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Perspectives in Plant Ecology, Evolution and Systematics 8 (2006) 45–66

Perspectives in Plant Ecology, Evolution and Systematics
www.elsevier.de/ppees

Biological Flora of Central Europe: *Viola elatior*, *V. pumila* and *V. stagnina*

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Received 29 August 2005; received in revised form 16 January 2006; accepted 24 January 2006

Abstract

Viola elatior, *V. pumila* and *V. stagnina* (syn. *V. persicifolia*) are very rare in central and western Europe and red-listed in many central European countries. To improve their conservation and to base management efforts on sound scientific knowledge, we here review the available information on their biology. A comparative approach is adopted to identify similarities and differences between the species. Special emphasis will be on taxonomy, community ecology and population biology.

All three species belong to the section *Viola*, subsection *Rostratae*. Since they are morphologically rather similar and have often been misidentified, we supply the most important characters for separating the three taxa. The species share a continental distribution with a centre of occurrence in the temperate zone of eastern Europe and western Siberia, and reach their western range margin in central and western Europe. They have become rare and endangered through melioration and fragmentation of their habitats. All three species are iteroparous hemicryptophytes with a complex life cycle, a mixed mating system with chasmogamous and cleistogamous flowers, and a persistent seed bank. *Viola pumila* and *V. stagnina* occur in floodplain meadows and wet grasslands, whereas *V. elatior* is a typical species of alluvial woodland fringes and other ecotonal habitats bordering floodplain meadows. *Viola elatior* and *V. pumila* are confined to calcareous or at least base-rich substrates, whereas *V. stagnina* may also occur on strongly acidic soils. The violets are able to occupy a broad range of site conditions in terms of soil nutrient status and productivity. However, on fertile sites the species depend on regular disturbances that weaken competitors and enhance the germination of dormant seeds. Current information about mycorrhizal colonisation, biochemical and physiological data, and herbivores and pathogens is scarce or lacking, probably due to the rarity of the three species in central Europe.

Keywords: Ecology; Morava-Dyje floodplain; Plant traits; Species biology; Upper Rhine; *Viola persicifolia*

Introduction

The present paper reviews the taxonomy, morphology, distribution, habitat requirements, life cycle and

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doi:10.1016/j.ppees.2006.01.001

ecology of the endangered species *Viola elatior* Fries, *V. pumila* Chaix and *V. stagnina* Kit. (syn. *V. persicifolia* auct., non Schreb.). We used information available from the literature supplemented by unpublished data, and followed the outline for the Biological Flora of Central Europe described by Matthies and Poschlod (2000). Summarising information about all three species, which are very similar with respect to their ecology, distribution and morphology, allows us to better elaborate the differences between them.

Except for violets (treated here), the taxonomy and nomenclature of vascular plants in the present paper follow Wisskirchen and Haeupler (1998). The classification of plant communities follows Oberdorfer (1983). In the section "Morphology", 10%- and 90%-percentiles and usually (in parentheses) also minimum and maximum values are given for quantitative characters, based on own measurements. Information on the general distribution in the section "Geographical distribution" is based mainly on revised herbarium specimens; if no herbarium samples could be inspected from a particular country, at least one reference is given to a flora, distribution atlas, or specialist paper. The distribution maps were produced with the program DMAP (Morton, 2005).

Taxonomy and morphology

Taxonomy

The three species dealt with in this paper belong to the genus *Viola* L., *Viola* (sect. *Viola*) subsect. *Rostratae* Kupffer (Kirschner and Skalický, 1990; Ballard and Sytsma, 2000). The cosmopolitan genus *Viola*, much larger than other genera of Violaceae, comprises about 400 (Valentine, 1962) or even 525–600 species (Ballard et al., 1999). It is widely distributed throughout regions with boreal to subtropical climates of the Northern Hemisphere, and in higher altitudes of mountain systems near the equator and in the Southern Hemisphere (Ballard et al., 1999). It includes woody plants, hemicryptophytic perennials and annuals.

The genus was studied in the world-wide scale by Becker (1925). He recognised 14 sections, some of them with a few to many infrasectional groups without formal rank. Representatives of six sections occur north of the equator. The central European violets are classified into the sections *Nominium* Ging. (e.g. *V. odorata*, *V. canina*, *V. reichenbachiana* and *V. palustris*), *Melanium* Ging. (e.g. *V. arvensis*, *V. lutea* and *V. tricolor*), and *Dischidium* Ging. (*V. biflora*; Becker, 1925; Valentine, 1962). The species treated here were classified together with other rosulate and arosulate European, Asian and North American species with leafy stem and hooked, rostrate style (e.g. *V. canina*, *V. reichenbachiana*, *V. riviniana* and *V. rupestris*) as *V.* [unranked] *Rostratae* Becker within *V.* sect. *Nominium*. Since the latter includes also *V. odorata* L., type of the genus, it should according to the Code be named *V.* sect. *Viola*. The infrageneric classification was later modified by Gershoy (1934), and Juzepčuk and Klokov (1949). Nikitin (1998), applying many infrageneric taxa, suggested a very splitting classification of eastern European violets. In some studies, *Rostratae* is given the subsectional rank as *V.* subsect. *Rostratae* Kuppfer (e.g. Kirschner and Skalický, 1990), or sectional rank as *V.* sect. *Trigonocarpea* Godr. and *V.* sect. *Mirabiles* (Borb.) Vl. Nikit. (e.g. Nikitin, 1995, 1998). The subsection *Rostratae* is species-rich and comprises about 35 species (Valentine, 1958, 1962).

A recent phylogenetic study (Ballard et al., 1999) has shown that *V.* sect. *Viola*, based on internal transcribed spacer DNA sequences for 44 taxa of eight sections, represents rather a derived group, in its circumscription including about a half of the infrasectional groups placed by Becker (1925) into *V.* sect. *Nominium*, as well as the mostly Hawaiian woody violets, formerly classified into *V.* sect. *Nosphinium* Becker (Ballard and Sytsma, 2000), and that *V. elatior*, *V. pumila* and *V. stagnina* as members of *V.* subsect. *Rostratae* are in a basal position in comparison to other *V.* sect. *Nominium* groups classified in the same clade. The phylogenetic relationship within *V.* subsect. *Rostratae* requires further research as this species-rich group was underrepresented in the study.

Viola stagnina KIT. ex SCHULT., Oestr. Fl., ed. 2, 1: 426. 1814.

Syn.: *Viola canina* subsp. *stagnina* (KIT. ex SCHULT.) ROUY et FOUCAUD, Fl. France 3: 9. 1896. – *V. persicifolia* auct., non SCHREB.

Exsiccates: BAENITZ Herb. Eur. no. 3134 (ut *V. lactea*), 6396 (ut *V. stricta*), 7250 (f. *umbrosa*), 7972 (ut *V. hornemanniana*). – BECKER Violae Exs. no. 19, 65. – CALLIER Fl. Siles. Exs. no. 154, 155, 156 (ut *V. pumila*), 782, 783. – Exs. Torun. no. 100. – Fl. Exs. Bavar. no. 786. – Fl. Siles. Exs. no. 933. – GÜNTHER Herb. Viv. sine no. – MAGNIER Fl. Select. no. 22, 22bis. – NEUMAN, WAHLSTEDT & MURBECK Violae Suec. Exs. no. 25 ('f. umbrosa'), 26 ('f. typica'). – PETRAK Fl. Bohem. Morav. Exs. no. 64. – Pl. Finl. Exs. no. 811, 812, 1250. – Pl. Polon. Exs. no. 326. – REICHENBACH Fl. Germ. Exs. no. 1080 (ut *V. lactea*). – SAMUELSSON Pl. Suec. Exs. no. 1178. – SCHULTZ Herb. Norm. no. 224, 224bis, 224ter, 2414. – Societé pour l'échange des plantes vasculaires de l'Europe et du basin mediterranéen no. 7621, 7622, 10444, 10445 (omnia ut *V. persicifolia*).

Viola pumila CHAIX, Pl. Vapincenses: 35. 1785.

Syn.: *Viola pratensis* MERT. & W. KOCH, Deutschl. Fl., ed. 3, 2: 268. 1826. – *V. canina* subsp. *pratensis*

(Mert. & W. Koch) Čelak., Květ. Okolí Praž.: 83. 1870. – *V. canina* subsp. *pumila* (Chaix) Rouy & Foucaud, Fl. France 3: 12. 1896. – *V. accrescens* Klokov in Klokov & Visjulina, Fl. URSR 7: 632. 1955. – *V. persicifolia* auct., non Schreb.

Exsiccates: Baenitz Herb. Eur. no. 3445 (ut f. *lactea*), 5634, 7972. – Becker Violae Exs. no. 21, 66, 66a. – Billot Fl. Gall. Germ. Exs., cent. 3, no. 27. – Callier Fl. Siles. Exs. no. 784. – Fiori, Beguinot & Pampanini Fl. Ital. Exs. no. 821. – Fl. Exs. Bavar. no. 515a, 515b. – Günther Herb. Viv. sine no. (ut *V. pratensis*). – Herb. Fl. Ross. no. 909, 1506 (var. *orientalis*). – Hochstetter Gewächse des Brünner Kreises no. 127 (ut *V. pratensis*). – Neuman, Wahlstedt & Murbeck Violae Suec. Exs. no. 29. – Puel & Maille Flores régionales no. 66. – Schultz Herb. Norm. no. 432. – Societé dauphinoise no. 5193. – Societé Linnéenne de la Seine maritime no. 453. – Societé pour l'échange des plantes vasculaires de l'Europe et du basin mediterranéen no. 9459, 16263. –Wołoszczak Fl. Polon. Exs. no. 509.

Viola elatior Fries, Novit. Fl. Suec. alt.: 277. 1828.

Syn.: *Viola montana* L., Sp. Pl.: 935. 1753. – *V. persicifolia* Schreb., Spicil. Fl. Lips.: 163. 1771. – *Viola canina* subsp. *persicifolia* (Schreb.) Čelak., Květ. Okolí Praž.: 83. 1870. – *V. canina* subsp. *elatior* (Fries) Rouy & Foucaud, Fl. France 3: 10. 1896.

