

BIOLOGICAL FLORA OF CENTRAL EUROPE

Biological flora of Central Europe: *Muscari tenuiflorum* Tausch

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Abstract

Muscari tenuiflorum Tausch is a bulbous, perennial, facultative wintergreen geophyte native to Central Europe, where it is rare and vulnerable. In Central Europe, *M. tenuiflorum* occurs in xerothermic plant communities in regions with low precipitation. This article reviews the taxonomy, morphology, karyology, ecology and population biology of the species.

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Taxonomy and distribution

Taxonomy

Muscari tenuiflorum Tausch–Schmalblütige Traubenhyazinthe

Synonyms: *Bellevalia tenuiflora* (Tausch) Nyman; *Leopoldia tenuiflora* (Tausch) Heldr.; *M. alpinum* Gay ex Baker; *M. buschiricum* Parsa; *M. iranicum* Parsa; *M. tubiflorum* Steven; *M. wallii* Rech. f. (Davis and Stuart, 1980, 1984; Garbari et al., 1996; Rechinger, 1990).

The genus *Muscari* Mill., which comprises about 50 species distributed from temperate Europe, the Mediterranean to Central Asia, belongs to the subfamily Hyacinthoideae Link. of the family Hyacinthaceae Batsch (Speta, 1998a, b). The volume and infrageneric arrangement of *Muscari* is not yet settled.

An approach of taxonomical splitting has been put forward by Garbari and Greuter (1970). They proposed

a division of *Muscari* into the genera *Muscari* Mill., *Leopoldia* Parl., *Muscarimia* Kostel. ex Los. and *Pseudomuscari* Garbari & Greuter mainly on the basis of karyological investigations (Garbari, 1966, 1968, 1969). However, this approach was criticized several times. Authors dealing with the evolution of *Muscari* (e.g. Davis and Stuart, 1980, 1984; Speta, 1982, 1989) found transitions in character expression and suggested to treat the genera of Garbari and Greuter (1970) only as subgenera. A molecular study of plastid DNA sequences proved the monophyly of *Muscari* and supports a broader genus concept (Pfosser and Speta, 1999).

M. tenuiflorum belongs to the subgenus *Leopoldia* (Parl.) Peterm. The species of this subgenus have slightly zygomorphic fertile flowers that are brownish, yellowish or greenish and differ remarkably from the bluish or violet sterile flowers at the top of the inflorescence (Bentzer, 1973; Speta, 1989). *M. tenuiflorum* was described by Tausch (1841). He did not give a detailed geographical locality, but he stated the general occurrence of *M. tenuiflorum* in Austria and Bohemia. In his

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monographic survey about *Leopoldia* Heldreich (1878) transferred *M. tenuiflorum* into the genus *Leopoldia* and created the combination *L. tenuiflora* Tausch (Heldr.). This synonym was and is used by authors preferring a narrower genus concept (e.g. Garbari et al., 1996; Lozina-Lozinskaya, 1935). Further nomenclatural studies seem to be necessary, as diagnostic characters of some of the names mentioned above do not fit in every respect to the Central European plants. It concerns e.g. the length of fertile flowers (up to 11 mm) and the insertion of stamina (6–7 mm above base of flower) in *M. wallii* according to Rechinger (1951; for corresponding data see Inflorescence and flower).

Geographical distribution

Global distribution

The distribution of *M. tenuiflorum* ranges within the submeridional and south-temperate zone (sensu Meusel et al., 1965) from south-eastern Europe to Anatolia, Transcaucasia and the Iranian Highland (Fig. 1). There are occurrences isolated from the main range in Central Italy (Brilli-Cattarini, 1964; Brilli-Cattarini and Ballelli, 1979), north-east Italy (Garbari et al., 1996) and in Central Europe. In the latter, *M. tenuiflorum* is restricted to the Bohemian and Central German dry region. The investigation of herbarium specimens revealed that there are still further occurrences in Saudi Arabia, i.e. Tabal Aja and Bir Iba (specimen E 00118784 and E 00129893 of the Edinburgh herbarium).

The altitudinal range of *M. tenuiflorum* extends to 1250 m.a.s.l. in Italy (Garbari, 1982), to 2400 m.a.s.l. in Turkey (Davis and Stuart, 1980, 1984) and to 2600 m.a.s.l. in Iran (Rechinger, 1990). The range of *M. tenuiflorum* can be shortly described with the formula: sm-stemp c4–6 EUR–VORDAS (Jäger and Werner, 2002).

Distribution in Germany

M. tenuiflorum reaches its north-western range edge in Germany, where it currently occurs within 16 approximately 12 × 12 km grid cells in southern Saxony-Anhalt and northern Thuringia (Fig. 2). Some occurrences have been reported from Bavaria, by e.g. Ascherson and Graebner (1905–1907), Vollmann (1914), Hegi (1939), Walter and Straka (1970) and Rauschert (1978). However, these records cannot be confirmed (Haeupler and Schönfelder, 1988). Today, *M. tenuiflorum* is extinct in Bavaria, and the historical occurrences are believed to have been introduced (Schönfelder and Bresinsky, 1990).

