvia pratensis is a Southern Continental European species, generally found in warm temperate, dry environments (Hultén & Fries, 1986). However, cultivated material is known to withstand cold winters (Yeo, 1995; see Section 5.3).

The species’ restricted distribution in the British Isles is likely linked to specific habitat and microclimate requirements. British populations occur mainly on sunny, gentle-to-steep sloping ground, facing south to west, on free draining soils (Scott, 1989). The average annual rainfall from all 37 native hectares in the British Isles is 733 mm (Preston et al., 2002), a low total compared to the national average per hectad. This coincides with a low Ellenberg value for moisture of 3, indicating the species’ preference for drier sites. The mean January temperature in native hectares is 3.7°C, fitting within the normal distribution for native plant species in the British Isles. The mean July temperature in hectares is 16.3°C, among the highest for species native to the British Isles. An Ellenberg value for light requirements of 8 indicates that it is found in situations where light is generally >60% relative illumination in the summer months (Hill et al., 2004). Sites with such climatic and topographical characteristics provide a warm, dry microclimate in which the species has managed to survive at the edge of its global range in the British Isles. Ellenberg (1988) stated the following climatic indicator values for Central Europe: a water value of 4, between dry and moist sites; a temperature value of 6, between fairly warm to warm conditions; a light value of 8, a light-loving plant; and a continentality value of 4, suboceanic.

| Vice-county number | Vice-county           | Number of sites 1999 | Number of sites 2002–2003 |
|--------------------|-----------------------|-----------------------|--------------------------|
| 8                  | South Wiltshire       | 1                     | 1                        |
| 13                 | West Sussex           | 2                     | 1                        |
| 15                 | East Kent             | 1                     | 2                        |
| 16                 | West Kent             | 1                     | 2                        |
| 17                 | Surrey                | 1                     | 1                        |
| 23                 | Oxfordshire           | 13                    | 14                       |
| 24                 | Buckinghamshire       | 1                     | 2                        |
| 34                 | West Gloucestershire  | 3                     | 2                        |
| 35                 | Monmouthshire         | 1                     | 1                        |

TABLE 1 Number of extant Salvia pratensis sites per vice-county in the British Isles based on surveys performed in 1999 from Rich et al. (1999) and in 2002–2003 from King (2004)
Substratum

In the British Isles, *Salvia pratensis* is a calcicole, found on nutrient-poor, calcareous, free draining, sandy soils derived from parent rock of oolitic limestone or chalk (Scott, 1989). Long-recorded populations generally considered native occur only on dry calcareous substratum, most commonly the Oxfordshire strata of Jurassic limestone, on soils where the rock is near to the surface (Lousley, 1950).

During a survey of British *S. pratensis*, Scott (1989) observed soil profiles at 11 populations, all of which had rendzina soils. The most regularly observed profiles were brown rendzina soils with average surface soil horizons of 11 cm of dark brown, fine to medium granular, sandy loam. Below this, a parent rock of weathered oolitic malleable shattered stone was most regularly observed, with many joints and root matrices extending from the upper horizon. This layer descended to 30 cm where the stratum became too solid for surveying to continue. At the interface between the surface soil horizon and parent rock, a thin dark yellow-brown layer comprising an accumulation of weathered material was observed.

A slightly varied rendzina soil was observed at Stuart Fawkes Nature Reserve, Gloucestershire, where one of the largest populations in the British Isles can be found. Here, a calcareous brown earth was found with a moist, dark brown, surface soil containing a greater proportion of small stones, again 11 cm deep. Below this, there was a 6-cm layer of very stony dark brown loam subsoil, and at 17 cm, a light olive brown, calcareous clay. This calcareous brown earth profile was found below the main population; however, a smaller colony 300 m east grows on a soil more characteristic of that described in the paragraph above. This area was found to be positioned over a landslip section of soil, where calcareous brown earth and brown rendzina merge, though both fall under the rendzina soil group.

*Salvia pratensis* is given an Ellenberg ‘reaction value’ of 8 by Hill et al. (2004), meaning the average soil pH associated with the species is between 7 and 9; however, there is evidence that there is not an obligate need for basic soils. Salisbury (1952) suggested that the distribution of the British populations could be better linked to the fact that these soils are well drained and in warm situations. This is supported by the prolonged survival of some populations (generally considered non-native) on neutral soils throughout Southern England. Furthermore, in Continental Europe, the species is less restricted to calcareous soils, extending onto more mesotrophic but not acid soils. Hegland et al. (2001) describe Dutch populations as occurring more regularly on dry floodplain grasslands than on calcareous grasslands. In Central Europe, Ellenberg (1988) gave the
species a ‘reaction value’ of 8; between the indicators for ‘weakly acid to weakly basic’ conditions and ‘basic to lime loving plants’, that is, mostly seen on limestone or chalk, but not limited to these conditions. Together with the species' Ellenberg values for light and temperature, this may further exemplify the view of Salisbury (1952) that dry, nutrient-poor soil characteristics are of greater importance than a basic pH.

3 | COMMUNITIES

In the British Isles, *Salvia pratensis* is predominately a grassland plant of lightly grazed or unmanaged open grasslands on weakly to strongly calcareous soils (Rich et al., 1999; Rodwell, 1991 et seq.; Scott, 1989); thus, the National Vegetation Classification (NVC) community in which it occurs most frequently is CG3 *Bromus erectus* grassland which provides such conditions. It is also occasionally found on ungrazed sites with calcareous soils in CG5 *Bromus erectus–Brachypodium pinnatum* grassland, which tends to be less open than the CG3 *Bromus erectus* grassland but still retains some relatively short, open areas. It is found only rarely in CG4 *Brachypodium pinnatum* grassland, which is dominated by coarse, competitive perennial grasses leaving little room for regeneration. It appears to be rare on calcareous soils in CG2 *Festuca ovina–Avenula pratensis* grassland, probably due to the grazing pressure which maintains this community (Rodwell, 1991 et seq. only list it from this community, which is an artefact of the data sampling for the NVC). It also occurs occasionally on weakly calcareous soils in the more calcareous examples of the mesotrophic grasslands in MG1 *Arrhenatherum elatius* grassland and MG5 *Centarea nigra–Cynosurus cristatus* grassland, provided these are also open. Oddly, it also occurs occasionally in the heavily improved MG7 *Lolium perenne* leys, where it may perhaps be a persistent relict of former calcareous grassland types. It also grows rarely on the edges of scrub and woodland in W21 *Craetaegus monogyna–Hedera helix* scrub where scrub is invading former grasslands. The most frequently associated species across all sites are *Bromopsis erectus*, *Dactylis glomerata*, *Festuca rubra*, *Plantago lanceolata*, *Trifolium pratense*, *Trifolium repens* and *Trisetum flavescens* (Table S1).

In Continental Europe, the species is found in a wider range of habitats including floodplain grasslands and alpine meadows but is predominantly a calcicolous throughout its range, extending onto more mesotrophic but not acid soils. In the Netherlands, *S. pratensis* is a diagnostic species of *Medicaginii–Avenetum pubescentis* associations of dry floodplain grasslands, with characteristic riverine species such as *Medicago sativa* subsp. *falcata*, along with calcicole species such as *Avenula pubescens*, *Eryngium campestre* and *Orobanche caryophyllacea* (Hegland et al., 2001). It is placed with grey dune plants in the class of Koelerio-Corynephoretea (Hegland et al., 2001; Schaminée et al., 1996). In Central and Eastern Europe, *S. pratensis* is frequently found on roadside verges, unimproved dry pastures and hay meadows, often in abundance (Hedge, 1972; Slavík, 2000). In Central Europe, Ellenberg (1988) includes *S. pratensis* as characteristic of more or less calcicole arid and slightly arid grasslands and characteristic of *Arrhenatherum* grasslands in the lowlands to submontane habitats.