Exsiccates: Becker Violae Exs. no. 41, 142. – Billot Fl. Gall. Germ. Exs., cent. 3, no. 28, 28bis. – Callier Fl. Siles. Exs. no. 157. – Fl. Exs. Austro-Hung. no. 2866. – Fl. Exs. Bavar. sine no. 936, 937. – Fl. Rom. Exs. no. 451. – Gandoger Fl. Gal. Exs. no. 983. – Günther Herb. Viv. sine no. (ut *V. persicifolia*). – Herb. Fl. As. Med. no. 437. – Herb. Fl. Ross. no. 1057, 1057a. – Karelin & Kiriloff Soc. Imp. Natur. Cur. Mosqu. no. 127 (ut *V. persicifolia*). – Magnier Fl. Select. no. 3210. – Neuman, Wahlstedt & Murbeck Violae Suec. Exs. no. 30. – Reichenbach Fl. Germ. Exs. no. 1772 (ut *V. persicifolia*). – Samuelsson Pl. Suec. Exs. no. 1179. – Schultz Herb. Norm. no. 615, 615bis. – Societé pour l'échange des plantes vasculaires de l'Europe et du basin mediterranéen no. 15299. – Tausch Herb. Fl. Bohem. no. 181 (ut *V. persicifolia*).

The name *Viola montana* L. has been usually used for a taxon of the *V. canina* group sometimes known under the name *V. ruppii* All. The Linnean name was typified by Nikitin (1988; see also Nikitin 1995), and its type is identifiable as *V. elatior*, so it is the earliest available name for that species to be used according to the Code. The name *Viola persicifolia*, which is for example used in the German standard list of plant names (Wisskirchen and Haeupler, 1998), has been repeatedly employed for all three species treated here. As shown by Rauschert (1973), it most probably refers to *V. elatior* but a formal typification is still lacking. However, the use of both names would cause further confusion and should be avoided for practical reasons, so it is necessary to propose these names for rejection according to the Code (see Kirschner and Skalický, 1989).

Morphology

The species of the subsection *Rostratae* are perennial herbs with or without a ground rosette, with thin or moderately thick persistent primary roots, and moderately long to short, shortly creeping, oblique or ascending rhizomes, or with many-headed rootstock and without stolons.

Leaves alternate, petiolate, crenately serrate, with stipules differing from lamina in shape. Peduncles thin, in upper part nodding. Flowers chasmogamous (CH) (open, with petals) and cleistogamous (CL) (closed, petals mostly lacking), forming racemose inflorescences. Sepals peltate, with the front part narrowly or linearly triangulate, pointed and back part (appendage) broadly quadrangular. The lowermost petal with a spur, and the two neighbouring stamens with nectarial appendages projecting into the spur. Style hooked, rostrate. Lateral petals directed obliquely below. Corolla pale violet to white, non fragrant. Capsule loculicidal, obtusely triangulate in cross-section, dehiscing with three keeled coriaceous to almost woody valves which fold shortly after opening and shoot out seeds. CH and CL seeds with small elaiosome.

The leaf anatomy of eastern European and Caucasian violets, incl. *V. elatior*, *V. stagnina* and other members of *V.* subsect. *Rostratae*, was studied by Nikitin (2002; see therein for further references). Leaves are dorsiventral, with mesophyll differentiated into palisade and spongy parenchyma. In rostrate violets, the central leaf vein protrudes equally on both sides of the lamina, and lamina is amphistomatal or hypostomatal. Typical of subsect. *Rostratae* is the presence of idioblasts containing tannin components in the epidermis, which are supposedly not found in other eastern European violets. Leaves with hairs 0.3–0.6 mm long; so leaf indument is shorter than in some species of subsect. *Viola*. Petioles are winged, semicircular in crossection, with two furrows on the adaxial side and colenchyma strands in most cases only in lateral wings.

The morphology of *V. elatior* was studied in detail by Łukasiewicz (1962) and Troll (1964). It is a typical allohomorhiz pleiocorm species with thick and branched primary root persistent for several years. Shoots are erect or very shortly ascending, develop numerous adventive roots and one to a few innovation buds near their base. Golubev (1962) depicts a single root profile of *V. pumila* consisting of a primary root that is intensively branched into side-roots, reaching a soil depth of about 40–50 cm.

As described by Meusel and Kästner (1974), *V. stagnina* forms usually a leaf rosette during the first year, and the primary shoot develops several stretched internodes and in some individuals even flowers during the second growing season. In the third year, first flowering shoots develop from innovation buds near the base of the primary shoot. The innovation proceeds always from basal buds, and only small parts of shoots persist, forming sometimes a many-headed rootstock on a persistent thickening primary root, similar to that of *V. elatior*. In other plants the branches of persistent basal shoot parts are rather long, with many adventive roots, resembling a rhizome. New plants develop also from buds on oblique or horizontally growing roots, which was probably first observed by Gershoy, (1934); see Klimeš et al., 1997) and later confirmed by Schmidt (1961, p. 53) in cultivated plants of all three species treated here. *Viola elatior*, *V. pumila* and *V. stagnina* also have a similar foliation pattern with scale formed leaves near the shoot base, followed by frondose leaves with large stipules, whose relative size increases towards the apex (Troll, 1964; Meusel and Kästner, 1974).

The pleiocorm with sympodially formed shoot base of the arosulate species of *Viola* subsect. *Rostratae* seems to be the most derived growth form within *V.* sect. *Viola*, compared (i) with the long lasting monopodial growth of the main axis in *Viola* subsect. *Viola* (e.g. *V. hirta and V. odorata*) and in the rosulate species *V.* subsect. *Rostratae* (e.g. *V. reichenbachiana* and *V. riviniana*) or (ii) with the monopodial-sympodial system of shoots in *V. mirabilis* (Meusel and Kästner, 1974). The loss of the basal rosette may be explained as an adaptation to stress in sites where basal rosettes were repeatedly damaged or torn off (Th. Marcussen, pers. comm.).

Flowers are supported by frondose leaves, which are similar to those found in the vegetative part of the stem. Sometimes, they are referred to as being 'solitary, in leaf axils'. As shown by Troll (1964), all violets have racemose inflorescences, which is not obvious due to rosette growth habit. Owing to their close relationships, the three species treated in this paper share a number of morphological features. Since the species are rather rare in central Europe, they have not always been treated appropriately in floras, which has led to much confusion and frequent misidentifications. Therefore, the morphological characters of the three species are depicted in Fig. 1 and summarised in Table 1, and an identification key is presented below:

1 Leaves, stipules and stems shortly pubescent to densely shortly pubescent (hairs mainly on veins on both surfaces, stem angles and on their margins); stipules of middle and upper stem leaves as long or longer than petioles, in the upper part of the stem (2.3–)3.1–5(–5.4) cm long and 0.4–1.2(–1.4) cm wide; bracteoles (4.4–)5.8–11.2(–14) mm long, usually attached closely below the bend of the peduncle; plants (13–)20–51(–72) cm tall ....***V. elatior***

1* Leaves, stipules and stems glabrous, subglabrous or with scattered hairs (hairs on both surfaces of young leaves and stipules and on their margins); stipules of middle and upper stem leaves shorter, as long or longer than petioles, in the upper part of the stem up to 2.8(–4.6) cm long and 0.6(–1.1) cm wide; bracteoles up to 5.1(–5.6) mm long, usually attached in the upper third of the peduncle; plants up to 33(–47) cm tall **2**

2 Laminas and stipules glabrous or stipules rarely ciliate; laminas of middle and upper stem leaves usually cuneate or narrowly cuneate, rarely truncate at the base and often decurrent; stipules of middle and upper stem leaves mostly longer than petioles, (0.4–)1–2.8(–4.6) cm long and 0.1–0.6(–1.1) cm wide; plants usually dark green; petals mostly pale blue-violet, with dark lilac veins ....***V. pumila***

2* Laminas and stipules of young leaves at least on veins and in their upper parts with scattered hairs; laminas of middle and upper stem leaves truncate, subcordate or cuneate; stipules of middle and upper stem leaves mostly shorter, rarely as long or even longer than petioles, (0.8–)0.9–2.6(–3) cm long and (0.1–)0.2–0.4(–0.5) cm wide; plants light green; petals milk-white or rarely lilac, with dark lilac veins ....***V. stagnina***

Detailed descriptions of species treated and their hybrids are provided for instance by Becker (1902, 1909) and Gerstlauer (1905).

Morphological variation of all three species is rather high and includes both general habit and individual organs. It seems, however, to be caused mainly by different habitat conditions and therefore appears to be unimportant from the taxonomical point of view.

Stipules vary remarkably in size, shape and the degree of margin division. For example, in one specimen of *V. elatior*, both almost entire and divided (with regular deep incisions) stipules can be found. But in general, stipules in *V. pumila* are wider and usually longer than in *V. stagnina*, and those in *V. elatior* are longer and wider than in *V. pumila*. The variation in plant height is also remarkable and caused a lot of confusion. *Viola pumila* has usually been considered a small plant; an extreme example of this belief can be found in Gams, (1925; cf. Klokov, 1955) where 1–1.5(–3.5) cm is given as the stem height. This is true only about flowering plants collected in late April or early May, whereas the normal

Fig. 1. Morphology of the species: (1) *Viola elatior*, (2) *Viola pumila*, (3) *Viola stagnina*; a general habit, b middle cauline leaf (scale bar for a and b: 1 cm), c flower (scale bar: 0.5 cm), d detail of upper lamina surface, e detail of stem (scale bar for d and e: 1 mm). Drawn by A. Skoumalová.