Most occurrences of *M. tenuiflorum* in Germany are found within the Central German dry region, situated in the rain shadow of the Harz mountains. In that area, long-term annual rainfall does not exceed 500 mm year⁻¹ (Bohnstedt, 1959). Due to low annual rainfall in combination with edaphic and microclimatic conditions (Schubert et al., 1995), a number of other plant species rare in Germany are found here and have been classified phytogeographically as continental (ponctic/pannonic) plant species (e.g. Drude, 1902; Meusel,

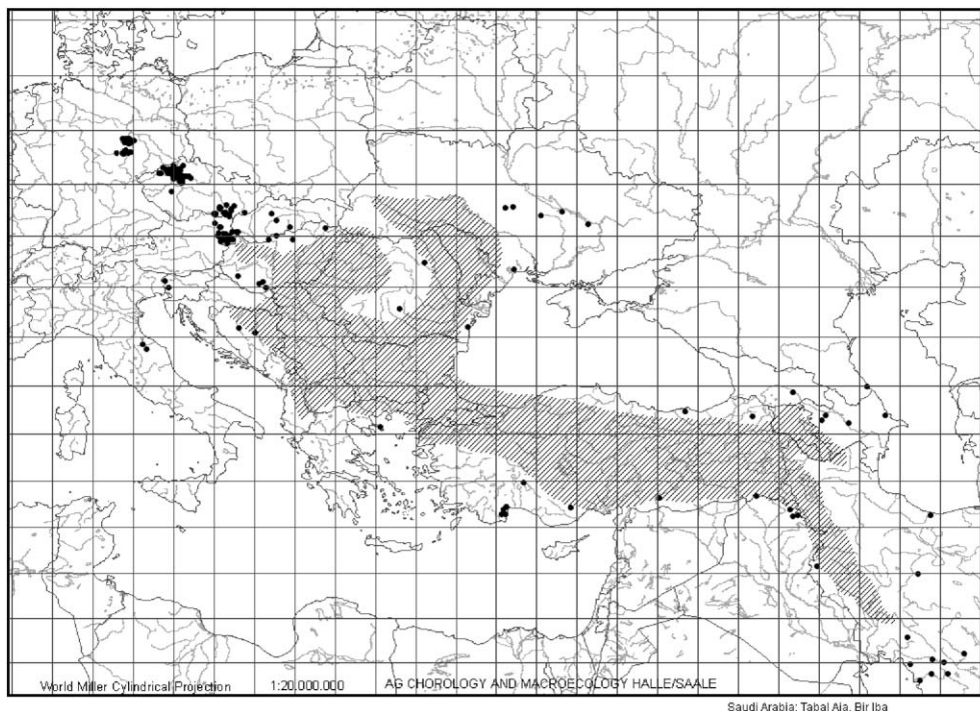


Fig. 1. Global distribution of *M. tenuiflorum*.

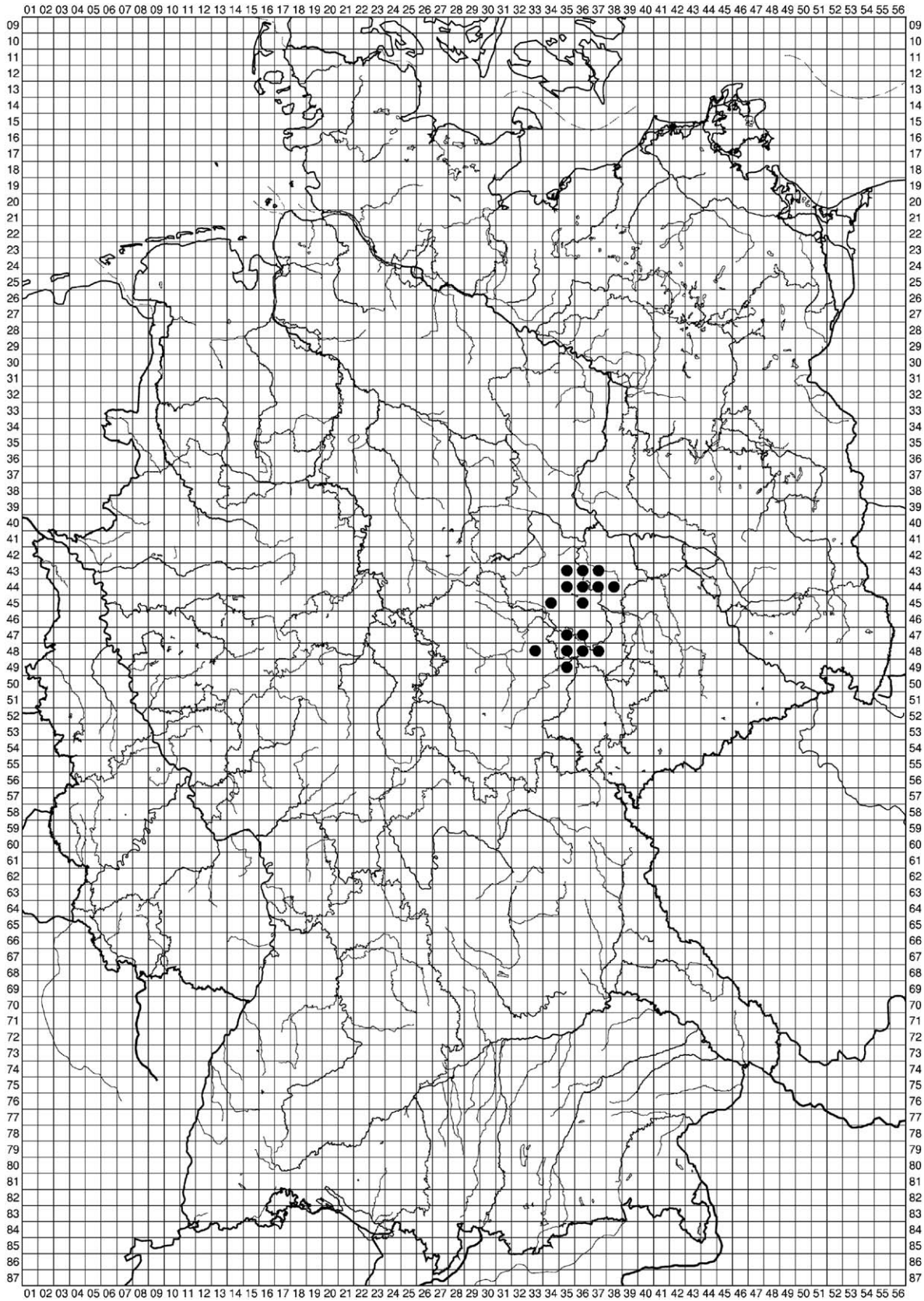


Fig. 2. Distribution of *M. tenuiflorum* in Germany. That map was compiled according to Benkert et al. (1996) taking into account data from Korsch et al. (2002) and own observations. Doubtful records were omitted, e.g. in the area of the Kyffhäuser mountains, where the species was probably confused with *M. comosum* (Barthel and Pusch, 1999; Rauschert, 1978). Further local distribution maps concerning Central Europe were published by Rauschert (1978; with localities in Bohemia, Czech Republic) and Große (1985).