4 | RESPONSE TO BIOTIC FACTORS

4.1 | Grazing

*Salvia pratensis* is known to be extremely palatable to grazing animals. Sheep and deer will graze it heavily and cattle will remove aerial plant sections down to sward height (Scott, 1989). Lousley (1950) described a population in the North Downs, Kent, where rabbit grazing had prevented flower production. Rabbits have been observed to bite through inflorescence stalks (Lousley, 1950), but among-site comparisons of grazing by Scott (1989) suggested that they avoid the leaves. Sites heavily grazed by sheep and cattle were found to have up to 100% of flowering stems removed. By surveying plants prior to and during grazing, Scott (1989) identified selective grazing by sheep: Open flowers were initially removed, followed by unopened flowers and then flowering stems. The leaves and basal rosette will be eaten by sheep last, but at one heavily grazed site, all above-ground plant matter was eaten within 3 days. Cattle will unselectively graze all plant parts, commonly leaving the basal rosette, unless at high intensity. Grazing of flowering shoots may promote the production of adpressed vegetative shoots (Smith, 2019), although vegetative spread is generally limited. Of the few populations with year-round grazing regimes in the Netherlands, Hegland et al. (2001) found that sites with more intense grazing had smaller proportions of juvenile or progressive plants than sites with seasonal grazing or mowing regimes. High-intensity grazing can destroy basal buds, significantly impacting the survival rate to a reproductive age (Hegland et al., 2001; Scott, 1989). Intense grazing, or grazing at the wrong time of year, is therefore likely to contribute to population decline. Yet, while grazing can greatly reduce the biomass of *S. pratensis*, seasonal grazing is beneficial in maintaining suitable habitat and promoting establishment through soil disturbance (see Section 11).

4.2 | Other plants

Hegland et al. (2001) found that populations of greatest viability in the Netherlands were located at sites with the most diverse vegetation cover (by species richness) and the rarest species. Open areas with more bare soil and less vegetation cover were found to support more flowering *S. pratensis* plants. In addition, a higher proportion of species normally associated with nutrient-rich community structures were generally found to render the *S. pratensis* population less viable (having a greater proportion of older plants). Competition from nutrient-loving species may contribute to site unsuitability more than high nutrient levels alone (see Section 6.5.3).
5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

Populations in the British Isles range from a single long-lived plant to many hundreds of plants (King, 2004; Scott, 1989). A demographic survey of 10 sites by Moughan (2012) found that population area ranged from 2 m² to approximately 1,066 m², with an estimated 2–459 plants, and an estimated 1–239 flowering plants, per population. An 11th site, Holly Court Farm, was an outlier, with a population area estimate of 6,372 m², potentially translating to >16,000 plants (>7,000 flowering). The Cotswolds, particularly the vice-county of Oxfordshire, hosts sites with the largest abundance of plants per population (King, 2004; Scott, 1989). Within a vice-county, it is common that only one or two sites/populations are present (Table 1). Greater densities of plants and seedlings are found at sites that experience disturbance (Hegland et al., 2001). Populations surveyed in Britain were found to be more compact in growth form when growing at high density with up to 50 plants per square metre (Rich et al., 1999).

5.2 | Performance in various habitats

The level of disturbance and hence amount of open soil was the most significant parameter affecting population structure of Salvia pratensis in dry grasslands in the Netherlands (Hegland et al., 2001). Here, a positive correlation between the amount of bare ground and proportion of juvenile plants (those with <1 leaf pair and a rosette ≤5 cm) was documented (Hegland et al., 2001). Disturbance and bare soil are required for increased recruitment from seed and a younger more dynamic population structure. Of 51 plots surveyed in the Netherlands, Hegland et al. (2001) observed seedlings in only seven plots, six of which were in late-mown grassland. A more progressive population structure was also observed in late-mown grassland. Seedling establishment is limited in tall undisturbed grassland which tends to have an accumulation of moss and litter at ground level (Scott, 1989).

5.3 | Effect of frost, drought etc.

Salvia pratensis is given a hardiness rating of ‘H1’ by Compton (2011), meaning it can withstand the severest of European continental climates down to −20°C and below. Its occurrence in arid calcareous grasslands in Europe and the presence of a tap root suggests a reasonable level of drought tolerance, but there are no specific data available.

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

Salvia pratensis is an erect, rosette-forming herb, with short basal internodes. The mode of branching is monopodial, or, when the apical meristem is lost, sympodial from dormant basal buds. A deep tap root forms over time, with spreading, fibrous and yellow-tinged rootletts. In a study investigating phenotypic variation in S. pratensis populations of various sizes in the Netherlands, Ouborg et al. (1991) measured 17 morphological characteristics of first-generation plants grown from wild seed in a greenhouse (14/10 hr light/dark; 20/15°C; n = c. 300 plants). After 8 months, the longest leaf was 27.6 cm. The average number of leaves at 60 days was 11, increasing to 39 at 8 months when the average number of basal rosettes was three. Larger populations were found to exhibit significantly higher phenotypic variation.

6.2 | Mycorrhiza

Salvia pratensis is known to form associations with arbuscular mycorrhizal fungi (Harley & Harley, 1987), including with the ubiquitous taxa Glomus claroideum, G. geosporum, G. intraradices and G. mosseae (Zaller et al., 2011). Glomus geosporum has been shown to significantly increase the shoot and root biomass of S. pratensis in controlled growth experiments in field soil mixed with 50% sand (Zaller et al., 2011).

6.3 | Perennation: Reproduction

Salvia pratensis is a hemicyryptophyte, probably capable of living 30 years or more (Rich et al., 1999). One plant originating from the Dordogne, France, has been retained in cultivation for 26 years by T. Rich. The species reproduces by seed, but there are suggestions that it can spread vegetatively to a limited extent; Šerá and Šerý (2004) assumed that lateral spread via vegetative propagation can occur up to 0.3 m per year. Overwintering occurs as vegetative shoots in rosettes. Ouborg (1993) found that it can take 4–5 years for an individual to form a rosette large enough to produce flowers.

6.4 | Chromosomes

A chromosome number for S. pratensis in the British Isles has not been established; however, several varied figures have been recorded from a broad area. The commonly cited and currently accepted chromosome number is 2n = 18 (Hedge, 1972; Sell & Murrell, 2009; Stace, 2019). This number was most recently reported from the Český kras region in the Czech Republic (Slavík, 2000) and from the Castelló region of the Iberian Peninsula (Bošcaiu et al., 1998). This value also agrees with samples from Bulgaria (Markova & Ivanova, 1982), Germany (Scheel, 1930), Italy (Del Carratore & Garbari, 1996; Kieft & van Loon, 1978; van Loon, 1980; Löve & Löve, 1982) and Poland (Frey et al., 1981). Contrary to these findings, however, the chromosome number of 2n = 16 has also been recorded in some cases including: seeds from cultivated S. pratensis grown at Rotterdam Botanic Garden in the Netherlands (Haque, 1981; Haque & Ghoshal, 1980); plants from the...
Serpukhovsky area of west Russia (Patudin et al., 1975) and in the Ukraine (Slavik, 2000). Plants from the Ukraine with $2n = 16$ chromosomes may be the species *Salvia dumetorum* (Slavik, 2000), but this taxon is believed to be better placed within *S. pratensis* by some (Hedge, 1972). A chromosome number of $2n = 32$ has also been recorded from cultivars grown at Hamborg Botanic Garden, Germany (Scheel, 1930) and from some natural Bulgarian plants (Markova & Ivanova, 1982). Chromosome counts of $n = 9$ and $n = 16$ suggest that polyploid variants may exist. This is not unexpected as members of *Salvia* sect. *Pliethiosphae* are known to hybridise (Haque, 1981; Hedge, 1972; Scheel, 1930).