Table 1. Morphological differentiation of *Viola elatior*, *V. pumila* and *V. stagnina*

	Viola elatior	*Viola pumila*	*Viola stagnina*
Height	(13–)20–51(–72) cm	(3.5–)7–33(–47) cm	(7–)10–27(–32) cm
Stem	Erect, rarely shortly ascending, round or indistinctly angulate, with short patent dense to scattered hairs	Erect, rarely shortly ascending, round glabrous or minutely papillose	Erect or less frequently shortly ascending, round glabrous or papillose
Lamina of middle and upper stem leaves	Lanceolate, (1.9–)2.8–4(–5.4) × longer than wide, 4.7–8(–8.5) cm long and (1.2–)1.6–2.6 cm wide, remotely crenately serrate, cuneate, sometimes truncate, rarely subcordate at the base, shortly decurrent on the petiole, hairy, grass green	Lanceolate or narrowly oblong, (1.6–)1.9–3(3.4) × longer than wide, (1–)1.5–3.7(–5.5) cm long and (0.5–)0.6–1.5(–2.2) cm wide, crenate, crenately serrate or almost entire, truncate, cuneate or subcordate at the base, both above and below glabrous, rather tough and dark-green	Lanceolate or narrowly triangulate, at least (2–)2.3–3.5(−3.9) × longer than wide, (2.5–)2.7–5.2(–5.5) cm long and (0.8)1.1–1.7(−2.3) cm wide, crenately serrate, obtuse at apex and truncate, cuneate or subcordate, rarely cordate at the base, glabrous or in young leaves towards the base and apex and below on nerves hairy, rather thin and light green
Petioles of middle and upper stem leaves	(0.9–)1.7–3.6(–5.4) cm long, unwinged or often narrowly winged, (0.7–)0.8–1.6 (–2.2) mm wide, with short scattered hairs	(1–)1.6–3.6(–3.7) cm long, winged to almost unwinged, (0.4–)0.5–1.3(–1.7) mm wide, glabrous	(0.7–)1.6–3.2(–3.5) cm long, narrowly winged mainly towards the base of lamina, (0.6–)0.7–1.3(–1.5) mm wide, glabrous
Stipules	In middle und upper stem leaves conspicuously large, narrowly elliptic or (narrowly) lanceolate, (2.3–)3.1–5(–5.4) cm long and 0.4–1.2(–1.4) cm wide, usually only near the base irregularly dentate, otherwise entire	Narrowly lanceolate to lanceolate in outline, (0.4–)1–2.8(–4.6) cm long and 0.1–0.6(–1.1) cm wide, irregularly sharply dentate to almost entire, in lower leaves shorter than a quarter of the petiole, in middle stem leaves longer than half of the petiole, in upper stem leaves usually longer than petiole, often ciliate, otherwise glabrous	Broadly lineate, narrowly elliptic or narrowly lanceolate in outline, (0.8–)0.9–2.6 (–3) cm long and (0.1–)0.2–0.4 (–0.5) cm wide, in the lower part of the stem always shorter than half of the petiole, in upper stem leaves usually longer than petiole, sharply and irregularly, often remotely dentate on the margin or sometimes almost entire, usually ciliate but otherwise almost glabrous
Peduncles	Often pubescent in their uppermost part, (4.3–)6.4–10(–11) cm long	Glabrous, (4.6–)5–14(–14.5) cm long	Glabrous, (3.5–)3.8–7.5(–8.3) cm long
Bracteoles	(4.4–)5.8–11.2(–14) mm long, inserted in the bend and often exceeding the peduncle	(2–)3–5.1(–5.6) mm long, inserted below the bend of the peduncle	(1.7–)2.3–5(–5.5) mm long, inserted in the upper third of the peduncle
Sepals	(7–)7.7–12.4(–14) mm long (including appendages), narrowly triangulate or narrowly lanceolate, appendages (1–)1.3–3.5 mm long, rectangulate	(6–)7–10(–10.5) mm long (including appendages), narrowly lanceolate or narrowly triangulate, appendages (1.2–)1.3–2(–2.2) mm long, truncate	(5–)5.5–8(–9) mm long, (including appendages), narrowly triangulate, acute, appendages, (1–)1.3–2(1–2.5) mm long, rectangulate, truncate to slightly emarginate
Petals	Broadly obovate, pale blue to blue-violet, whitish near the spur mouth, with blue-violet veins, the lower petal (including spur) (11–)13–20(–22) mm long	Narrowly obovate, violet or pale blue-violet, rarely whitish, always whitish near the base, with violet veins, the lower petal (including spur) (10–)11–14(–16) mm long	Oblanceolate to narrowly obovate, rounded at apex, milk-white or slightly lilac, with dark veins, the lower petal (including spur) (8.5–)10–13.5(–16) mm long
Spur	(2.7–)2.9–5(–5.5) mm long, obtuse, thick, longer than calyx appendages, greenish	(2–)2.5–3.5(–4) mm long, longer than calyx appendages, greenish	Obtuse, 2–3.5(–4) mm long, often slightly longer than calyx appendages, greenish
Style	Bearded in the bend	Glabrous in the bend	With a few hairs in the bend

Table 1. (*continued*)

Capsules of chasmogamous flowers	Narrowly ovoid, acute, glabrous	Narrowly ovoid, acute, glabrous	Narrowly ovoid, ± acute, (6–)7–9(–10) mm long, glabrous
Seeds	1.9–2.2 mm long and 1.2–1.4 mm wide, deep brown when ripe	1.7–1.9 mm long and 1.1–1.2 mm wide, deep brown when ripe	1.5–1.7 mm long and 0.9–1.1 mm wide, brown when ripe

Values represent (minimum), 10%- and 90%-percentiles and (maximum), based on own measurements.

height (found in herbarium specimens in BRNU) was 7–27 cm and fruiting specimens can be up to 47 cm tall. In general, *V. pumila* and *V. stagnina* do not differ much in height, while *V. elatior* is usually taller than the former two.

Plants with CL flowers collected later in the season are often branched and have broad, ovate or even triangular leaves with truncate (in *V. pumila*) to cordate lamina base. The rich branching is typical mainly of the specimens of *V. stagnina* collected in mown meadows during late summer or early autumn.

The differences in the indument of upper lamina surface seem to be a useful diagnostic character to distinguish between *V. pumila* and *V. stagnina*. The former remains glabrous, while the latter tend to have at least some hairs near the base and top of the upper lamina surface. This difference becomes even more pronounced under greenhouse conditions (Th. Marcussen, pers. comm.).

Some variation was believed to be taxonomically important. In The Netherlands, *V. stagnina* var. *lacteaeoides* has been recognised and considered endemic to the Pleistocene part of the country (Weeda, 2001). It differs from the nominate variety by slender, almost dwarfish growth habit and dark green leaves, as well as by the straight stigma. Its taxonomic status requires further studies (Weeda, 2001). *Viola accrescens*, described from Ukraine, where it replaces *V. pumila* (Klokov, 1955; Nikitin, 1998), should be taller (6–42 cm) than *V. pumila* and should differ from it mainly in papillose stems, ciliate stipules, broader leaves and milk-white corollas. Apart from longer spurs, the few specimens we had the opportunity to study did not exceed the variation range of central and western European populations. Thus, in our opinion, *V. accrescens* does not merit specific status.

Distribution and habitat requirements

Geographical distribution

Viola elatior is known from France, northern Italy, Switzerland, Germany, Austria, Czechia, southern Sweden, Estonia (Kuusk et al., 1996), Latvia (Kuusk et al., 1996), Lithuania (Kuusk et al., 1996), Poland, Slovakia, Hungary, Slovenia, Croatia (Domac, 1994), Serbia, Bosnia and Herzegovina, Romania, Bulgaria, Belorussia (Parfenov et al., 1987), Moldavia (Juzepčuk and Klokov, 1949; Gejdeman, 1986), Ukraine, European Russia as well as in western Siberia (Peškova, 1996), Kazakhstan, Tadzhikistan, Turkmenia, Uzbekistan and the Xinjiang province in northwestern China (Wu and Raven, in prep.).

Viola pumila grows in France, northern Italy, Switzerland (Aeschiman and Burdet, 1994), Germany, Austria, Czechia, southern Sweden, Estonia (Kuusk et al., 1996), Poland, Slovakia, Hungary, Serbia (Josifović, 1972), Romania, Bulgaria, Belorussia, Moldavia (Gejdeman, 1986), Ukraine, European Russia, Georgia (Kechoveli, 1984), Kazakhstan and Uzbekistan (Vvedenskij, 1959). In contrast to the opinion of Zuev (in Peškova, 1996), the revision of violets in the herbarium NSK (Central Siberian Botanical Garden in Novosibirsk) has shown that *V. pumila* occurs also in Siberia, and most records in Peškova (1996) of *V. stagnina* in western, central and eastern Siberia refer in fact to *V. pumila*.

Viola stagnina is known from Great Britain (Valentine, 1975; Pullin, 1986; Pullin and Woodell, 1987), Ireland (Pullin, 1986), France, Switzerland, Belgium (extinct; Lambinon et al., 1992), The Netherlands, Denmark (Clausen, 1931), Germany, Czechia, Austria, Sweden, Norway (Røren, 1993), Finland (Meusel et al., 1978), Estonia, Latvia (Kuusk et al., 1996), Lithuania (Kuusk et al., 1996), Poland, Slovakia, Hungary, Serbia (Josifović, 1972), Romania, Moldavia (Gejdeman, 1986), Ukraine, Belorussia, European Russia (Juzepčuk and Klokov, 1949), and in southwestern Siberia even though most Siberian records (Zuev in Peškova, 1996) are based on the misidentifications of *V. pumila* (see above).