1943). These species show a similar local distribution as *M. tenuiflorum* in Central Europe, e.g. *Hornungia petraea*, *Iris aphylla*, *Scorzonera parviflora* and *Stipa dasyphylla*. Korsch (1999) subsumed plant species with this local distribution pattern in Germany under the “*Astragalus exscapus*-type”.

First record in Central Germany: A detailed historical outline about the first records of *M. tenuiflorum* and *M. comosum* in Central Germany and the confusion of these species was provided by Rauschert (1966). *M. tenuiflorum* was recorded in Central Germany for the first time in the 16th century by Valerius Cordus († 1544). The record was published after the death of Cordus, by K. Gesner in 1561. Cordus found *M. tenuiflorum* which he called “*Hyacinthus syluestris*”, in the vicinity of the porphyry hill “Petersberg” north of Halle/Saale.

Morphological and anatomical characterization

Morphology

M. tenuiflorum is a bulbous perennial with a short, flattened underground stem covered by enlarged and fleshy cataphylls and leaf bases (= bulb scales) functioning as storage organs. The bulb is cream-white to light yellow, 2.5–4.5 cm high and 1.8–3.2 cm in diameter when mature, covered by a greyish/brown papery tunic. Bulb scales are imbricate. Up to 25 adventitious roots are formed in a year, branched to second degree, up to 8 cm long, 0.5–1.5 mm thick, white when alive, light yellow to light brown when dead. Contractile roots (2–3 mm thick) occur mainly in juvenile plants, rarely in adults. The assimilating leaves are narrow, up to 1.2(–1.5) cm wide and up to 35(–46) cm long including underground parts. They are green to greyish-green, slightly glaucous, slightly succulent and light yellow at the base of the above ground part. Total height of the stem including inflorescence is 25–55(–75) cm. The stem system of a mature plant is a sympodium. A stem generation of an adult plant consists usually of 1 cataphyll, followed by 3–6 assimilating leaves, another single cataphyll which bears the renewal bud in its axle and the single inflorescence (raceme) in terminal position. The inflorescence consists of fertile and sterile flowers. The tubular perigone of fertile flowers (6–8 mm long, pale beige, the midvein of each tepal is a narrow light green line) is sharply constricted distally and coloured dark brown/black at its tip. Sterile flowers form a violet showy structure at the top of the inflorescence. The gynoecium consists of 3 locules, each with 2 superposed ovules. The fruit is a capsule. Seeds are black, ovate to globose, 2(–2.5) mm in diameter. Dry weight of fertile seeds varies between 2.5 and 5.1 mg (mean 3.8 ± 0.64 SD, $n = 148$).

Germination stage

Germination is epigeal as is typical for all species of the genus *Muscari* (Speta, 1998a). The cotyledon appears aboveground as an unifacial cylindrical leaf becoming 50–100 mm long and 1–2 mm wide. After germination, the seed remains attached to the tip of the cotyledon as long as the cotyledon absorbs nutrients from the endosperm. The seedlings have a typical hook shape (Fig. 3a).

As in many other liliiflorous species the seedling of *M. tenuiflorum* belongs to the “*Juncus*-type” described by Tillich (1992). The cotyledon is the only assimilating leaf organ in the first year. It can be subdivided into leaf base (= cotyledonary sheath with slit-shaped opening, see Fig. 3b) and hyperphyll (Tillich, 1995). The cotyledonary sheath encloses 2 cataphylls with closed leaf sheaths. The inner cataphyll surrounds the renewal bud for the following year (Fig. 3c). The bulb is formed within the cotyledonary sheath by enlargement of both cataphylls. At the end of the first season the bulb reaches a size of 10×3 (–4) mm.

Besides the primary root, up to 2 further adventitious absorptive roots are formed in the first year which can be branched to first degree. Only the primary root is contractile in its upper part and pulls the small bulb into the ground to a depth of 2–3(–3.5) cm.

Juvenile stages

The bulb of 1-year-old plants consists of the thin remains of the cotyledonary sheath, 2 cataphylls of the

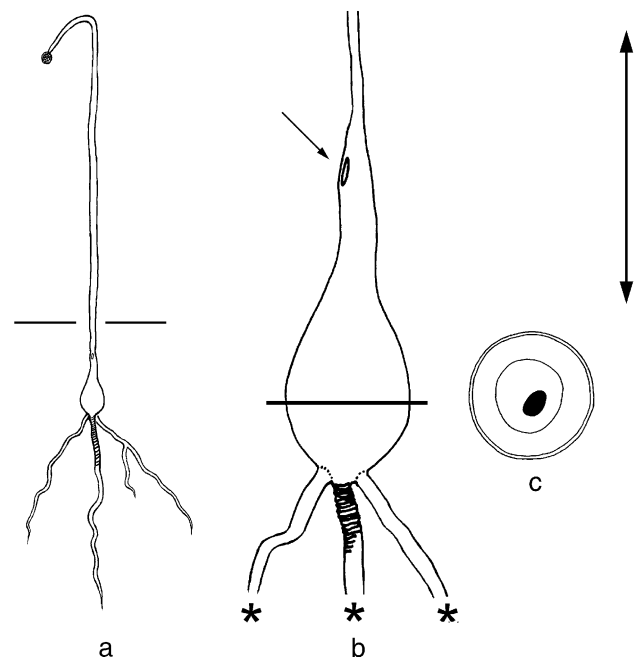


Fig. 3. Seedling of *M. tenuiflorum*. (a) Habit, (b) seedling bulb with slit-shaped opening of cotyledonary sheath (see arrow) and contractile root, (c) Cross-section through seedling bulb, renewal bud portrayed black. Scale bar: (a) 5 cm; (b, c) 1 cm.