Karyotype analysis was performed by Bošcaiu et al. (1998) for Spanish plants and by DelCarratore and Garbari (1996) for Italian plants. Both cases found chromosome sizes of 1–3 µm, with one satellite-bearing pair and all others being either subtelocentric or telocentric. Haque (1981) reported chromosome sizes ranging from 2.5 to 5.0 µm in $2n = 16$ cultivated plants.

### 6.5 | Physiological data

#### 6.5.1 | Response to temperature

Given its wide native range, *S. pratensis* is subject to a variety of growing temperatures, from areas with hot summers in the Mediterranean to much cooler conditions at the northern and western limits, like in the British Isles. Lasseigne et al. (2007) studied the effect of temperature on the growth of several cultivated *Salvia* species including cultivated *S. pratensis* seed from Britain. After 7 days in a growth chamber (day: 15 hr at 25°C; night: 9 hr at 20°C), plants were transferred to chambers of varying temperature regimes. A total of 10 test temperature environments were used, consisting of daytime temperature exposures between 20 and 40°C, and a night-time temperature of either 15 or 25°C, with 15/9 hr day/night, with all other conditions kept constant over 36 days. Above-ground dry biomass increased with warmer daytime temperatures to an optimum of around 33°C. Above this, temperature became limiting and growth declined, but plants were able to survive daytime temperatures of 40°C with no visible signs of injury. Of the *Salvia* species tested, *S. pratensis* was one of the least sensitive to high daytime temperatures. Root dry weight was not significantly affected by the daytime temperature, which in the opinion of Lasseigne et al. (2007) further exemplified the species’ ability to survive at high temperatures. Night-time temperature did not significantly affect the above-ground dry weight, root dry weight, nor root-shoot ratio. Net leaf photosynthetic rate was not significantly affected by the day, nor by the night-time temperature, ranging from a high of 9.40 µmol m⁻² s⁻¹ at 20°C to 7.92 µmol m⁻² s⁻¹ at 40°C.

#### 6.5.2 | Response to flooding

Mommer et al. (2006) investigated the effects of flooding on a range of plant species found along the River Rhine in the Netherlands. *S. pratensis* was found to exhibit a significant intolerance to complete submersion in water, decaying rapidly in both light and dark conditions. Median lethal time (where 50% of plants had died) was 11 days of submersion in full light, and when light was excluded, the plant was estimated to survive <5 days. The leaves were found to have an extremely low aerenchyma content of c. 5% before submersion and c. 2% after 11-day submersion with light, with no measurable material after 11-day submersion in darkness. Although the species is severely damaged by flooding, it is able to grow in higher elevated and dry habitats on the Rhine floodplain (above 13 m with a maximum flooding period of 5 days per growing season; Mommer et al., 2006), likely due to the presence of sandy, free-draining soils.

### 6.5.3 | Response to nutrients

*Salvia pratensis* is characteristic of low-nutrient soils and a decline in populations due to soil improvement has been recorded in the British Isles (Rich et al., 1999). An analysis of 11 sites in England showed that sites supporting species with higher Ellenberg indicator values for nitrogen had smaller *S. pratensis* populations with more regressive demographic structures (Moughan, 2012). In Central Europe, Ellenberg (1988) gave the species an indicator value for nitrogen of 4, meaning it is more often found on nitrogen deficient and average nitrogen soils than on eutrophic soils. In cultivation, however, it is known to grow well in nutrient-rich potting mixes (K. McGinn pers. obs.), suggesting that the species’ intolerance of high nutrient levels may in part be an indirect effect of greater competition from surrounding vegetation (see Section 4.2).

Scott (1989) performed soil analyses for six populations in the British Isles and found that concentrations of potassium (K⁺) were low, ranging between 0.07 and 0.55 mEq/100 ml soil, whereas an adjacent area of improved grassland where *S. pratensis* was absent at one site had levels around 1.3 mEq/100 ml. Some sites, particularly Stuart Fawkes Nature Reserve, Gloucestershire, had high magnesium concentrations, but an overall relationship between the distribution of the species and high magnesium concentrations was not supported (Scott, 1989).

### 6.6 | Biochemical data

*Salvia* species, particularly *S. officinalis*, produce essential oils that are utilised in traditional medicines (see Section 10). Anačkov et al. (2009) isolated essential oils from 50 specimens of *S. pratensis* to identify compounds potentially used as adulterants in commercial *S. officinalis*-based medicines. A composition of 0.073% essential oil was found in air-dried inflorescences. The oils extracted contained 42 constituents, of which the sesquiterpene hydrocarbons group accounted for over 50% of substances identified and the most prevalent essential oil was (E)-caryophyllene, forming over 25% of the total essential oil volume. Veličković et al. (2003) found that the most represented components were thymol (30%), (E)-caryophyllene...
(28%), p-cymene (9%) and caryophyllene oxide (4%). Extracts of cal- 
lus tissue from S. pratensis have been shown to exhibit antimicrobial 
properties (Maslova et al., 2019). While S. pratensis appears to con- 
tain a lower amount of essential oil than other Salvia species, the 
antimicrobial activity of its essential oils has been found to be higher 
than that of S. officinalis (Mossi et al., 2011; Veličković et al., 2003).

Harborne (1992) identified that delphinidin 3',5'-dimethyl ether- 
based malvidin pigments are responsible for flower colour in S. 
pratensis. This group of pigments was found in eight other species 
of Lamiaceae originating from the Old World, all of which possess 
violet-blue flowers pollinated by bees (Harborne, 1992).

7 | PHENOLOGY

Salvia pratensis is a main flowering period of late May–early July 
in the British Isles (Rich et al., 1999). However, when inflorescences 
are removed early or mid-season by hay cutting or grazing, sec- 
ondary flowering shoots are sometimes observed, extending the 
flowering period into early October. Scott (1989) found that 13% 
of plants cut in mid-June flowered again in mid-August. Fruiting oc- 
curs around 1 month after flowering, with seeds released from mid- 
July (Scott, 1989). Seedlings in the wild emerge from July onwards 
(Smith, 2019).

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

Salvia pratensis is polycarpic and populations are typically gynodi- 
oecious, having both female (male-sterile) and hermaphrodite in- 
dividuals, the latter being more abundant (see final paragraph in 
this section). It is, however, possible for individuals to have both 
female and hermaphrodite shoots (Smith, 2019). The species has 
a mixed mating system and is self-compatible, but insect pollina- 
tion is required for within-flower selfing (Scott, 1989; van Treuren 
et al., 1993). Hermaphrodite flowers are protandrous (Ouborg & van 
Treuren, 1994; Scott, 1989).

Experimental work by van Treuren et al. (1993) showed that the 
species predominantly outcrosses in both wild and cultivated 
populations, with rates (±SE) ranging from 38.2% (±9.2) to 81.8% 
(±8.7) in four natural populations (n per population = 23, 51, 92, 129) 
and 71.5% (±5.8) to 95.5% (±5.4) in four experimental populations 
(n per population = 27, 54, 27, 54). Outcrossing of hermaphrodites 
was found to be promoted by higher plant densities and a lower fre- 
quency of female plants. Interestingly, the study did not find sup- 
port for a relationship between population size and outcrossing rate, 
as the largest populations with >1,000 plants exhibited the lowest 
outcrossing rate. Crossing experiments performed by Ouborg and 
van Treuren (1994) found significant inbreeding depression after 
one generation in all selfed populations, regardless of population 
size. This inbreeding depression was demonstrated for mean seed 
weight, proportion of germination, plant size, regenerative capacity 
and survival. Subsequent field experiments showed that survival 
rates were 16%–63% lower in selfed relative to outcrossed progeny 
and the effect of inbreeding load increased over the 8 months during 
which observations were made.