In all three species, the eastern parts of species ranges are poorly known and data available in standard floras are sometimes contradictory. They share a relatively similar distribution that covers roughly the submeridional and temperate zone of western Eurasia from the Atlantic Ocean in the west to the Altai mountains in the east (Meusel et al., 1978; Hultén and Fries, 1986). Towards the western edge of their range, the species become increasingly rare and show a strict confinement

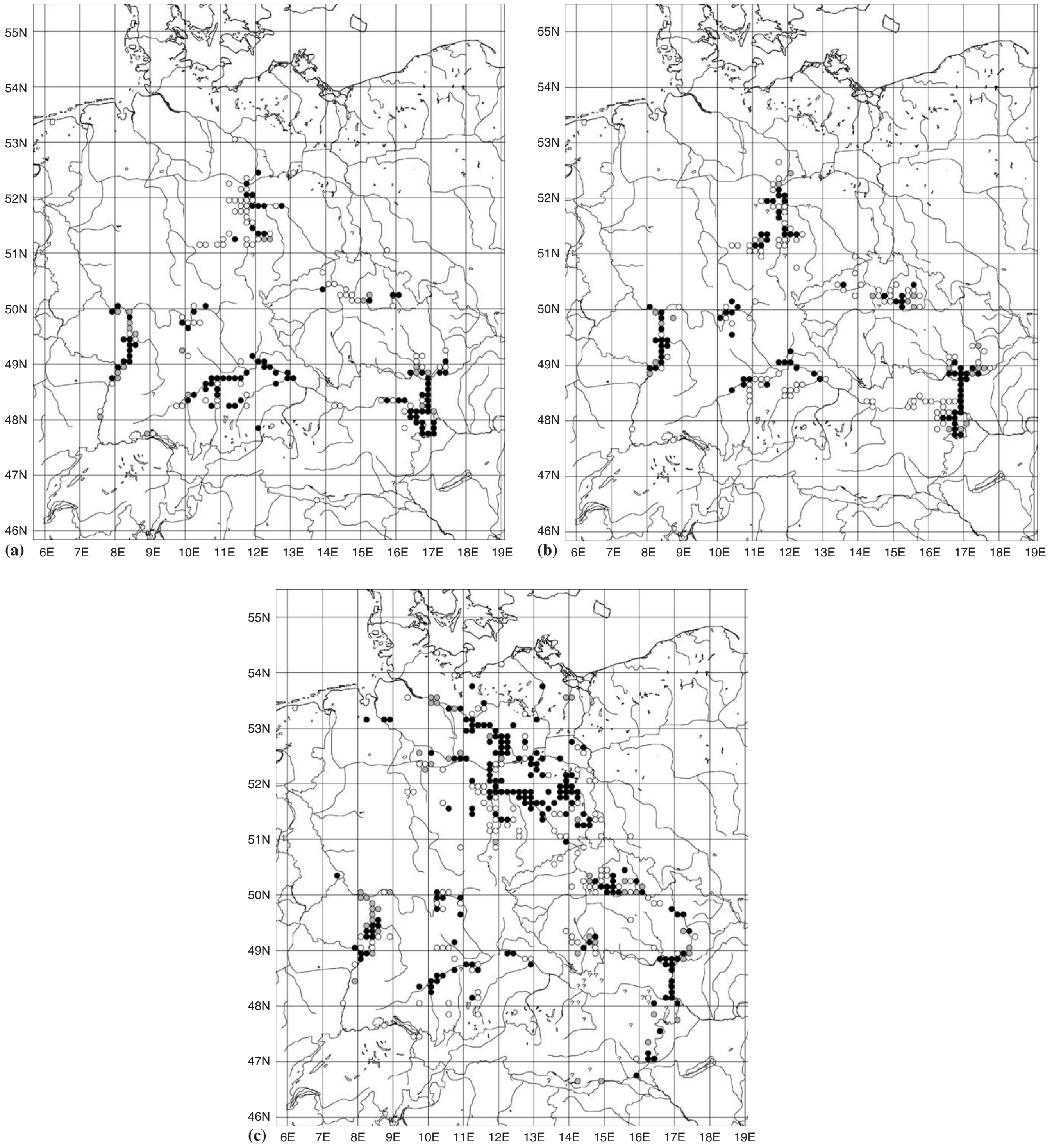

Fig. 2. Distribution of *Viola elatior* (a), *V. pumila* (b) and *V. stagnina* (c) in Austria (records provided by H. Niklfeld), Czechia and Germany (records provided by R. May, BfN, 2005). Open circles denote records before 1950, grey circles those from 1950 to 1980 and black circles those after 1980. Question marks denote doubtful records.

to large river corridors (Fig. 2). This is typical of a number of other characteristic flood-meadow species such as *Allium angulosum*, *Cnidium dubium* and *Scutellaria hastifolia* (Burkart, 2001). While the core area of *V. elatior* and *V. pumila* comprises the summer-warm continental climates of the submeridional and southern temperate zone, *V. stagnina* shows a more northern distribution covering even the southern part of the boreal zone and highly oceanic regions (Meusel et al., 1978; Hultén and Fries, 1986). *Viola elatior* and

V. pumila are almost absent from northern central Europe. The northernmost extrazonal occurrences are found in the south of the Swedish mainland (*V. pumila*; Persson, 1969) and the limestone areas of Öland (both species), Gotland (*V. elatior*) and Estonia (both species; Hultén and Fries, 1986). In contrast, *V. stagnina* is widely distributed in the southern parts of Sweden and also in southern Finland and Norway with outposts even under oceanic climates such as in The Netherlands (Weeda, 2002), England (Pullin and Woodell, 1987) and Ireland (Pullin, 1986).

Central European strongholds of the violets are found in central and southern Poland (Zając and Zając, 2001), and the northern part of the Pannonian Basin (e.g. Balátová-Tuláčková, 1969). Further to the west the violets are confined to the valleys of the rivers Morava/March, Dyje/Thaya, Saale, Elbe/Labe, Main, Danube and Upper Rhine (e.g. Haeupler and Schönfelder, 1988; Benkert et al., 1996). Moreover, *V. stagnina* is also found across the entire diluvial north central European lowland between The Netherlands and Poland with increasing abundance towards the east (Hultén and Fries, 1986).

Habitat

In central Europe, the species are restricted to floodplain habitats of large lowland river corridors with relatively dry and summer-warm climatic conditions. While *V. pumila* and *V. stagnina* are mostly found in managed or recently abandoned grasslands, *V. elatior* occurs also along irregularly disturbed ecotones between herbaceous and woody vegetation such as forest edges as well as tracks and clearings in alluvial forests (Hölzel, 2003; Eckstein et al., 2004). A new secondary, purely artificial habitat was discovered only recently along the Main River in Germany where *V. elatior* occupies overgrown rock fills along parallel ripraps (Wolters, 2002).

All these alluvial habitats are characterised by strong fluctuations of the groundwater level and a high variability in soil water potential. Of the three species *V. stagnina* occurs more frequently outside floodplains than *V. elatior* and *V. pumila*, viz. in fen and swamp habitats with a more constant water regime. Generally, there is a distinct separation along a moisture gradient between *V. elatior* and *V. pumila* with a relatively high drought tolerance and *V. stagnina* with a clear preference for damp sites (Hölzel, 2003). In eastern Europe, *V. elatior* and mainly *V. pumila* are found in steppe and forest steppe habitats (Becker, 1916; Gams, 1925; Juzepčuk and Klokov, 1949), which is in line with their preferences for relatively dry sites in central Europe. The occurrences of *V. pumila* in rather xeric grasslands in western and central Europe have been reported e.g. near Gap in the French Alps (Becker, 1916) and at a few sites in southern Moravia in Czechia (J. Danihelka, unpubl. data).

Communities

Formerly, all three violets were regarded as character species of the alliance Cnidion dubii (Oberdorfer, 1983). An analysis of 335 relevés from central Europe revealed distinct differences in community preferences (Hölzel, 2003): *Viola pumila* is most often found in relatively dry eutrophic to mesotrophic Cnidion meadows that obtain a regular management by mowing or grazing. In contrast, *V. elatior* shows a clear preference for very extensively managed, late mown or abandoned oligotrophic to mesotrophic Molinion caeruleae meadows where an overlap with *V. pumila* may occur. A second, even more important but poorly documented stronghold of *V. elatior* comprises open, irregularly disturbed nitrophilous tall forb communities of the class Artemisietea vulgaris within or along hedges and alluvial hardwood forests (mostly Querco-Ulmetum minoris). Also, its secondary habitats along parallel ripraps comprise mainly ruderal stands dominated by *Rubus caesius* and other nitrophilous plant species (Wolters, 2002).

In contrast to *V. pumila*, *V. stagnina* shows a clear preference for the wettest types of Cnidion meadows often in direct contact to damp tall-sedge communities (Caricion gracilis) or flood-swards (Agropyro-Rumicion). A second stronghold of *V. stagnina* outside floodplains comprises meso- to oligotrophic wet grassland communities (Calthion palustris, Agropyro-Rumicion, Juncus-Molinia caerulea community, Caricion fuscae, Filipendulion ulmariae) at fairly to strongly acidic fen and gley sites with a more constant ground water level.

In direct comparison, plant communities with *V. stagnina* are characterised by species indicating wet and/or acidic site conditions such as *Ranunculus flammula*, *Galium palustre*, *Agrostis canina*, *Lythrum salicaria*, *Mentha arvensis*, *Carex panicea*, *Hydrocotyle vulgaris*, *Phalaris arundinacea*, *Thalictrum flavum* and *Juncus effusus* (Hölzel, 2003). In contrast, species occurring together with *V. pumila* are mostly nutrient-demanding grassland species and ruderals such as *Alopecurus pratensis*, *Lathyrus pratensis*, *Elymus repens*, *Potentilla reptans* and *Cirsium arvense* as well as species characteristic of a highly variable soil water regime, such as *Serratula tinctoria* and *Galium boreale*. Many species co-occurring with *V. elatior* are typical of very extensive management or fallow conditions, such as *Filipendula ulmaria*, *Rubus caesius*, *Succisa pratensis* and *Genista tinctoria*, whereas species typical of regularly managed grasslands, such as *Rumex acetosa*, *Silene flos-cuculi* and *Achillea millefolium* agg., are absent.

Response to abiotic factors

Viola elatior and *V. pumila* are confined to calcareous or at least base-rich substrates. In contrast, *V. stagnina* may also occur on strongly acidic soils, which facilitates its occurrence in regions with predominantly acidic bedrock, such as in the diluvial lowland of northern central Europe where the other two species are completely absent (Hölzel, 2003). Although the older literature emphasises a strict confinement to relatively nutrient-poor habitats (e.g. Ellenberg et al., 1992; Quinger, 1993), the violets are able to occupy a broad range of site conditions in terms of soil nutrient status and productivity. However, in more fertile sites they crucially depend on regular disturbances, which weaken strong competitors. Generally, increased productivity due to raised nutrient levels, e.g. in course of the fertiliser application, must be regarded as critical for population survival.