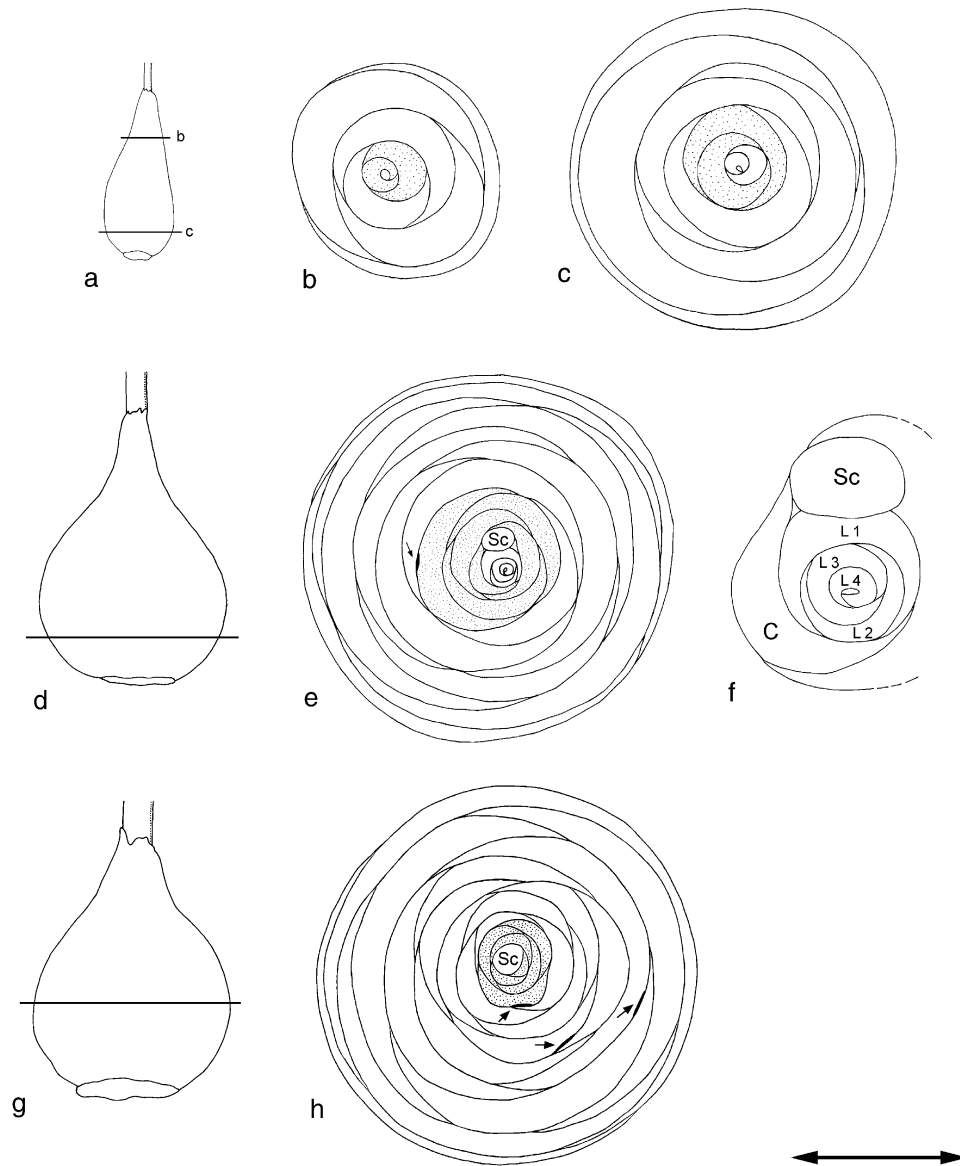


Fig. 4. Shape of juvenile and mature bulbs with corresponding cross-sections, performed in June. Leaf organs of the current generation are dotted. Lines in (a), (d) and (g) indicate where bulbs were cut. Fig. (f) is a detail from (e): Sc = scape, C = cataphyll, L1-L4 = leaf initials of the stem generation of the next year. Arrows point to remnants of scapes of previous years. Scale bar: (a, d, g): 2 cm; (b, c, f): 0.4 cm; (e, h): 1 cm.

previous year and the base of the single unifacial leaf of the current shoot-generation (up to 9 cm long), which encloses the terminal renewal bud for the next year. The bulb enlarges up to 5(–6) mm. Up to 4 adventitious roots are formed, 1 or 2 of which are contractile and pull the bulb up to 4 cm into the ground. Bulbs of 2-year-old plants are up to 1.5 cm high and 6(–7) mm in diameter. Two-year-old plants produce a narrow bifacial foliage leaf (2 mm wide, up to 9 cm long), which is preceded by a small cataphyll. Up to 7 adventitious roots can be observed. The precise age of further juvenile stages that have been studied is not exactly known. A cross-section through a 3 or 4-year-old individual is presented in

Figs. 4a–c. The stem generation of this year is composed of a single foliage leaf (3 mm wide, 12 cm long) and a cataphyll. The leaf initials for the next year are already present in June. In juvenile stages with 2 foliage leaves, a stem generation is usually composed of 1 cataphyll and the 2 foliage leaves followed by another cataphyll. The morphological analysis of such bulbs revealed, that the stem generation of the previous year was composed in the same way. This shows that the leaf number does not permanently increase from year to year. Therefore we estimate that plants with 2 foliage leaves are at least 6 or 7 years old. Shape and size of the bulb change with increasing age (Fig. 5). While bulbs of younger juvenile