The stamens in Salvia flowers are modified to form a spoon- 
shaped lower lever arm which functions to disperse pollen onto pol- 
linators’ bodies (Reith et al., 2007). A hole in the spoon-shaped lever 
allows access for a pollinator’s proboscis and the force of the probos- 
cis entering it is converted into an inwards and upwards movement, 
causing the thecae to be lowered onto the thorax or abdominal re- 
gions of the pollinator (Reith et al., 2007). Pollinators then access 
a reward of nectar from nectaries sited at the base of the corolla. 
Honeybees (Apis mellifera) and bumblebees (Bombus spp., including 
quens and workers) are abundant pollinators (Claßen-Bockhoff 
et al., 2004; Zhang & Claßen-Bockhoff, 2019), but a diverse range 
of other bee species and a few other insect species visit S. pratensis 
flowers (Table 2). Salvia pratensis is said to be less specialised in its 
pollinators relative to other Salvia species (Reith et al., 2006). Insects 
are known to be capable of collecting nectar or pollen without trig- 
gering the staminal mechanism and therefore, not pollinating the 
flower (Table 2; Reith et al., 2007). Nectar robbers (which pierce 
the corolla to obtain nectar) and nectar thieves (which forage nor- 
mally but transfer little pollen due to a mismatch in floral and insect 
morphology) are documented (Reith et al., 2006). Scott (1989) ob- 
erved that nectar robbing at some sites can occur on up to 100% 
of flowers, whereas at other sites, no occurrences were apparent.

The corollas of hermaphrodite flowers are notably larger, 
measuring 15–30 mm, compared to c. 10 mm in female flowers 
(Stace, 2019). Aborted stamens are present in female flowers, where 
the base of the staminal lever is often intact but with no anthers. 
Rarely, intermediate flowers can be observed, where one or both 
anthers are formed on retracted stamens; these anthers are often 
small, deformed and paler brown in colour than in hermaphrodite 
flowers (Scott, 1989). Zhang and Claßen-Bockhoff (2019) found that 
the smaller structures of female flowers are a better fit to pollina- 
tors relative to hermaphrodite flowers. The shorter corolla, shorter 
corolla tube and lower stigma in female flowers resulted in more 
efficient pollen deposition from pollinators’ bodies (Bombus spp., 
predominantly B. terrestris) onto stigmas. Significantly more pol- 
linator visits were observed to be stigma-touching in female than 
in hermaphrodite flowers (>65% and <30% respectively; n = 400). 
The authors suggested that this factor underpins the maintenance 
of sexual dimorphism in the species. There are suggestions that seed 
set may be higher for female relative to hermaphrodite flowers, but 
data collected by Zhang and Claßen-Bockhoff (2019) did not show 
significant differences.

Scott (1989) found that 1%–9% of flowers in eight British popu- 
lations were female, with higher frequencies observed in fields that 
were shaded or subject to herbicide treatment. Intermediate flow- 
ers were observed at frequencies of 1%–13%. In four Dutch popu- 
lations, female flowers were observed at frequencies of 0%–4% in 
two small populations (<30 individuals) and 22%–24% in two large
Invertebrate feeders and flower visitors recorded from *Salvia pratensis*. Nomenclature follows de Jong et al. (2014)

| Species/classification | Present in UK? | Ecological notes | Source (see footnote) |
|------------------------|----------------|-----------------|-----------------------|
| **Arachnida**          |                |                 |                       |
| **Acarina**            |                |                 |                       |
| Eriophyidae            |                |                 |                       |
| *Aceria salviae* Nalepa (syn. *Eriophyes salviae* Nalepa) | No | Larvae and adults; phytophagous; galling; Lamiaceae, monophagous on *Salvia* spp. | 1, 2 |
| **Insecta**            |                |                 |                       |
| **Coleoptera**         |                |                 |                       |
| Apionidae              |                |                 |                       |
| *Squamapion elongatum* Germar | No | Larvae; root gall; Lamiaceae, monophagous on *Salvia* spp. | 2 |
| *Squamapion leucophaeatum* Wencker | No | Larvae; stem borer; Lamiaceae, monophagous on *Salvia* spp. | 2 |
| Buprestidae            |                |                 |                       |
| *Trachys quercicola* Marsecker | No | Larvae; leaf miner; Lamiaceae, monophagous on *Salvia* and *Stachys* spp. | 2 |
| **Chrysomelidae**      |                |                 |                       |
| *Cassida canaliculata* Laicharting | No | All developmental stages; monophagous on *Salvia* | 2, 3 |
| *Dibolia femoralis* Redtenbacher | No | Larvae; leaf miner; Lamiaceae, monophagous on *Salvia* spp., *S. pratensis* is the main host plant | 2 |
| *Dibolia schillingii* Letzner | No | Larvae; leaf miner; Lamiaceae, monophagous on *Salvia* spp. | 2 |
| *Longitarsus obliteratus* Rosenhauer | Yes | Larvae and adults; phytophagous; leaves | 1 |
| **Curculionidae**      |                |                 |                       |
| *Datonychus paszlavszkyi* Kathy | No | Larvae; stem borer; Lamiaceae, monophagous on *Salvia* spp. | 2 |
| *Phrydichus topiarius* Germar | No | Larvae; petiole and stem borer; Lamiaceae, monophagous on *Salvia* spp. | 2 |
| **Nitidulidae**        |                |                 |                       |
| *Brassicogethes aeneus* Fabricius | Yes | May pollinate; pollen beetle; polyphagous | 6 |
| **Diptera**            |                |                 |                       |
| **Agromyzidae**        |                |                 |                       |
| *Ophiomyia labiatarum* Hering | Yes | Stem miner; Lamiaceae, oligophagous | 2 |
| *Phytomyza salviae* Hering | No | Larvae; leaf miner; Lamiaceae, oligophagous | 2 |
| *Phytomyza scotina* Hendel | No | Larvae; leaf miner; Lamiaceae, monophagous on *Salvia* spp. | 2 |
| **Cecidomyiidae**      |                |                 |                       |
| *Dasineura salviae* Kieffer | No | Larvae; flower gall; Lamiaceae, monophagous on *Salvia* spp. | 2 |
| **Syrphidae**          |                |                 |                       |
| Hoverflies—not listed to genera or species level | Yes | Flower visitor (or no details given) | 7 |
| **Hemiptera**          |                |                 |                       |
| **Aphididae**          |                |                 |                       |
| *Aphis salviae* Walker | No | Leaf; Lamiaceae, monophagous(?) on *Salvia* spp. | 2 |
| **Cercopidae**         |                |                 |                       |
| *Philaenus spumarius* Linnaeus | Yes | Leaf gall; polyphagous | 2 |
| **Cicadellidae**       |                |                 |                       |
| *Eupteryx atropunctata* Goeze | Yes | Larvae and adults; phytophagous; leaves | 1 |
| **Miridae**            |                |                 |                       |
| *Hadrodemus m-flavum* Goeze | No | Phytophagous | 1 |
| **Tingidae**           |                |                 |                       |
| *Derephysia foliacea* Fallen | Yes | Phytophagous | 1 |
### Hymenoptera