Average flooding durations per year of more than 25 days (*V. pumila* and *V. elatior*) and more than 50 days (*V. stagnina*) are easily tolerated. Individual flooding events may even last for more than 50 and 100 days, respectively (N. Höltzel, unpubl. obs.). There are reports about negative effects of high water levels on seedling growth and early reproduction through CL capsules in *V. stagnina* (Wells et al., 1995). However, after dieback of aboveground organs in the course of prolonged flooding, mature plants of all three violet species rapidly resprout. Drought tolerance is lowest in *V. stagnina* and highest in *V. pumila*. Consequently, *V. stagnina* is particularly sensitive towards drainage and desiccation of wetlands.

In central Europe, *V. elatior* and *V. pumila* are confined to summer-warm lowland regions with monthly averages in July above 17 °C (e.g. Korsch, 1999), whereas *V. stagnina* can grow even under relatively cool sub-boreal conditions (Hultén and Fries, 1986).

As found in an experiment with planted seedlings of the three species, competition for light determined the leaf accumulation rate and reproduction (Eckstein, 2005), since reproductive plants were almost exclusively found on plots where the surrounding vegetation was removed by clipping. The decreased leaf accumulation rate and reproduction under vegetation canopy was probably due to lower rates of carbon gain under shady conditions. Competition for light influences reproductive output also in other species of the genus *Viola* (Mattila and Salonen, 1995; Jensen and Meyer, 2001; Moora et al., 2003), indicating that at least violet species from semi-natural habitats are light demanding for successful sexual reproduction. In the same experiment (Eckstein, 2005), water addition and soil water availability (i.e. site) accounted for 75 and 31% of the variation, respectively, in seedling survival and height growth across species.

Abundance

Even in areas where the species are relatively common, local populations exhibit a very scattered and patchy distribution often with large areas of seemingly suitable but unoccupied habitat in between. Accordingly, all species usually occur with low frequency in vegetation samples from adequate habitats. Even within occupied sites the species are usually rather rare. Based on the 335 phytosociological relevés compiled by Hölzel (2003) the species were rare (Braun-Blanquet abundance value +) in 55–60% of the samples. In contrast, only in 7% (*V. pumila*) to 18% (*V. elatior*) of all samples the species were recorded as abundant, i.e. common but with less than 5% cover. With the exception of carpet-forming clones of sterile hybrids (e.g. *V. pumila* × *V. stagnina*) only the tall and sometimes tuft-like *V. elatior* is able to gain dominance values of more than 5% or sometimes even 20% cover per sampling area. High abundance of the violets is often correlated with low interference by the established vegetation such as in early successional stages after heavy disturbances of the topsoil.

Life cycle and biology

Life cycle

All three species share a similar life history, although the importance of certain life-cycle transitions for population growth may differ among species (Eckstein et al., 2004; L. Eckstein et al., unpubl. data). As in many other perennial iteroparous species, the most important demographic processes (transitions) were related to growth (into a higher stage class) or survival (in the same class; Franco and Silvertown, 2004). Large vegetative plants most frequently developed into generative plants. Reduction in size of marked individuals between years (i.e. regression back into a lower stage class) was rare and had only a small influence on population growth rate. During the study period (2001–2002), probably owing to weather conditions, most populations had intrinsic population growth rates below one (L. Eckstein et al., unpubl. data). The fecundity of the species measured as 'anonymous reproduction' (Caswell, 2001), i.e. the number of seedlings in a certain year divided by the number of flowering plants the year before, was higher in populations from the Upper Rhine (1.5–4.0) than from the Dyje (0.04–1.4). Since seed bank dynamics (see the section 'Germination') could not be modelled in this field study, these are included in the fecundity values. Differences in growth rate and fecundity may be related to differences between regions in management (Eckstein et al., 2004; see also Section 'Response to competition and management') or weather conditions.

There are no published data on the maximum life span of the three violets. However, root diameters of 0.5–1 cm in 5–6-year-old plants (Łukasiewicz, 1962) suggest that individual ramets are truly perennial. Through disintegration of the pleiocorm, genets are – as in many clonal plants – theoretically immortal.

Spatial distribution of plants within populations

In central Europe, *V. pumila* and *V. stagnina* occur mostly as patches of scattered individuals within the floodplain meadows. Though their populations may consist of hundreds or thousands of individuals, their spatial extent within a habitat is restricted. This is also true for *V. elatior*, which often grows in linear habitats, i.e. along woodland margins and fringes between alluvial forests and meadows. The latter species may build very dense stands that consist of a few large multiple-stemmed flowering plants. This clumped spatial distribution of the three species within habitats could be caused by (1) clonal growth, (2) a restricted ballistic seed dispersal within the surrounding tall meadow vegetation (Section 'Morphology'), and (3) development of populations from the persistent seed bank after major, locally restricted disturbance events.

Phenology

All three violet species belong to a guild within the communities of floodplain habitats that flower in early spring. From late April to early-June generative plants will bear one to several open (CH) flowers, and capsules mature from early-June to early-July. As true CL species (Plitmann, 1995), later in the season the same individuals may develop flowers that never open (CL flowers) and are obligatorily self-pollinated (see also the sections 'Reproduction' and 'Genetic data'). Under field conditions, first CH flowers in *V. pumila* appear after April 20, whereas in *V. elatior* and *V. stagnina* flowering starts not earlier than in early May and ends in June (Gerstlauer, 1905; Göbel, 2001). In a pollination experiment, *V. elatior* and *V. pumila* flowered about one week earlier than *V. stagnina* (Eckstein and Otte, 2005). The significant earlier start of flowering in *V. pumila* under field conditions is probably due to the drier and therefore more rapid warming of its open habitat within managed grasslands. In *V. stagnina* and *V. pumila*, first seeds from CH flowers are released from early to mid June, and those in *V. elatior* after July 1. The production of CH and CL capsules is temporarily separated in the study species, with CL capsules emerging after cessation of CH flowering (Eckstein and Otte, 2005). This temporal segregation of floral types, which also occurs in other members of the genus (Culley, 2002), suggests that production of CH and CL flowers is triggered by different environmental cues (Le Corff, 1993). Species with non-overlapping production of floral types may regulate the production of CL capsules according to the reproductive success of the CH flowers (Redbo-Torstensson and Berg, 1995). Under favourable weather conditions, CL flowering and seed production may proceed until October (Göbel, 2001; Eckstein and Otte, 2005; N. Hölzel, unpublished data; observations in herbarium specimens).

Depending on the weather in a particular year, aboveground parts of shoots wither and die back in November or early December, and only their lowermost parts hidden in the litter and topsoil with innovative buds survive over the winter (Sylvén, 1906; Łukasiewicz, 1962; Meusel and Kästner, 1974). This is in contrast with some rosulate species of *Viola* subsection *Rostratae*, e.g. *V. reichenbachiana* and *V. riviniana*, where also some leaves of the ground rosette survive.

Under natural conditions, plants of the three violet species have usually developed an unbranched vegetative leaf rosette with a few stretched internodes at the end of the first season (cf. Section 'Morphology'; Sylvén, 1906; Meusel and Kästner, 1974). In culture, plants show the first CL capsules during their first year, whereas under field conditions flowering (CH and CL) usually starts during the second season.

Reproduction

All three species are capable of vegetative reproduction. Rather old pleiocorms of *V. elatior* (and probably of *V. pumila*) can disintegrate and give rise to new individuals without any connection to other parts of the original pleicorm (Łukasiewicz, 1962). This is also true for *V. stagnina*, where persistent basal shoot parts with numerous adventive roots sometimes resemble a short creeping rhizome (Meusel and Kästner, 1974). The other way of vegetative reproduction is the formation of root buds, giving rise to new shoots and later to new individuals (Gershoy, 1934; Schmidt, 1961; Meusel and Kästner, 1974; Klimeš et al., 1997).

All three species are characterised by a mixed mating system because they produce both CH flowers and closed CL flowers. Most open self-compatible flowers are potentially cross or self-pollinated. However, there is an extreme degree of floral reduction in CL flowers (Richards, 1997), which are obligatorily selfed. Cleistogamy occurs in at least 256 species from 56 angiosperm families (Lord, 1981). The CH–CL system of the three violets provides a reproductive system with both potentially variable (CH) and relatively invariable (CL) offspring, that may represent a 'fail-safe' or 'bet-hedging' strategy, optimising reproductive output in

Table 2. Mass per seed, ripe seeds per capsule and capsules (CH plus CL) per plants of *Viola elatior*, *V. pumila* and *V. stagnina*

Type	*V. elatior*	*V. pumila*	*V. stagnina*	
Mass per seed (mg)				
CH/CL[a]	1.80	1.08	0.68	
CH[b]	1.82±0.19 (5)	1.60±0.18 (35)	0.74±0.06 (13)	
CL[b]	1.80±0.27 (22)	1.08±0.20 (15)	0.59±0.09 (18)	
Seeds per capsule				
Type	*V. elatior*	*V. pumila*	*V. stagnina*	
CH/CL[c]	30.7±11.7 (82)	34.8±11.7 (46)	no data	
CH[b]	11.4±6.7 (5)	11.6±5.1 (35)	13.1±8.5 (13)	
CL[b]	13.0±5.3 (23)	11.8±4.7 (15)	10.7±2.9 (18)	
Year	Region	*V. elatior*	*V. pumila*	*V. stagnina*
Capsules per plant				
2001	Dyje	4.4±6.8 (20)	2.3±1.3 (20)	2.6±1.6 (47)
	Rhine	6.1±7.8 (84)	2.3±1.7 (85)	4.6±4.7 (35)
2002	Dyje	2.1±1.1 (11)	3.1±3.2 (18)	2.3±2.2 (52)
	Rhine	5.6±8.1 (52)	2.7±2.8 (48)	2.5±2.2 (62)

Data are mean±SD (*n*).

[a] Field collection; ripe CH and CL capsules do not differ morphologically and could thus not be separated, source: Hölzel and Otte (2004a).

[b] Experiment II, CH = open flowers hand pollinated with pollen of different source, CL = marked CL capsules, source: Eckstein and Otte (2005).