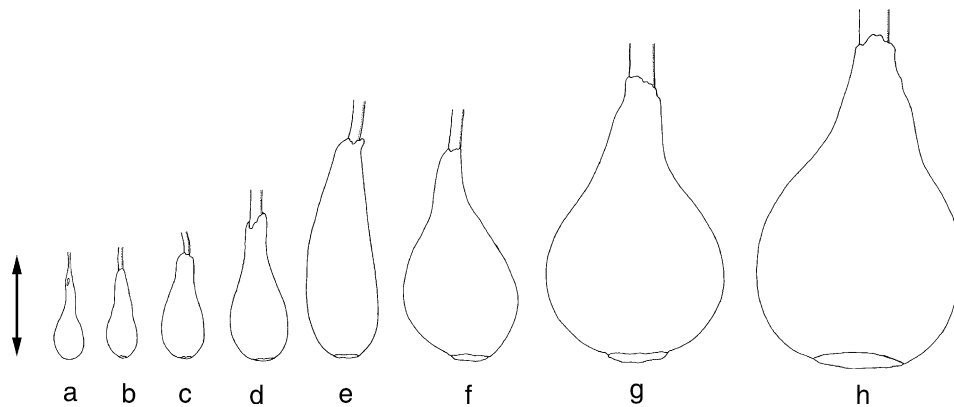


Fig. 5. Shape of bulbs of different age, a–g = juvenile bulbs, h = mature bulb. (a) seedling, (b) 1 year old with a single unifacial leaf. (c) 2 years old, with a single weakly bifacial foliage leaf. (d) 3 (?) years old with a single bifacial foliage leaf. (e) 4 (?) years old, with a single bifacial foliage leaf. (f) 5–6 (?) years old, with a single bifacial foliage leaf. g: 7–8 (?) years old, with 2 bifacial foliage leaves. (h) 10 (?) years old, with 3 foliage leaves. Scale bar: 1 cm.

stages are elongated, bulbs of more advanced stages appear more ovoid.

The age at first flowering is not exactly known. During its ontogeny the bulb enlarges in every growing season, finally reaching a critical size that enables the initiation and development of an inflorescence. Flowering was observed only in individuals with at least 3 foliage leaves. After thorough morphological investigations we estimate the minimum age from seed to maturity as 8–10 years at least.

Adult stages

The roots emerge at the base of the bulb. They are orientated more or less plagiotropically in the soil. Contractile roots, which are thicker than ordinary absorptive roots, are mainly found in disturbed habitats. Bulbs are typically found in a depth of 5–12 cm.

A schematic representation of the stem system of a mature plant at flowering is shown in Fig. 6. Every annual shoot consists of 1 cataphyll (rarely 2), 3–6 foliage leaves, another cataphyll and a single inflorescence in terminal position. In contrast to juvenile stages the renewal bud originates axillary, thus the stem system in adult plants is branched sympodially. Additionally to the current shoot 2 older stem generations and the renewal bud for the next year can be recognized in mature bulbs (see cross-section in Figs. 4d–f). Thus adult bulbs at flowering time are composed of 4 stem generations.

However, in late winter up to 5 stem generations can be recognized in mature bulbs. At that time, the gelatinous remains of 3-year-old leaf bases and cataphylls are still present as the outermost scales. Usually by early summer they form the papery tunic covering the bulb during anthesis. As an exception they were found being still gelatinous during flowering in a bulb of an individual from an agricultural field (see Communities).

Even exceptionally in that bulb remnants of scapes of 3 previous years were found (Figs. 4g and h).

The short note about the structure of the mature bulb presented by Kirchner et al. (1934) cannot be confirmed in every respect. The authors did not find the uppermost cataphyll of each stem generation. Furthermore, they found only 2 bulb scales in mature plants belonging to the previous year. As already pointed out by Speta (1982), the corresponding note in Kirchner et al. (1934) should read: “fleischige Schuppen zweier Jahrgänge waren weiterhin noch vorhanden” (fleshy bulb scales of 2 earlier years are present additionally).

Inflorescence and flower

Inflorescence structure: The inflorescence is a raceme. As already remarked by Schulz (1888) and Troll (1957) it consists of both fertile and infertile flowers. Total height ranges from 20 to 50(–75) cm (mean = 38 ± 9 SD, $n = 374$). The inflorescence of *M. tenuiflorum* can be divided into 3 zones (Fig. 7a), each with different size and function. The basal zone is 6–13 cm long and contains 15–35(–88) (mean = 19 ± 12 SD, $n = 392$) fertile flowers. Distally a second zone (2–6 cm long) follows with 8–20 (mean = 11 ± 7 SD, $n = 384$) infertile flowers. The flowers of both zones are nearly equal in appearance (pale beige; lobes of perianth dark brown to blackish), with the infertile flowers more violet. These flowers are infertile due to their stunted stigmas and ovaries and their anthers containing hardly any pollen. The infertile flowers desiccate and drop after anthesis. The third zone (1–3 cm long) at the top of the inflorescence consists of up to 45 sterile flowers (Fig. 7b). Flowers, pedicelli and rachis are bright-violet and form a showy structure similar to that of *M. comosum* described by Knuth (1898) and Kirchner (1911). Within the third zone the length of flowers and of pedicelli increases apically from 5 to 9 mm and 2 to 8 mm and