#### Apidae

| Species/classification                  | Present in UK? | Ecological notes                       | Source (see footnote) |
|----------------------------------------|----------------|----------------------------------------|-----------------------|
| Andrena carbonaria Linnaeus            | ?              | Flower visitor (or no details given)   | 7                     |
| Andrena dorsata Kirby                  | Yes            | Pollinator                             | 7                     |
| Andrena hattorfiana Fabricius          | Yes            | Pollinator                             | 7                     |
| Andrena labiata Fabricius              | Yes            | Flower visitor (or no details given)   | 7                     |
| Andrena nigripes Provancher            | No             | Flower visitor (or no details given)   | 1, 7                  |
| Anthophora manicata Linnaeus           | Yes            | Pollinator                             | 7                     |
| Anthophora fulviorhirs Brullé          | No             | Flower visitor (or no details given)   | 7                     |
| Anthophora quadrirrimaculata Panzer    | Yes            | Flower visitor (or no details given)   | 7                     |
| Apis mellifera Linnaeus                | Yes            | Pollinator; nectar thief               | 7, 7                  |
| Bombus hortorum Linnaeus               | Yes            | Pollinator                             | 7, 6                  |
| Bombus humilis Illigerb                | Yes            | Flower visitor (or no details given)   | 7                     |
| Bombus hypnorum Linnaeus               | Yes            | Pollinator                             | 7                     |
| Bombus lapidarius Linnaeus             | Yes            | Pollinator                             | 7                     |
| Bombus lucorum Linnaeus                | Yes            | Pollinator                             | 6                     |
| Bombus muscorum Linnaeus               | Yes            | Flower visitor (or no details given)   | 7                     |
| Bombus pascuorum Scopoli               | Yes            | Pollinator                             | 7, 6                  |
| Bombus pratorum Linnaeus               | Yes            | Pollinator; nectar thief               | 7, 6                  |
| Bombus ruderarius Mullerb              | Yes            | Pollinator                             | 7, 6                  |
| Bombus sylvarum Linnaeus               | Yes            | Pollinator; nectar robber              | 7                     |
| Bombus terrestris Linnaeus             | Yes            | Pollinator                             | 7, 6                  |
| Bombus wurfenii Radoszkowski           | No             | Nectar robber                          | 7                     |
| Eucera nigresens Perez                 | Yes            | Pollinator                             | 7                     |
| Halictus leucaheneus Ebmer             | No             | Flower visitor (or no details given)   | 7                     |
| Hylaeus communis Nylander              | Yes            | Nectar thief                           | 7                     |
| Lasioglossum convexiusculum Schenck    | No             | Flower visitor (or no details given)   | 7                     |
| Lasioglossum majus Nylander            | No             | Flower visitor (or no details given)   | 7                     |
| Lasioglossum malachurum Kirby          | Yes            | Flower visitor (or no details given)   | 7                     |
| Lasioglossum minutissimum Kirby        | Yes            | Flower visitor (or no details given)   | 7                     |
| Lasioglossum morio Fabricius           | Yes            | Nectar thief                           | 7                     |
| Lasioglossum nitidiusculum Kirby       | Yes            | Nectar thief                           | 7                     |
| Lasioglossum pauxillum Schenck         | Yes            | Flower visitor (or no details given)   | 7                     |
| Lasioglossum pygmaeum Schenck          | No             | Flower visitor (or no details given)   | 7                     |
| Lasioglossum sexnotatum Kirby          | Yes            | Nectar thief                           | 1, 7                  |
| Lasioglossum sexstrigatum              | No             | Nectar thief                           | 7                     |
| Lasioglossum xanthopum Kirby           | Yes            | Flower visitor (or no details given)   | 7                     |
| ‘Megachile pyrina (fasciata)’           |                | Pollinator                             | 7                     |
| Megachile paretia Geoffroy             | No             | Flower visitor (or no details given)   | 7                     |
| Osmia aurulenta Panzer                 | Yes            | Flower visitor (or no details given)   | 7                     |
| Osmia bicolor Schrank                  | Yes            | Flower visitor (or no details given)   | 7                     |
| Osmia bicornis Linnaeus                | Yes            | Pollinator                             | 7                     |
| Osmia caerulescens Linnaeus            | Yes            | Pollinator                             | 7                     |
| Osmia plicornis Smith                  | Yes            | Flower visitor (or no details given)   | 7                     |
### TABLE 2 (Continued)

| Species/classification | Present in UK? | Ecological notes | Source (see footnote) |
|------------------------|----------------|------------------|----------------------|
| **Osmia uncinata** Gerstaecker | Yes | Flower visitor (or no details given) | 7 |
| **Xylocopa iris** Christ | Yes | Flower visitor (or no details given) | 7 |
| **Cynipidae** | &nbsp; | &nbsp; | &nbsp; |
| **Neaylax salviae** Giraud | No | Fruit gall; Lamiaceae, monophagous on *Salvia* spp. | 2 |
| **Neaylax verbenacea** Nieves-Aldrey | No | Fruit gall; Lamiaceae, monophagous on *Salvia* spp. | 2 |
| **Tenthredinidae** | &nbsp; | &nbsp; | &nbsp; |
| **Agaostigma** W. F. Kirby spp. | Yes | Larvae; flowers and sometimes leaves | 5 |
| **Lepidoptera** | &nbsp; | &nbsp; | &nbsp; |
| **Coleophoridae** | &nbsp; | &nbsp; | &nbsp; |
| **Coleophora albitarsella** Zeller | Yes | Larvae; leaf miner; Lamiaceae, oligophagous | 2 |
| **Coleophora virgatella** Zeller | No | Larvae; leaf miner; Lamiaceae, oligophagous | 2 |
| **Cosmopterigidae** | &nbsp; | &nbsp; | &nbsp; |
| **Vulcaniella extremella** Wocke | No | Larvae; leaf miner; Lamiaceae, oligophagous | 2 |
| **Crambidae** | &nbsp; | &nbsp; | &nbsp; |
| **Pyrausta aurata** Scopoli | Yes | Larvae; leaf hidden; Lamiaceae, oligophagous | 2 |
| **Pyrausta virginalis** Duponchel | No | Larvae; leaf hidden; Lamiaceae, oligophagous | 2 |
| **Pyrausta cingulata** Linnaeus | Yes | Larvae; phytophagous on leaves; webbing | 1 |
| **Udea fulvalis** Hübner | Yes | Larvae; phytophagous on leaves | 1 |
| **Geometridae** | &nbsp; | &nbsp; | &nbsp; |
| **Siona lineata** Scopoli | Yes | Flower visitor (or no details given) | 7 |
| Various spp. e.g. *Eupithecia* Curtis | Yes | Flower visitor | 5, 6 |
| **Hesperiidae** | &nbsp; | &nbsp; | &nbsp; |
| **Ochloides sylvanus** Esper | Yes | Flower visitor (or no details given) | 6 |
| **Nepticulidae** | &nbsp; | &nbsp; | &nbsp; |
| **Trifurcula lituanica** Ivinskis & van Nieukerken | No | Larvae; stem miner; Lamiaceae, narrowly monophagous (*S. pratensis*) | 2, 4 |
| **Noctuidae** | &nbsp; | &nbsp; | &nbsp; |
| **Autographa gamma** Linnaeus<sup>b</sup> | Yes | Flower visitor (or no details given); nectar thief | 7 |
| **Nymphalidae** | &nbsp; | &nbsp; | &nbsp; |
| **Vanessa cardui** Linnaeus | Yes | Flower visitor (or no details given) | 7 |
| **Euphydryas aurinia** Rottemburg | Yes | Flower visitor (or no details given) | 7 |
| **Melanargia galathea** Linnaeus | Yes | Flower visitor (or no details given) | 6 |
| **Melitaea parthenoides** Keferstein<sup>b</sup> | No | Flower visitor (or no details given) | 7 |
| **Lasiommata petropolitana** Fabricius | No | Flower visitor (or no details given) | 7 |
| **Pieridae** | &nbsp; | &nbsp; | &nbsp; |
| **Anthocaris cardamines** Linnaeus | Yes | Flower visitor (or no details given) | 7 |
| **Aporia crataegi** Linnaeus | Yes | Flower visitor (or no details given) | 7 |
| **Colias hyale** Linnaeus | Yes | Flower visitor (or no details given) | 7 |
| **Pieris brassicae** Linnaeus | Yes | Flower visitor (or no details given) | 7 |
| **Pieris rapae** Linnaeus | Yes | Flower visitor (or no details given) | 7 |
| **Psychidae** | &nbsp; | &nbsp; | &nbsp; |
| **Apterona helicoidella** Vallot | No | Larvae; leaf miner; polyphagous | 2 |
| **Sesiidae** | &nbsp; | &nbsp; | &nbsp; |
| **Chamaesphcia doleriformis** Herrich-Schäffer | No | Larvae; root borer; Lamiaceae, monophagous on *Salvia* spp. | 2 |
| **Chamaesphcia schmidtiiformis** Freyer | No | Larvae; root borer; Lamiaceae, monophagous on *Salvia* spp. | 2 |
TABLE 2 (Continued)