[c] Field collection, ripe CH and CL capsules do not differ morphologically and could thus not be separated, source: L. Eckstein (unpubl. data).

fluctuating environments (Berg and Redbo-Torstensson, 1998; but see Mattila and Salonen, 1995), and may cause large between-year variation in the degrees of selfing and outcrossing. In the North-American *V. pubescens*, selfing rate varies significantly between years, probably as a result of weather induced differences in pollinator activity (Culley, 2002).

In a pollination experiment, the exclusion of pollinators had little effect on the production of CH capsules and seeds in the three violets (Eckstein and Otte, 2005). Abortion of CH capsules was about 90% in *V. elatior* and *V. pumila*, while CL capsules produced abundant seeds. Similar mass per seed of *V. pumila* in capsules from field populations (Hölzel and Otte, 2004a), and CL seeds from a pollination experiment (Table 2; Eckstein and Otte, 2005) suggests that the majority of ripe seeds in natural populations may come from CL pollination.

The production of seeds was studied in situ in 2001–2003 in the floodplains of the Dyje River (B. Lučeničová, unpubl. data). The success of CH flowers (percentage mature capsules) differed substantially both among species and years: it was 24–67% in *V. elatior*, 19–75% in *V. pumila* and 10–90% in *V. stagnina*. Also, the share of CH seeds varied much among years and species: they contributed 40–71% to the total seed production in *V. elatior*, 41–60% in *V. pumila* and 1–61% in *V. stagnina*. Actually, the production of CL seeds may be underestimated since permanent plots were mown in late July each year, and also the potential CL seed production in late summer was not studied.

There was no indication of inbreeding depression in *V. pumila* and *V. stagnina* with respect to seedling biomass (Eckstein and Otte, 2005); there are no data for *V. elatior*. In the North-American *V. canadensis* L., the relative fitness of selfed and outcrossed offspring varied among plant traits, but inbreeding depression and differences between floral types were generally low (Culley, 2000). Similarly, for the European species *V. hirta*, *V. mirabilis* and *V. riviniana* no indication of inbreeding depression was found (Berg and Redbo-Torstensson, 1999). These results suggest that deleterious alleles, which may become homozygous as a consequence of selfing, have been purged out of the populations of the study species. In contrast, results from the same pollination experiment indicate that there may be outbreeding depression among distant populations in *V. stagnina* (Eckstein and Otte, 2005). Since populations of *V. stagnina* are highly isolated in the study area (Eckstein et al., 2004), gene flow is very low, and consequently genetic differentiation among populations rather high (L. Eckstein et al. unpubl. data).

There is a clear ranking of the three species with respect to seed mass (Table 2) with *V. elatior* seeds being about three times heavier than those of *V. stagnina*. CL seeds of *V. pumila* and *V. stagnina* have a significantly lower mass than CH seeds (Table 2). The same difference was found in the European *V. hirta*, whereas there were no differences between floral types in *V. mirabilis* and *V. riviniana* (Berg and Redbo-Torstensson, 1999). In *V. elatior* larger CL seeds showed better germinability (Eckstein and Otte, 2004), but for

V. pumila and *V. stagnina* there is no information, whether smaller seed mass of CL seeds (in comparison with CH seeds) will have any effects on traits such as survival, persistence, germinability and seedling growth. However, there was observational evidence that germination was lower in CL seeds than in CH seeds from our experimental plants, and germination percentages were lower in CL than in CH seeds in other species of *Viola* and in the CL *Oxalis acetosella* (Berg and Redbo-Torstensson, 1999, 2000; see Section 'Germination').

The total number of ripe capsules (CH plus CL) of field populations in the floodplains of the Dyje and Rhine varied from 2 to 6 in *V. elatior*, from 2 to 3 in *V. pumila*, and from 2 to 5 per flowering plant in *V. stagnina* among years and regions (Table 2). Hay making in June disrupts seed production, and the number of (CL) capsules produced during the second growth after mowing depends on climatic conditions. Potted plants in a pollination experiment in a common garden produced on average 8–12 CH flowers plus between 25 CL capsules in *V. elatior* and *V. pumila*, and 80 CL capsules in *V. stagnina* (Eckstein and Otte, 2005). However, due to the abortion of flowers, at the end of the season only 5.5±2.3 (mean±SD, $n = 24$) and 6.9±3.8 ripe capsules (CH plus CL) were found per plant in *V. elatior* and *V. pumila*. In *V. stagnina*, 12.3±4.6 ripe CH capsules developed, but the fate of CL capsules could not be followed because of the extremely high capsule production of this species.

Large capsules haphazardly collected from mature plants of unknown age from field populations contained about 30 and 35 seeds in *V. elatior* and *V. pumila*, respectively (no data available for *V. stagnina*). In contrast, potted plants in their second year of growth (first CH flowers) from a pollination experiment produced about 12 ripe seeds per capsule in all three species (Table 2; Eckstein and Otte, 2005).

The probability of flowering during the second year of life (CH flowers) is significantly related to the plant size, viz. height and number of leaves in the previous year in all three species (Eckstein, unpubl. data). Also in seedlings, which may produce some CL capsules during their first year, 'flowering' probability is size dependent (Eckstein, 2005).

The diaspores of all three species are ovoid seeds with a small elaiosome. Therefore, dispersal is potentially diplochorous. Owing to their hard shell, in a first phase of dispersal, seeds are expelled from the capsules when the valves dry out (Beattie and Lyons, 1975; Müller-Schneider, 1983). Average dispersal distance of seeds of some North-American violets by ballistic dispersal ranged between 0.8 and 2.1 m (Beattie and Lyons, 1975). The ballistic dispersal distance (studied ex situ) in plants from South Moravian populations of *V. elatior* and *V. pumila* was 1.35 m ($n = 435$, min $= 0$, max $= 2.39$, SD $= 0.78$) in CH and 1.19 m ($n = 245$, min $= 0$, max 3.07, SD $= 0.69$) in CL seeds of the former, and 1.36 m ($n = 101$, min $= 0$, max $= 2.88$, SD $= 0.80$) in CH and 0.68 cm ($n = 177$, min $= 0$, max 2.54, SD $= 0.60$) in CL seeds of the latter. Differences in the dispersal distance of CH and CL seeds were significant in both species (B. Lučeničová, unpubl. data). In a second phase, ricinoleic acid in the appending elaiosomes (Bresinsky, 1963) may potentially attract ants, which may carry the seeds into their nests (Beattie and Lyons, 1975). Here, the fat-containing elaiosome is removed and the seeds, still viable, deposited on the ants refuse heap. However, for the three species treated here, there are no observations of ant dispersal.

Germination

In an experiment in which seed banks from natural populations were sampled during 13 occasions over 2 years and analysed under constant conditions in a greenhouse, all three species showed similar seasonal germination patterns (N. Hölzel, unpubl. data). Seeds came out of dormancy during autumn and reached their highest germinability during winter and early spring, whereas between May and September almost no germination occurred. In both years the highest germination was observed in samples from mid March with maximum densities per m^2 of 420 in *V. elatior*, 140 in *V. pumila*, and 160 in *V. stagnina*. These laboratory results suggest that all three species have a pronounced main germination period during early spring.

In an experiment under outdoor conditions, in *V. elatior* and *V. pumila* spring germination started after a temperature sum of ca. 300 °C or 33 days with daily averages above 5 °C (counted from the last day with a daily average <1 °C), which is usually between mid-March and the first week of April (Hölzel and Otte, 2004a). In both species a first distinct peak was reached about one week after the onset of germination. Ninety per cent of the final germination occurred within 4 weeks in *V. pumila*, whereas in *V. elatior* the same percentage germination was reached after 11 weeks. An even higher degree of bed-hedging was observed in *V. stagnina*: In this species first distinct germination peaks occurred only in spring of the second and third year after sowing. Maximum germination rates reached 59% and 66% in *V. elatior* and *V. pumila*, respectively, but only 18% in *V. stagnina*. In the latter there were presumably still viable but dormant seeds when the experiment was stopped. Fresh seeds of the three violets showed almost no germination under laboratory conditions even after various types of stratification treatments (Hölzel and Otte, 2004a). Presumably, their thick-coated seeds crucially depend on soil biological agents and imbibition to come out of dormancy. When seeds of

Table 3. Maximum seed densities (seed m^{-2}) in the soil seed bank under populations of *Viola elatior*, *V. pumila* and *V. stagnina* (Hölzel and Otte, 2004b)

Sampling depth (cm)	*V. elatior* ($n = 3$)	*V. pumila* ($n = 21$)	*V. stagnina* ($n = 4$)
0–10	2660	630	770
0–5	2170	560	770
5–10	490	140	70

V. elatior and *V. pumila* were stratified under outdoor conditions either in moist or flooded soil, the seeds from flooded soil showed higher germination rates in the growth chamber in February, March and April (Smolka, 2003).

As in many other violets, all three species share the ability to build up persistent soil seed banks (Hölzel and Otte, 2001, 2004b). In *V. pumila* and *V. stagnina* measured densities in the soil seed bank rarely exceeded 500 seeds m^{-2} (Table 3). In *V. elatior*, under a very dense population in an irregularly late mown Molinion-meadow, up to 2660 seeds m^{-2} could be found, which is probably an exceptionally high figure. Usually, more than 80% of all seeds are concentrated in the upper 5 cm of the soil layer. Generally, persistent seed banks seem to be an important part of the life strategy in all three species. There are numerous reports about sudden emergence in the course of topsoil disturbances after long-term absence from the aboveground vegetation (cf. Pullin and Woodell, 1987; Quinger, 1993; Croft and Preston, 1996; Hölzel, 1999; Käsermann, 1999a, b; Romahn and Kieckbusch, 2001; Weeda, 2002).

Response to competition and management

In a competition experiment with seedlings of the rare *V. elatior* and the common *V. mirabilis* in Estonia, the former species appeared to be more sensitive to light availability (Moora et al., 2003). During the second year of growth, the density of *V. elatior* decreased in untreated plots, where competition for light was more severe. In contrast, diffuse competition of a grass canopy had no significant effect on seedling survival of *V. elatior*, *V. pumila* and *V. stagnina* (Eckstein, 2005), and only minor effects on height growth. However, the latter experiment was carried out during a year with a hot and dry summer, in which water addition and site conditions (soil water availability) probably overruled interspecific interactions by graminoids and other herbs.