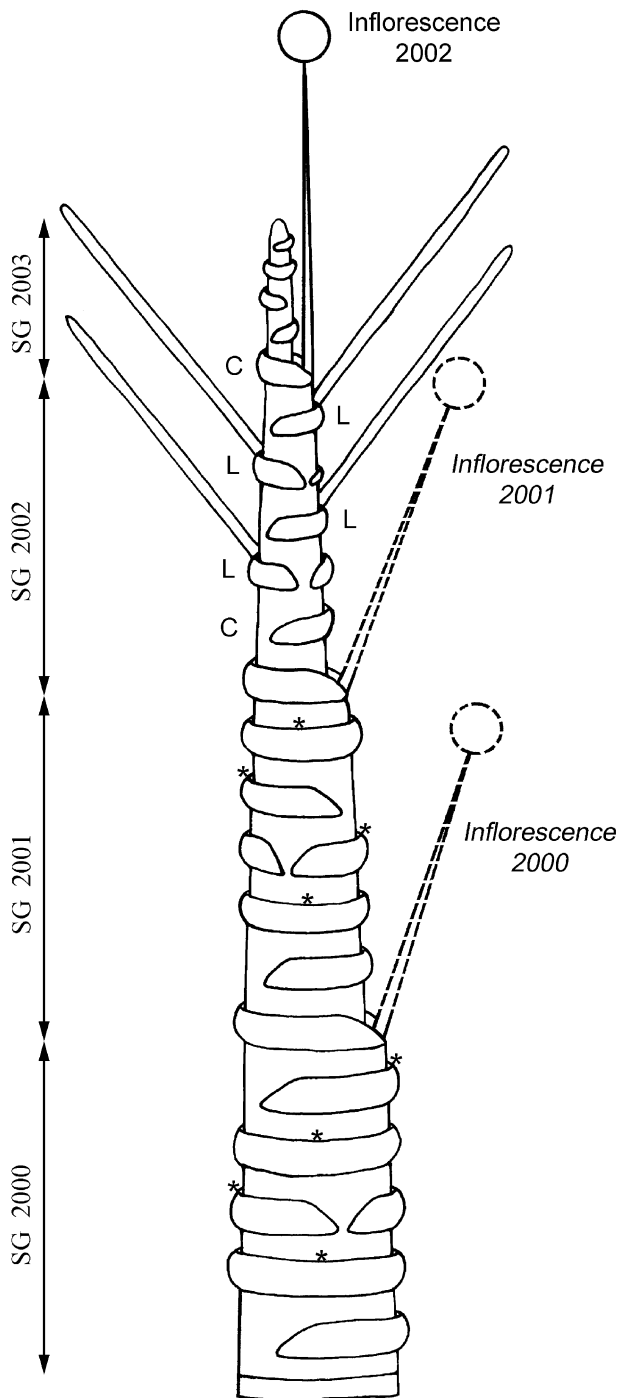


Fig. 6. Stem system of an adult plant; schematic representation with extremely lengthened internodes. C = cataphyll, L = foliage leaf, SG = stem generation. * indicates scars, where the foliage part of the leaves originated.

shortens again at the very top of inflorescence. Flowers of the third zone can contain rudimentary stamens with white anthers and stunted ovaries.

The pedicelli of the flowers of the first and second zone are 3–4(–6) mm long and are slightly sunken into

the rachis. The bracts are 1 mm long. Characteristic 0.5-mm-long prophylls exist which seem to originate laterally like in other *Muscari* species (see Speta, 1982) and are not in addorsed position. While pedicels and rachis are green, bracts and prophylls are usually violet.

Flower structure: The tubular perigone of fertile flowers is 6–8 mm long and sharply constricted distally (Figs. 7c and d). Six small terminal lobes surround a circular mouth (1.5 mm). The 6 stamens are arranged within the perigone tube in 2 rows, like in all species of the genus (Speta, 1982, 1998a). The filaments are inserted in or above the middle of the perigone tube (3–5 mm above ground of flower; Fig. 7e). The dorsifixed anthers are black and 1.5 mm long and contain approximately 2000 pollen grains each. The superior ovary (3 mm high, 2 mm in diameter) consists of 3 locules (Figs. 8a and b), each containing 2 ovules. The style is 2 mm long.

Nectar is produced in 3 septal nectaries (see arrow in Fig. 8b). Only inner nectaries were observed (see also Daumann, 1970). In each of the 3 septa there is a slit surrounded by nectariferous tissue, thus nectar is released at 3 sites at the base of the ovary (see arrow in Fig. 8a). In *M. racemosum* inner nectaries were also observed that are connected with the slit at the top of the ovary by an open channel (Fahn, 1952). The nectar released should pass through the channel and accumulate at the base of the ovary. However, the mechanism described by Fahn (1952) was not observed in *M. tenuiflorum*, although there is also a small groove above each nectary. The top of the ovary of *M. tenuiflorum* is always dry, and the nectar is released exclusively at its base.

When the seeds ripen, the gynoecium enlarges and a dry capsule is formed (Figs. 8c and d). Within the subgenus *Leopoldia* the shape of the capsule is used as taxonomical character (Bentzer, 1973).

Leaf anatomy

A transversal section of a leaf is given in Fig. 9. An uniseriate layer of palisade parenchyma is present on the adaxial and abaxial side. Thus leaves of *M. tenuiflorum* are isolateral. The spongy parenchyma surrounds the vascular tissue and large intercellular spaces. These intercellular spaces originate rhixigenously, as has been observed in other species of the Liliaceae s. l. by Fuchs (1911). In broad leaves up to 29 vascular bundles can be found. Within the mesophyll, mucilage and raphides do occur. In leaves of *M. tenuiflorum* there is no special supporting tissue, like collenchyma or sclerenchyma fibres. For that reason leaves can be easily destroyed by mechanical stress, for instance by trampling. The specific leaf area is $18.2 \pm 4.0 \text{ mm}^2 \text{ mg}^{-1}$, the dry matter content is $13.3 \pm 2.0\%$ (SD, $n = 9$).