| Species/classification | Present in UK? | Ecological notes | Source (see footnote) |
|-------------------------|----------------|------------------|----------------------|
| Sphingidae              |                |                  |                      |
| Hemaris sp. Dalman     | Yes            | Flower visitor (or no details given) | 7                    |
| Macroglossum stellatum | Yes            | Flower visitor (or no details given) | 7                    |
| Hyles euphorbiae Linnaeus | Yes      | Flower visitor (or no details given) | 7                    |
| Tortricidae             |                |                  |                      |
| Epinotia kochiana      | No             | Larvae; stem borer; phytophagous on leaves; Lamiaceae, monophagous on Salvia spp. | 2                    |
| Cnephasia asectlana     | Yes            | Larvae; phytophagous; leaf miner; polyphagous | 1                    |
| Doubleday               | Yes            | Larvae; phytophagous; leaf miner; webbing | 1                    |
| Gastropoda              |                |                  |                      |
| Various species including Arion ater Linnaeus, Comu aspersum O.F. Muller and Helix pomatia Linnaeus | Yes | Above-ground parts; polyphagous | 5, 8a |

Source: 1, DBIF (2018); 2, Ellis (2017); 3, Heisswolf et al. (2005); 4, Ivinskis et al. (2012); 5, Scott (1989); 6, King (2004); 7, Reith et al. (2006) and references therein; 8, Rich (1995).

aThe original authors used a synonym.

8.2 | Hybrids

The hybrid between S. nemorosa and S. pratensis, S. × sylvestris, is common in Central and South-East Europe where the two species are sympatric. Salvia × sylvestris is also known to have arisen in cultivation (Stace, 2019; Stace et al., 2015). In the British Isles, this hybrid is naturalised on sand dunes at Burnham Overy Saithe, West Norfolk, where it was discovered in 1953 and rerecorded as still being present in 1997 (Stace, 2019; Stace et al., 2015). Earlier records of the hybrid as a casual and garden escape are known from Hertfordshire, West Norfolk and Jersey (Stace et al., 2015). Stace et al. (2015) describe this hybrid as being partially fertile and Hegen (1927) found that 60% of its nutlets contained an embryo.

In comparison to S. pratensis, S. nemorosa has a denser inflorescence, far smaller flowers and longer, coloured (pink to purple as opposed to green) bracts (Stace et al., 2015). Salvia × sylvestris is intermediate in these characters, but can be very close to S. nemorosa, having colourful (purple, blue, pink or white) bracts, at least the lower flowers longer than the corolla, and a corolla colour similar to the bracts (Stace et al., 2015). All three taxa are grown in gardens and S. × sylvestris has been known in cultivation for several centuries (Stace et al., 2015). Salvia pratensis and S. nemorosa have been the focus of artificial hybridisation and selection by plant breeders, resulting in an array of named cultivars of S. × sylvestris. These cultivars have been bred to combine the larger flowers of S. pratensis with the coloured bracts of S. nemorosa (Stace et al., 2015). There are 33 cultivar names associated with S. × sylvestris that are accepted or tentatively accepted by the Royal Horticultural Society (RHS) Horticultural Database, many of which are protected by plant breeders’ rights (Royal Horticultural Society, 2020). Salvia × sylvestris ‘Blauhügel’, ‘Viola Klose’ and ‘Tänzerin’ have received ‘Awards of Garden Merit’ from the RHS (Royal Horticultural Society, 2020). As a result, S. × sylvestris has become a popular and widely available garden plant.

Salvia × digenea Borbás is a hybrid between S. amplexicaulis Lam. and either S. nemorosa or S. × sylvestris (the parentage is disputed; Stace et al., 2015). Along with S. × sylvestris, these taxa form a taxonomically complex group that is often treated under S. nemorosa in horticulture (Compton, 2011).

8.3 | Seed production and dispersal

Salvia pratensis produces nutlets with an average weight of 2.4 mg (1–3.3 mg; derived from 12 ‘1,000 seed weight’ measurements; Royal Botanic Gardens Kew Seed Information Database, 2020). Each nutlet contains a single seed. Hagemann et al. (1967) quantified the average oil content per seed as 19% and the average protein content as 24%, although seed moisture content was not stated within the analyses. Chetverikova et al. (2008) measured a moisture content of 6.64% of weight of seeds dried at 105°C (±0.11 SE; n = 90 seeds).

Šerá and Šerý (2004) estimated the reproductive capacity of a theoretical S. pratensis population with 100% cover within 1 m² as 33,458 seeds (SD = 11,050) per season. This value was calculated based on a comparison of three populations, as an average for...
polycarpic, perennial plants, with a small amount of vegetative lateral growth representing a medial input into reproductive success. At six British populations, Scott (1989) observed seed set to mostly exceed 90%, but reduced to 84% in plants where flowers had been ‘robbed’ and to 83% where plants produced flowers in mid-August when fewer pollinators were available. Plants were found to produce up to 1,500 seeds each, but high rates of loss due to mammal predation were observed. Haque and Ghoshal (1981) found that open-pollinated plants exhibited lower seed set compared to hand-pollinated plants.

Each flower can produce up to four nutlets which drop from the calyces once they mature and dry (Scott, 1989). Barochory (seed dispersal by gravity alone) is considered the chief dispersal route for *S. pratensis* and most seeds fall close to the parent plant (Diacon-Bolli et al., 2013; Ouborg et al., 1991; van Treuren et al., 1991). However, a range of other seed dispersal mechanisms have been documented. Römermann et al. (2005) demonstrated the potential for epizoochory (seed dispersal on the exterior of animals) via an experimental approach using dry sheep and cow pelts and a mechanical shaking device. The experiments showed that 50% of *S. pratensis* nutlets tested remained attached to sheep’s wool after 1 hr of shaking, but only 2% remained in cattle hair (n = 100 seeds each treatment; three replicate runs each). Such dispersal potential may be higher in wet conditions. The potential for epizoochory was also described by Bouman and Meeuse (1992), whereby the sticky mucus produced by glandular hairs on the calyces may promote the adherence to animal fur, with mature seeds remaining inside the calyces. This mode of dispersal has been documented for other *Salvia* species (Zona, 2017). The nutlets also produce thick mucilage upon wetting which may similarly aid in dispersal by adherence to animals, although direct field-based observational evidence is lacking for *Salvia* species (Scott, 1989; Zona, 2017). Hydrochory has been suggested as an explanation for the distribution of Dutch *S. pratensis* along the river system of the Rhine (Hegland et al., 2001) and may account for the Middlesex population (Rich, 2000). Ridley (1930) stated that *S. pratensis* nutlets may float in water for up to 8 days and experimental work by Zona (2017) showed that seeds of *Salvia* species can float for many hours. In addition, Bonn (2004) found that seeds of *S. pratensis* can survive passage through the digestive system of sheep, but at very low rates. Dispersal methods other than barochory would suggest that the distance of seed dispersal can be much greater than that of 1 m stated by some authors. Historical long-range human-mediated dispersal has also been documented via the transport of grass seed contaminants (Rich et al., 1999).