Field studies show that a regular management through mowing, which is considered to reduce the asymmetry in competition for light (Lepš, 1999), has positive effects on the germination of *V. pumila* and increases the density of various life-cycle stages in all three violets (Eckstein et al., 2004; Bissels et al., in press), with managed populations containing 6–90 times more seedlings than abandoned populations. This indicates that especially the early life-cycle stages are rather weak competitors. Seedling density was negatively correlated with the percentage cover of bryophytes, whereas density of large vegetative plants increased significantly with increasing bryophyte cover (Eckstein et al., 2004). This may be because seedling emergence is impeded by bryophytes, whereas those plants that manage to establish within the bryophyte carpet may benefit from higher soil moisture in the bryophyte layer in later phases of the life cycle. Similarly, for *V. stagnina* regular management, reducing the abundance of competitors (Pullin and Woodell, 1987), and soil disturbance through flooding and animal activity, enhancing germination of dormant seeds from the soil seed bank (Croft and Preston, 1996), were identified as suitable and necessary management measures. The high percentage seedling emergence in *V. elatior* and *V. pumila* under a litter cover of up to 0.8 kg m^{-2} (Eckstein and Donath, 2005), shows that seedlings of these species apparently have enough reserves to penetrate a moderate litter layer, and that their thick-coated seeds need constant moisture and/or high microbial activity for germination. Additionally, the experimental results suggest that the successful establishment of these rare species at suitable sites can be enhanced by the transfer of seed containing plant litter as is currently done along the northern Upper Rhine (Donath et al., 2003; Hölzel and Otte, 2003).

A comparison of *V. elatior* and *V. pumila* indicated that the former species invested more biomass into vegetative tissues (Eckstein and Otte, 2004). *Viola elatior* showed an efficient use of nitrogen for growth and the development of storage organs (roots) to sustain growth and reproduction during unfavourable periods. This is a typical trait combination of stress-tolerant plants (Grime, 2001). At the same time, *V. elatior* can grow very tall, which may enable the species to develop a high competitive ability. This combination of traits appears to be well adapted to its primarily successional habitats (the section ‘Habitat’). This higher competitive ability is obviously paid for by a low mowing compatibility which is reflected by the absence of the species from regularly early mown meadows. *Viola pumila* is probably a weak competitor also in later life-cycle stages since it remains rather low-growing or is climbing-ascending among neighbouring grasses to keep up with the vegetation but never overtopping it. The low competitive ability in *V. pumila* is compensated for by a high tolerance towards early and frequent mowing or pasture. Also, the scattered occurrence of *V. pumila* and *V. stagnina* within populations (the section 'Spatial distribution of plants within populations') and low cover-abundance scores in vegetation relevés (the section 'Communities') indicate relatively low competitive abilities.

Herbivores and pathogens

Some capsules in South Moravian populations of all three species (studied in 2002–2003; B. Lučeničová, unpubl. data) were infested by the larvae of *Orbitis cyaneus* (L.) of the Curculionidae family (Coleoptera). Larvae develop inside the capsules and feed on young seeds; the infested capsules can be recognised by perforated valves and contain a few or even no undamaged seeds. The infestation rate in six CH capsules was between 9.7% (*V. elatior* in 2002) and 66.7% (*V. stagnina* in 2003; but only 6 CH capsules developed!), that of CL capsules between 14.6% (*V. stagnina* in 2003) and 41.4% (*V. stagnina* in 2002). These data suggest that the insects can substantially reduce seed production.

Mycorrhiza

The comparison of arbuscular mycorrhizal (AM) fungi in the roots of the rare *V. elatior* and the common *V. mirabilis* in Estonia with DNA-techniques revealed twelve AM fungal sequence types, ten of which were shared by both species, suggesting mainly quantitative differences in mycorrhizal colonisation between the species (Öpik et al., 2006). The variability of AM fungal community composition was higher in *V. elatior* than in *V. mirabilis*, probably due to rare fungal types colonising only the roots of the former species.

There is no information on the presence or absence of mycorrhiza and its type for *V. pumila* and *V. stagnina*.

Physiological data

No data available for the species.

Biochemical data

No data available for the species.

Genetic data

Chromosome counts in the treated species are summarised in Table 4. *Viola stagnina* has $2n = 20$, and *V. elatior* and *V. pumila* have $2n = 40$. The only count of $2n = 40$ in *V. stagnina* (Krogulevič and Rostovceva, 1984) is erroneous, made actually in *V. pumila* (voucher specimens seen in the herbarium NSK by J. D.). In contrast to *V. canina*, *V. riviniana* and *V. rupestris*, no plants with accessorial (B) chromosomes have been recorded so far (cf. Valentine, 1958, 1962; Schmidt, 1961, Table 4).

The basic chromosome number in the genus *Viola* is $x = 6$ (Clausen, 1926; Valentine, 1962; Ballard et al., 1999). Its relation to $2n = 20$, found in the 'diploid' members of subsection *Rostratae*, remains unclear. Nordal and Jonsell (1998), studying allozymic variation, first recorded fixed heterozygosity in *Viola* and suggested that *V. rupestris* with $2n = 20$ is a tetraploid, while *V. canina* and *V. riviniana* with $2n = 40$ are octoploids. Marcussen and Nordal (1998) and Marcussen and Borgen (2000) demonstrated the same for *V.* subsect. *Viola*. It can be assumed that chromosome numbers in V. subsect. *Rostratae* and V. subsect. *Viola* are highly derived, and that the species of these subsections with $2n = 20$ have to be considered (palaeo)tetraploid, derived from $x = 5$. True diploids (with $2n = 10$) are known neither within subsection *Rostratae* (cf. Clausen, 1927; Valentine, 1958, 1962) nor within the whole section *Viola* (Clausen, 1927; Marcussen and Borgen, 2000). So subsection *Rostratae* consists of tetraploids (e.g. *V. reichenbachiana*, *V. rupestris* and *V. stagnina*), octoploids (*V. canina*, *V. elatior*, *V. pumila* and *V. riviniana*), and (sub-)dodecaploids (*V. lactea* with $2n = 58$; Valentine, 1962; *V. sieheana* with $2n = 60$; Th. Marcussen, pers. comm.).

Studying chromosome pairing in the hybrids between western European rostrate violets, Moore and Harvey (1961) suggested the alloploid origin of *V. canina*, *V. lactea* and *V. pumila* and assumed that these species have one genome in common, probably that of *V. stagnina*. Clausen (1927), basing purely on morphological evidence and tetraploid chromosome number, interpreted *V. elatior* as autopolyploid derivate of *V. stagnina*.

A study on eight populations of *V. elatior* from Austria, Germany, Italy and Switzerland, using protein polymorphisms revealed that 82% of the genetic variance rested among populations, whereas the remaining 18% were found among individuals within populations (Gygax, 2001). When eight individuals of one population of *V. pumila* were included in the analysis of molecular variance (AMOVA), 19% of the genetic variation was found between species, 67% among populations and 14% within populations. In contrast, in an analysis based on amplified fragment length polymorphism (AFLP) in 930 individual plants of the three violet species from 50 populations, 51% of the genetic variance rested among the three species, only 18% among populations (within species) and as much as

Table 4. Chromosome numbers of *Viola elatior*, *V. pumila* and *V. stagnina* and the hybrid *Viola canina* × *V. stagnina*

	Country	Reference
Viola elatior		
$n =$ ca. 20	Switzerland? Cultivated	Clausen (1927)
$2n = 40$	Not indicated	Gershoy (1934)
$2n = 40$	Poland	Skalińska et al. (1977)
$2n = 40$	Germany	Lippert and Heubl (1989)
$2n = 40$	Slovakia	Májovský et al. (1987)
$2n = 40$	Slovakia	Murín and Májovský (1992)
Viola pumila		
$2n = 40$	Not indicated	Gershoy (1934)
$2n = 40$	Germany	Schöfer (1954)
$2n = 40$	Sweden	Moore and Harvey (1961)
$2n = 40$	Sweden	Persson (1969)
$2n = 40^*$	Russia, Siberia, Irkutsk Region	Krogulevič and Rostovceva (1984)
$2n = 40$	Czech Republic	Měsíček and Jarolímová (1992)
Viola stagnina		
$n =$ ca. 10	Sweden	Heilborn (1926)
$n = 10$	Not indicated	Clausen (1926)
$n = 10$	Denmark? Cultivated	Clausen (1927)
$n = 10$	Denmark	Clausen (1931)
$2n = 20$	Not indicated	Gershoy (1934)
$n = 10$	Germany	Tischler (1934)
$2n = 20$	Germany	Schmidt (1961)
$2n = 20$	British Isles	Moore and Harvey (1961)
$2n = 20$	Poland	Skalińska et al. (1977)
$2n = 20$	Germany	Lippert and Heubl (1989)
$2n = 20$	Czech Republic	Měsíček and Jarolímová (1992)
$2n = 20$	Norway	Røren et al. (1994)
$2n = 20$	Czech Republic	V. Jarolímová (unpubl. data)
Viola canina × *V. stagnina*		
$2n = 30$	Norway	Røren et al. (1994)
$2n = 30$	Czech Republic	V. Jarolímová (unpubl. data)

Note: The count marked with an asterisk was published under *V. stagnina* but the voucher specimen in NSK is *V. pumila.*

31% among individuals within populations (Table 5). The differences between the two studies are most probably due to a lower number of populations sampled across a much larger geographic range by Gygax (2001), which results in larger among-population genetic differences.

AMOVA analyses for each of the species separately revealed that 60–64% of the genetic variance rested within populations, 30–37% among populations and 3–6% between regions. The genetic differentiation among populations (F_{ST}) was 0.40, 0.36 and 0.38 in *V. elatior*, *V. pumila* and *V. stagnina*, respectively (L. Eckstein et al., unpubl. data). Similarly, population differentiation of the North-American *V. pubescens* was 0.29 and 0.34 in two studies that included six and nine populations, respectively (Culley and Wolfe, 2001; Culley and Grubb, 2003). Each of the three violet species was characterised by a number of unique AFLP-markers, i.e. markers with a frequency of $>90\%$ in one of the violet species (Table 5). *Viola elatior* and *V. pumila* shared 14 bands, i.e. the frequency of these markers in *V. stagnina* was $<10\%$.