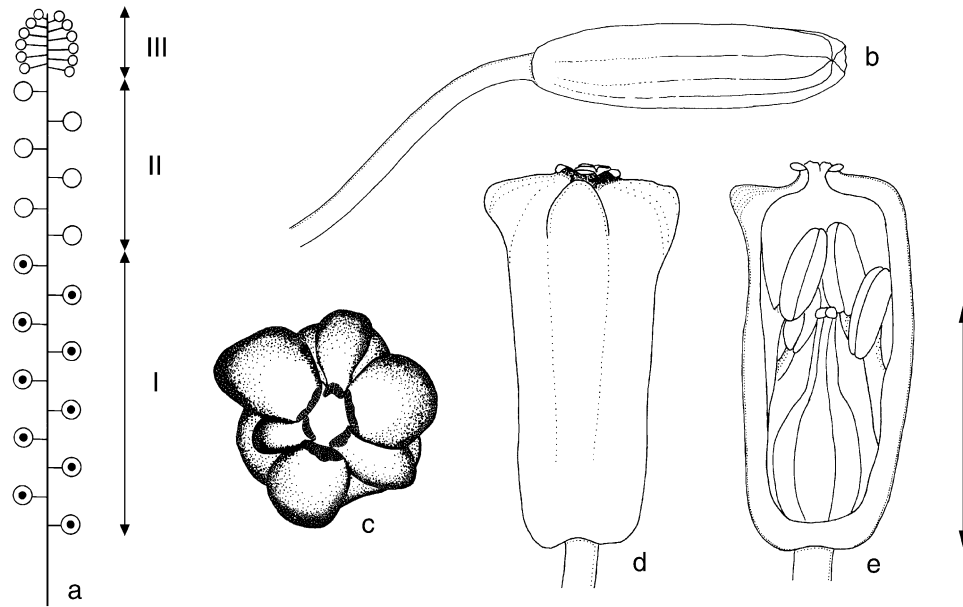


Fig. 7. Inflorescence structure and flowers of *M. tenuiflorum*. (a) schematic representation of the inflorescence structure, I–III indicate different zones of the inflorescence. (b) Flower from showy structure. Figs. c, d, e: fertile flower. (c) View on top of flower, (d) side view, (e) longitudinal section. Scale bar in (b–e): 5 mm.

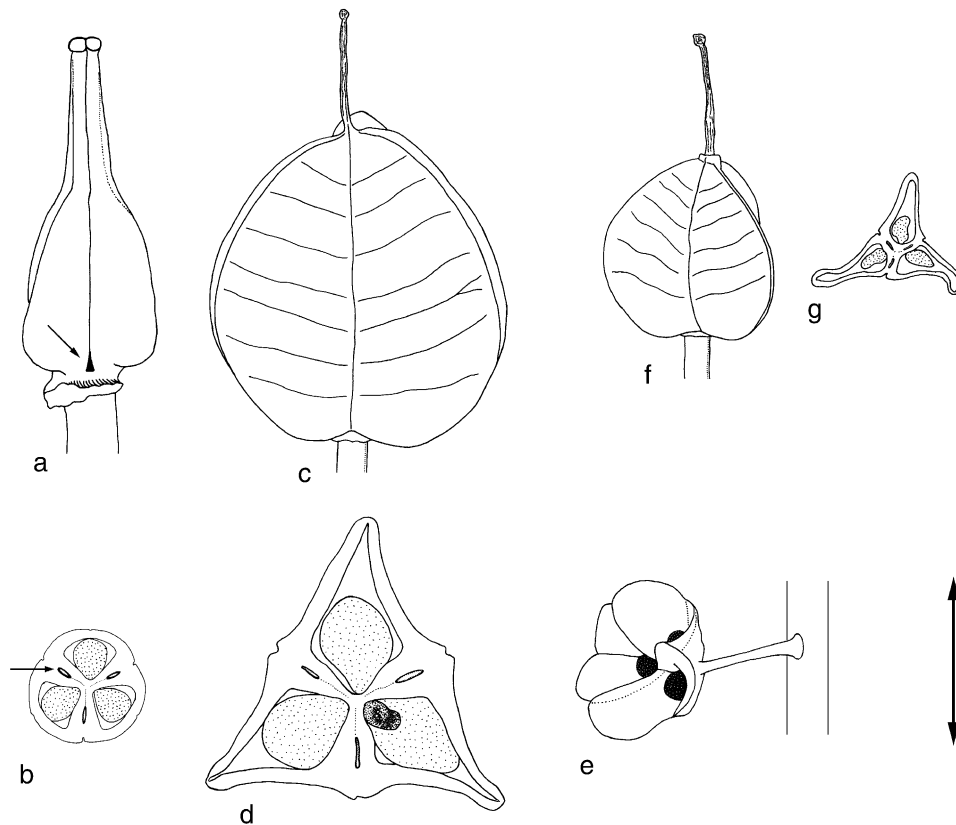


Fig. 8. Gynoecium and fruit of *M. tenuiflorum*. Fig. a: arrow points to the base of the gynoecium, where the nectar is released, (b) cross-section through gynoecium. Fig. c: capsule before anthesis, (d) cross-section through capsule with 3 seeds and an aborted ovule. Fig. e: open capsule. Fig. f: gynoecium, 3 weeks after pollination with *M. comosum* pollen, (g) cross-section. Scale bar: (a, b) 2.5 mm; (c, d, f, g) 5 mm; (e) 10 mm.

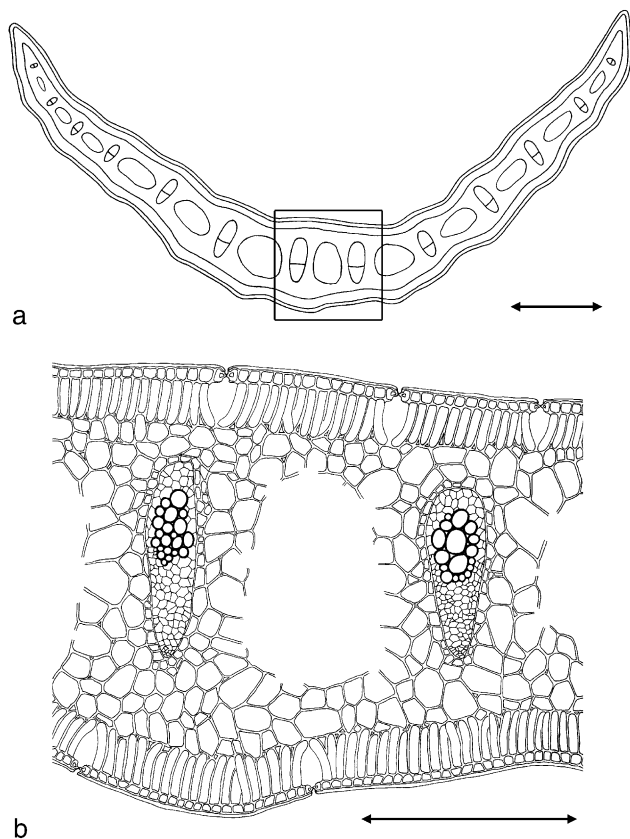


Fig. 9. Transverse section of leaf. Fig. (a): schematic representation; (b) cellular representation. Scale bar: (a) 1 mm; (b): 0.5 mm.