### 8.4 Viability of seeds: Germination

*Salvia pratensis* seed is able to germinate immediately from nutlets after wetting. Both viable and non-viable seeds produce a thick layer of mucilage from expelled epicarp cell contents 10–15 min after wetting (Scott, 1989). For ripe seed sown within 10 days of harvest, Scott (1989) observed an average germination of 72% (62%–91%; n = 596 seeds, originating from four sites), with no significant variation between dark and light treatment. Seed subject to wetting, drying and rewetting on alternate days successfully germinated. Samples reached 50% of their germination total within the first 7 days and 95% after 12 days. Underripe seeds collected while green but subject to after-ripening for several days showed some viability, with an average germination of 33% (23%–50%; n = 360 seeds, originating from three sites).

In 12 lab-based tests conducted on agar at the Millennium Seed Bank, an average of 95% germination was achieved (77%–100%; a mean of 35 seeds per test; Royal Botanic Gardens Kew Seed Information Database, 2020). These tests were conducted in a range of conditions, from 15 to 26°C and mostly with 12/12 hr light/dark. Germination took place over an average of 8 days (S. Miles, pers. comm., 9/12/20). All tests were conducted following storage at −20°C, but dried to 15% relative humidity prior to storage, as per normal seed banking protocols for desiccation tolerant species (S. Miles, pers. comm., 9/12/20).

Ouborg and van Treuren (1995) found that a minimum seed size of 1.3 mm was necessary for germination to occur; seeds smaller than this were non-viable. Out of eight seed size classes, an optimum size of 1.4–1.6 mm was suggested as seeds within this range produced seedlings with significantly longer roots and cotyledons (n = 75 seeds per size class, but only 25 for the largest size class). In the four Dutch populations surveyed, the proportion of non-viable seeds varied between 27% and 45% and this variation was not related to population size. Seeds resulting from self-fertilisation appear to be less viable; Ouborg and van Treuren (1994) found that such seeds weighed 12% less (mean ± SE: selfed = 2.29 ± 0.09 mg; crossed = 2.61 ± 0.08 mg) and had 29% lower germination (mean ± SE: selfed = 30 ± 3%; crossed = 42 ± 4%; n = 30 seeds per treatment).

Seeds of *S. pratensis* appear to be orthodox (desiccation tolerant) and storage of dry seeds in hermetically sealed containers at cool temperatures is recommended (Royal Botanic Gardens Kew Seed Information Database, 2020; Young & Young, 1992). Germination tests following 20 years of storage at the Millennium Seed Bank showed no significant loss in viability (S. Miles, pers. comm., 9/12/20). There are, nevertheless, accounts of limited germination following seed storage, but it is important to note that seed longevity will depend greatly on factors such as storage conditions. In a sample of 30 seeds 9–11 years old, Scott (1989) found no germination. Seeds sown after 1.5-year refrigeration (c. 4°C) were found to have 5% germination (n = 524), but this seed was selfed, from a single parent plant, with no seed excluded for size (J. Moughan, unpubl. data). No soil seed bank has been recorded for *S. pratensis* in Northern Europe (Thompson et al., 1997); however, seedlings have been observed to emerge just before the flowering season, suggesting that seed may be capable of lying dormant for at least 1 year (Scott, 1989).

Although *S. pratensis* seeds are likely orthodox, Chetverikova et al. (2008) included the species in a study on seed cryopreservation. Germination on petri dishes was consistently high (>75%) following storage for 1 month via quick deep freezing (−196°C; cooling rate of 700°C per min), programmed two-stage deep freezing (−196°C;
cooling first to −40°C at a rate of 1°C per min, followed by placement in liquid nitrogen), non-deep freezing (−10°C), in addition to a control (±5°C). However, post-germination monitoring of 30 plants grown from each treatment showed that deep freezing caused significantly reduced length and width of rosette leaves.

8.5 | Seedling morphology

Germination is epigeal. Cotyledons have a slightly notched obtuse tip, cordate base, inconspicuous veins and a hairy petiole. The cotyledon margins are entire, and during the initial days, are slightly revolute. The first true leaves are hairy and more typical of adult leaves, with crenate margins and reticulate venation (Figure 3).

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

\textit{Salvia pratensis} is extremely palatable to mammal grazers, including cattle, sheep, deer and horses (see Section 4.1). A total of 14 invertebrate species have been recorded as feeders on \textit{S. pratensis} in the British Isles, including leaf miners, root borers and gall formers (Table 2). This total will be an underestimate as sawflies and molluscs are not listed to species level in Table 2. Scott (1989) noted considerable damage by insect larvae, most notably from the suborder Symphyta (sawflies), causing loss of up to 21% of flower whorls. Various Gastropoda feed on \textit{S. pratensis} and can cause mortality in damp conditions (Rich et al., 1999; Scott, 1989). In addition, 24 invertebrate species not present in the British Isles have been documented as feeding on \textit{S. pratensis} (Table 2). The leaf beetle species \textit{Cassida canaliculata} Laich is dependent on \textit{S. pratensis} as a host, on which it is said to be monophagous in Germany and carries out all stages of its life cycle (Heisswolf et al., 2005).

9.2 | Plant parasites

In total, 10 fungal parasites have been recorded on \textit{S. pratensis} in Europe, including rusts, smuts and mildews (Table 3). The anther smut \textit{Microbotryum betonicae} is believed to be monophagous on \textit{S. pratensis} (Ellis, 2017).

\textbf{FIGURE 3} Seedlings of \textit{Salvia pratensis} at (a) 3 days (outer layer around the seed representing a layer of mucilage from expelled epicarp cell contents), (b) 10 days and (c) 30 days after germination. Drawings by K. McGinn
The earliest known record of *S. pratensis* in the British Isles was in 1696 on the North Downs, Kent, where the plant still resides today (Druce, 1886; Marren, 2001; Pearman, 2017). The epithet, *pratensis*, originates from the species' preferred habitat of meadows. Although *S. pratensis* is not especially noted for its medicinal properties relative to *S. officinalis*, the common name, Meadow Clary, is indicative of its traditional use as a treatment for eye maladies; the mucilage from wetted seeds was used to rinse eyes and the word clary originates from the term ‘clear-eye’ (Fisher, 1987). Medicinal uses as a gargle for sore throats and as a cleanser of the teeth have also been noted (Rich et al., 1999).

In the British Isles, *S. pratensis* is nationally scarce, red-listed as near-threatened and a priority Biodiversity Action Plan species (Cheffings et al., 2005). It is protected under Schedule 8 of the 1981 Wildlife and Countryside Act, making it illegal to intentionally pick, uproot, destroy or sell the species when of British origin. The species is conserved ex situ at the Millennium Seed Bank with 19 England-origin collections (Botanical Society of Britain & Ireland & Royal Botanic Gardens Kew, 2020).

### 9.3 Plant diseases

No data available.

### 10 HISTORY

The earliest known record of *S. pratensis* in the British Isles was in 1696 on the North Downs, Kent, where the plant still resides today (Druce, 1886; Marren, 2001; Pearman, 2017). The epithet, *pratensis*, originates from the species' preferred habitat of meadows. Although *S. pratensis* is not especially noted for its medicinal properties relative to *S. officinalis*, the common name, Meadow Clary, is indicative of its traditional use as a treatment for eye maladies; the mucilage from wetted seeds was used to rinse eyes and the word clary originates from the term ‘clear-eye’ (Fisher, 1987). Medicinal uses as a gargle for sore throats and as a cleanser of the teeth have also been noted (Rich et al., 1999).

### 11 CONSERVATION AND MANAGEMENT

*Salvia pratensis* can be found in abundance in parts of its range in Central Europe (Hedge, 1972) and it does not appear on the European Red List of Vascular Plants (Bilz et al., 2011). The species is thus not of direct conservation concern internationally; however, it does grow in a declining habitat and is increasingly rare at the edge of its range.