Hybrids

Viola is one of the genera where interspecific hybridisation frequently occurs. First detailed accounts of natural hybridisation on central European or European scale were presented by Borbás (1890), Becker (1902, 1910) and Valentine (1975). Gershoy (1934), Schmidt (1961) and Valentine (1962) produced artificial hybrids and analysed their growth and fertility; for a summarising table see Valentine (1962). Among 11 European species, including *V. pumila* and *V. stagnina*, and six American species of *Viola* subsect. *Rostratae*, 44

Table 5. (a) Distribution of molecular variance among species (= groups), among populations (within species) and among individuals (= within populations) using analysis of molecular variance, and (b) number of unique (i.e. frequency of >90% in one species) and of shared bands (i.e. frequency in the third species <10%) in *Viola elatior*, *V. pumila* and *V. stagnina* and all two-species combinations. The analysis was based on 120 polymorphic AFLP markers obtained with four primer combinations and included 930 individual plants from 50 populations

(a)

Source of variation	DF	SS	VC	% variation	*P*
Among groups	2	7348.9	11.58	50.54	<0.0001
Among populations within groups	47	3930.6	4.11	17.95	<0.0001
Within populations	880	6353.6	7.22	31.51	<0.0001
Total	929	17633.1	22.91	100.00	

(b)

Species	Unique bands	Species combination	Shared bands
V. elatior	8	*V. elatior*/*V. pumila*	14
V. pumila	12	*V. elatior*/*V. stagnina*	7
V. stagnina	4	*V. pumila*/*V. stagnina*	9

Abbreviations: DF, degrees of freedom; SS, sum of squares; VC, variance components; *P*, significance level.

artificial hybrids were observed. Seeds of some hybrid combinations did not germinate, others died in seedling stage, whereas plants of many hybrid offspring, among them *V. stagnina* × *V. canina* and *V. pumila* × *V. lactea*, were moderately vigorous or vigorous. Many hybrids between parents of the same ploidy level and across ploidy levels were largely or completely sterile (Valentine, 1962); but see Nikitin (2001) for contradictory statement about the hybrid between *V. canina* s.l. and *V. pumila* (as *V. nemoralis* × *V. accrescens*).

The three species treated here cross both among themselves and with other members of the subsection *Rostratae* under natural conditions. Following hybrid combinations were recorded in the field in Germany and Czechia (Kirschner and Skalický, 1990; Bäßler, 2002): *Viola elatior* × *V. pumila* (*V.* × *skofitziana* Wiesb.; for descriptions and further information see Wiesbaur, 1886; Becker, 1902, 1909), *V. elatior* × *V. stagnina* (*V.* × *torslundensis* W. Becker) and *V. pumila* × *V. stagnina* (*V.* × *gotlandica* W. Becker) as well as *Viola canina* × *V. elatior* (*V.* × *mielnicensis* Zapal.), *V. canina* × *V. pumila* (*V.* × *semseyana* Borbás), *V. canina* × *V. stagnina* (*V.* × *ritschliana* W. Becker) and *V. pumila* × *V. reichenbachiana* (*V.* × *gerstlaueri* L. Gross). The hybrids *Viola pumila* × *V. riviniana* and *V. pumila* × *V. rupestris* were found in Sweden and France (Becker, 1910), the hybrid *V. riviniana* × *V. stagnina* in Norway (Th. Marcussen, pers. comm.). Recently, several hybrid combinations involving *V. elatior*, *V. pumila*, or *V. stagnina* were described from eastern Europe and southern Siberia by Nikitin (2001, 2003).

Some hybrid plants listed above were distributed in exsiccate collections; we have seen the specimens of *V. pumila* × *V. stagnina* (Societé pour l'échange des plantes vasculaires de l'Europe et du basin mediterranéen no. 16265, seen in BRNM; Becker Violae Exs. no. 118, seen in PR and W) and *V. pumila* × *V. riviniana* (Dörfler Herb. Norm. no. 3103, seen in PR).

Morphological characters and other traits of hybrids between *V. canina* and *V. stagnina*, probably the most common hybrid involving one of the species treated here, were studied in England and Ireland by Valentine (1975) and in Norway by Røren et al. (1994). According to the former, they are intermediate in leaf characters, resemble *V. canina* in flowers and *V. stagnina* in general appearance. According to Røren et al. (1994), hybrids are intermediate but come closest to *V. canina* from which they are most difficult to distinguish. When morphometry is applied, they somewhat overlap in the canonical variate analysis diagram with *V. canina* and *V. stagnina*, and no single character distinguishes them from their parents. In our limited experience from the surrounding of Olomouc in central Moravia (Czech Republic), they can be best recognised in the field through their vigorous growth and rich flowering but, at the same time, trough their complete sterility of CH and CL flowers (cf. also Valentine, 1975; Røren et al., 1994). A few hybrid specimens of *V. elatior* with *V. pumila* and *V. stagnina* we had the opportunity to study (in BRNU, OP, PR, W and WU) kept much of the indument of the hairy parent, as did those of *V. pumila* and *V. rupestris*. The sterile hybrids between *V. pumila* and *V. stagnina* occur in a few places along the Upper Rhine, where they

Table 6. Grid cell frequency and decline of *Viola elatior*, *V. pumila* and *V. stagnina* in Czechia (Danihelka, unpubl. data) and Germany (data of the German flora mapping project, provided by the internet source FLORAWEB; BfN, 2005)

	V. elatior		*V. pumila*		*V. stagnina*	
	Germany	Czechia	Germany	Czechia	Germany	Czechia
Grid cells with records	130	34	124	53	275	71
Frequency (%)	4.4	5.0	4.2	7.8	9.2	10.5
Grid cells with records only before 1950	59	18	76	26	116	31
Decline (%)	45.4	52.9	61.2	49.1	42.2	43.7

built relatively dense clonal carpets. For a safe identification of hybrids, a chromosome count is helpful if putative parents differ in ploidy level.

Hybrids among the species treated here seem to be rarer than generally believed. Among hundreds of plants we observed and studied in the floodplain of the Rhine River in Germany and along the Dyje River in southern Moravia during the last decade, we were able to identify only a few hybrid plants with certainty even though flower periods of all three species overlap, and *V. pumila* and *V. stagnina* or *V. elatior* and *V. pumila* sometimes grow intermingled at one site. Recent introgression can almost be ruled out as hybrids are usually sterile. This pattern is in contrast with the situation known in *Viola* subsect. *Viola* (Marcussen and Borgen, 2000; L. Eckstein, pers. observ.) or in the *Viola* subsect. *Boreali-Americanae* (Valentine, 1962) where hybridisation is very common, and in the latter, hybrids are often fertile and introgression occurs.

Status of the species

The three species treated here are among those central European vascular plants that require priority conservation measures (Schnittler and Günther, 1999). The species are red-listed in several central European countries. Across central Europe, which represents between 5% and 33% of the species range (Schnittler and Günther, 1999), *V. elatior*, *V. pumila* and *V. stagnina* can be considered as endangered (IUCN category: EN). The rarity of the three violet species in central Europe can be exemplified by data from the German flora mapping project (BfN, 2005). *Viola elatior* and *V. pumila* occur in less than 5% of all grid cells. *Viola stagnina* is roughly twice as frequent as the other two species, which is mostly due to its wider distribution on acidic substrates in the northern central European lowland. All three species have undergone a significant decline during the last century that comprises 40% to more than 60% of all formerly occupied grid cells. The situation in Czechia was similar (Table 6). Declines are most dramatic in *V. pumila* and *V. elatior* at the northern edge of their central European range in eastern Germany along the rivers Saale and Elbe and in *V. pumila* along the Danube in Bavaria (BfN, 2005). Further, the remaining populations are often small and highly fragmented (Eckstein et al., 2004). Many of these remnants exist under sub-optimal habitat conditions along linear structures such as ditches, track and field margins (Liepelt and Suck, 1989; Böger, 1991; Hölzel, 1999). Large and vital populations are usually confined to nature reserves where they receive an adequate management (Hölzel et al., 2002; Eckstein et al., 2004). Processes responsible for the decline of the study species are: (i) grassland transformation into crop fields after 1945, grassland eutrophication, abandonment and afforestation of meadows, (ii) lowering of the ground water table and drainage, (iii) removal of small-scale habitat elements (e.g. fringes, hedgerows, ditches), (iv) intensive grazing, (v) peat and sand mining and soil filling, and (vi) reduced flood dynamics (Korneck et al., 1998). During the last decade, the abandonment of regular grassland management and consequent accumulation of thick layers of litter and spread of shading shrubs and trees are sources of major negative impact especially in eastern central European countries with dramatic changes in agricultural land use in the course of transition to market economy.

Acknowledgements

We are much indebted to W. Gutermann for nomenclatural consultations, R. May and H. Niklfeld for records of the three species, M. Öpik and M. Zobel for information on mycorrhiza, B. Wolters for unpublished information on secondary habitats of *V. elatior*, B. Lučeničová for numerous results from her unpublished diploma thesis, A. Skoumalová for the fine drawings of the species, A. Morton for consultation on mapping software and J. Scholz-vom Hofe for field assistance. Annette Otte, E.J. Jäger, Th. Marcussen, K. van den Hof, D. Simmering and an anonymous referee provided insightful comments that improved the quality of the manuscript. The work was supported by grants of the Deutsche Forschungsgemeinschaft (EC 209/2-1, EC 209/3-1), the Justus-Liebig-University Giessen and the Stifterverband für die Deutsche Wissenschaft (to R.L.E.), by the German Federal Agency for Nature Conservation (to N.H.), by the Ministry of Education of the Czech Republic, project no. MSM 0021622416 and by the long-term research plan no. AV0Z60050516 of the Institute of Botany, Czech Academy of Science (to J.D.). All help and support is gratefully acknowledged.

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