In the British Isles, *S. pratensis* is nationally scarce, red-listed as near-threatened and a priority Biodiversity Action Plan species (Cheffings et al., 2005). It is protected under Schedule 8 of the 1981 Wildlife and Countryside Act, making it illegal to intentionally pick, uproot, destroy or sell the species when of British origin. The species is conserved ex situ at the Millennium Seed Bank with 19 England-origin collections (Botanical Society of Britain & Ireland & Royal Botanic Gardens Kew, 2020). *Salvia pratensis* is likely to have always been rare in Britain but a significant loss of native populations and sites occurred before 1950, with native populations in Kent, West Sussex, Oxfordshire and Gloucestershire becoming locally extinct (Rich et al., 1999). This decline followed intensified farming practices, particularly the ploughing of downland and altered management techniques of grassland communities (Scott, 1989). It is thought to have been introduced from Eastern European sources between 1880 and 1930s as a seed contaminant of grass and clover seed, but such accidental introductions declined thereafter following the establishment of seed cleaning regulations (Rich & Karran, 2006).

In the Netherlands, *S. pratensis* is located mostly along dry floodplain grasslands, a habitat that diminished by >80% between the 1960s and 1990s, leaving small, fragmented populations (Hegland et al., 2001). The species is red-listed as vulnerable, legally protected...
and is a target species for conservation in floodplain grasslands, a priority habitat for Dutch conservation (Hegland et al., 2001; van der Meijden & Heukels, 1996; Ouborg & van Treuren, 1995). In Switzerland, it is classed as ‘of least concern’ on the country’s red list (Moser et al., 2002). In Southern Germany, it is described as very common (Schmeil & Fitschen, 1996). In countries at the north and north-western extremities, it is rare. The naturalised populations in Sweden are listed as endangered, as these populations have become fragmented due to changes in roadside management and pasture farming (Gärdenfors, 2005).

Both British and Dutch *S. pratensis* populations are now generally only found in places protected by conservation efforts (Hegland et al., 2001; Ouborg & van Treuren, 1995; Rich et al., 1999). Since the 1950s, the number of British populations has remained almost constant, restricted to sites managed with more traditional, less intensive farming practices (Rich et al., 1999). However, recent declines have been recorded in some populations, either due to a lack of management or the regular mowing of road verges with the trimmings left in situ (Smith, 2019). The species was lost from its only Welsh site in 2008 (see below).

The species’ habitat is heavily fragmented in the British Isles, with many populations reproductively isolated by distances of over 1 km, making gene exchange via pollen or seed dispersal unlikely. Genetic mixing is believed to have been more frequent in the past as a result of seeds being dispersed by the movement of livestock and hay (Smith, 2019). Reproductively isolated and declining populations are a cause for concern for a species that predominantly outcrosses as this brings the threat of inbreeding depression. It is feared that such populations could be ageing and not regenerative, especially when combined with pressures such as a lack of suitable site management. A survey of the demographic structure of British populations in 2011 supported this view, as populations at five out of 11 sites were considered regressive, with few seedlings and immature plants (Moughan, 2012). Two populations surveyed were considered to have dynamic, highly regenerative populations, and four were considered as normal, with an even spread of life stages.

A range of studies in the Netherlands have shown that small isolated populations of *S. pratensis* are experiencing the early stages of inbreeding depression and genetic erosion, most likely having become isolated fairly recently (Ouborg & van Treuren, 1994; Ouborg et al., 1991; van Treuren et al., 1991). In the British Isles, Kay and John (1995) examined the population genetics and demographic ecology of selected native *S. pratensis* populations using allozymes. The Welsh population with only three plants at the time of the study was found to have the lowest genetic variation, while the highest variation was found in the east and central England populations.

In 2008, *S. pratensis* became extinct from Rectory Meadows, Monmouthshire, its only native site in Wales, but a reintroduction programme in 2015 repopulated the site with 150 plants. As inbreeding depression likely contributed to the local extinction, the reintroduced plants were of various genetic stocks to increase genetic diversity. Seeds for these plants originated from 10 sites. The reintroduced plants comprised 110 individuals from English populations and 40 plants grown from a single Welsh individual conserved ex situ at Treborth Botanic Garden, Bangor, known to have originated from the Rectory Meadows population. Initial monitoring found that 12 plants had died, while 54 had been defoliated. A site survey in January 2019 suggested that 14 plants survived and a subsequent survey in June 2021 also counted 14 plants, with approximately two-thirds of a good size and flowering and/or fruiting (J. Woodman, pers. comm.). Some individuals had been lost between the two surveys, and others missed in the original count, but it is believed that no recruitment had taken place (J. Woodman, pers. comm.). The species has also been reintroduced to Dancers End in Buckinghamshire, and many other populations have been bolstered through planting (Smith, 2019).

Most British sites with native *S. pratensis* are managed as permanent pastures or hay meadows (Smith, 2019). Of 11 British sites surveyed in the summer of 2011 by Moughan (2012), five were observed to have no or little management (often with rabbit grazing and some small-scale conservation efforts such as scrub clearance and ground scarification). Three sites were observed to have year-round low-intensity livestock grazing, requiring some scrub control. Another three sites were managed well for *S. pratensis*, being seasonally grazed by livestock, with exclusions to allow flowering and seed set.

Management should seek to maintain suitable open grassland habitat, for example, by preventing scrub encroachment and the dominance of coarse grasses such as *Brachypodium pinnatum* (Scott, 1989). The use of herbicides and artificial fertiliser can greatly damage individual plants and populations as a whole (King, 2004). The removal of sward by hay cutting or grazing is advised, but it is important that this occurs after *S. pratensis* has flowered and set seed (in Britain, seed generally matures and drops in late July; Scott, 1989). Prolonged earlier cutting or grazing can have a very detrimental effect on *S. pratensis* populations by limiting reproduction (Hegland et al., 2001). Late mowing of experimental plots in October over 21 years in nutrient-poor limestone grasslands in Switzerland greatly benefitted *S. pratensis*, to the extent that it dominated plots (relative to plots that were mown in July, burned or without any biomass removal; Kahlert et al., 2005).

Scott (1989) made a series of recommendations for site management. He stated that sites should be grazed by livestock at high intensity in spring, to reduce competition from vigorous grasses. Stock should be removed at the beginning of May to allow the development of flowering shoots, then re-introduced at lower density from late July. For cattle, he suggested that grazing may be possible all year round, provided that the stocking density is low. Summer grazing every 4–5 years may be helpful to prevent the accumulation of unpalatable litter and reduce competition from surrounding vegetation. In addition, temporary stock proof enclosures during the flowering and fruiting period may be valuable, but they should not prevent rabbits from entering. For sites managed as hay meadows, a cut in late July or early August is recommended, which should allow around 50% of seed to ripen. Unripe seeds held on cut stems can after-ripen successfully to some degree (see Section 8.4), so hay should be left to dry in situ to maximise potential recruitment, but then be removed.
To provide a regeneration niche, site management should maintain a level of disturbance. Aftermath grazing, the grazing of hay meadows after hay has been cut, is successful in creating gaps in the sward and patches of loose soil in which seedling recruitment can occur (Smith, 2019). At Stuart Fawkes Nature Reserve in Gloucestershire, the introduction of hay cutting with subsequent cattle grazing has greatly increased the number of seedlings (Parker, 2009).

On road verges and at other sites where grazing is not feasible, Scott (1989) recommended a post-fructing cut, with the clippings collected up, and wherever possible, manual scarification to provide bare soil for seedlings. Where more regular cutting is necessary for road safety, he suggested a cut in late-April and then again in late-July/early-August. At unmanaged sites, the short sward and scrapes created by rabbits may maintain suitable habitat for S. pratensis, including niches for seedling establishment. Old ant hills and worm casts may similarly aid seedling establishment at unmanaged sites.

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