Fig. 10. Upper leaf surface with stomata. SEM-photograph. Scale bar: 20 μm .

Microanatomical characters

Stomata

The stomata of *M. tenuiflorum* (Fig. 10) belong to the anomocytic type and are 18–22 μm long and 10–12 μm wide (in closed state). Stomata occur both on leaves and

Table 1. Average number of stomata per mm^2 in different organs of *M. tenuiflorum*

		Mean	SD	Counts
Foliage leaf base	Adaxial	26.1	2.2	8
	Abaxial	21.0	1.3	8
Foliage leaf middle	Adaxial	54.4	3.9	8
	Abaxial	34.4	3.0	8
Foliage leaf tip	Adaxial	55.3	2.9	6
	Abaxial	38.5	2.2	6
Scape	Base	6.4	1.2	8
	Middle	10.3	2.5	8
Perigone		4.3	1.6	6
Gynoecium		5.1	1.0	12

on the scape, perigone and gynoecium, but their density varies considerably (Table 1). Even in the subterranean, non-assimilating part of scape and foliage leaves stomata are found in low numbers.

Stomatal density was higher on the adaxial surface of leaves than abaxially. On the perigone tube stomata occur especially on the midvein of each tepalum.

Pollen

Pollen grains of *M. tenuiflorum* are monads, monosulcate, ellipsoidal, isopolar and of bilateral symmetry like in most *Muscari* species. Pehlivan and Özler (2003) determined a pollen size of 51.1 \times 41.4 μm , while Schulze (1980) ascertained a length of 43.8–54.3 μm . The pollen wall shows reticulate ornamentation which is nearly twice as dense in *M. tenuiflorum* as in *M. comosum* (Radulescu, 1973). Both species can be distinguished by the structure of the sulcus membrane, which has rugulate ornamentation in *M. tenuiflorum* and reticulate ornamentation in *M. comosum* (Pehlivan and Özler, 2003).

Testa

The testa cells (Fig. 11) are isodiametric polygonal to elongated polygonal (terminology follows Barthlott and Ehler, 1977). The cuticle is strongly plicate. The structure of the testa cells is not uniform in the genus *Muscari* (Frattini et al., 1996; Herrmann, unpublished data) and should be taken into account in a future revision of the genus.

Embryology

Drawing of a cross-section through a seed is presented in Fig. 12. The embryo is rudimentary and belongs to the axile type according to the terminology proposed by Martin (1946). The shape of the embryo is linear, as is typical for Liliaceae s.l.

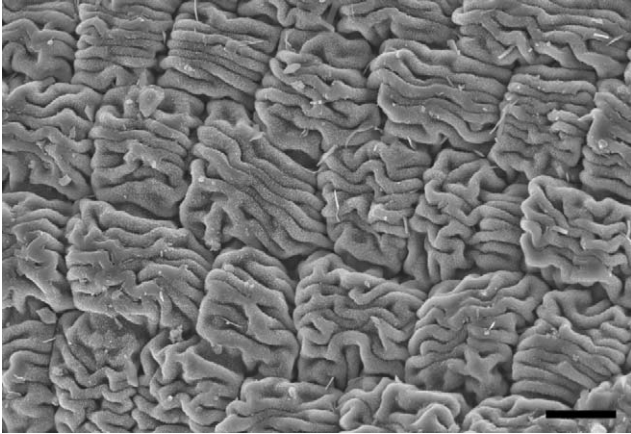


Fig. 11. Seed coat of *M. tenuiflorum*. SEM-photograph. Scale bar: 20 μm .

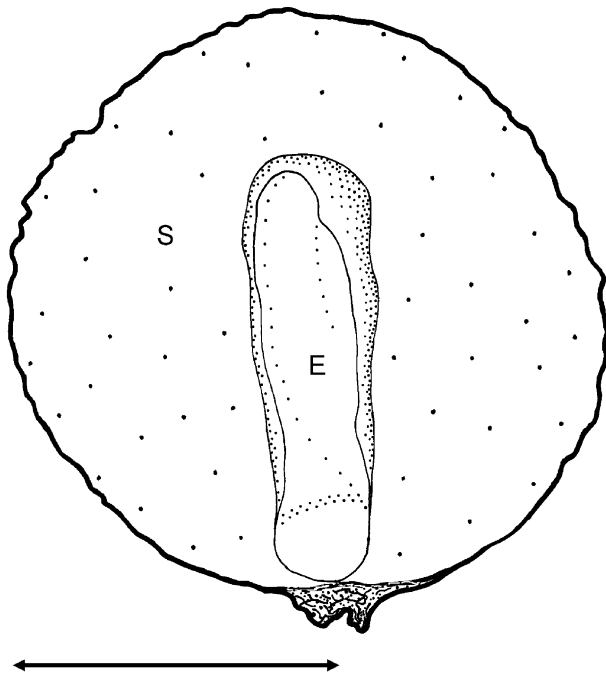


Fig. 12. Cross-section through seed. E = embryo, S = endosperm. Scale bar: 1 mm.

Habitat characteristics

Habitat

In Central Europe, *M. tenuiflorum* typically occurs in open grassland habitats which are characterized by intensive insolation, although the species is also found under more or less shaded conditions at the edge of shrubs and within forests. The habitats are well moistened in autumn, winter and early spring but dry in late spring and summer. In general, *M. tenuiflorum* is considered to

be a species of primary habitats, which arose without human intervention (Mahn, 1965).

Characters of the soils colonized by *M. tenuiflorum* in Central Germany were described by Rauschert (1978). The soils are mostly fine earth rich in nutrients and bases and belong to the type pararendzina and chernozem. In Central Germany *M. tenuiflorum* occurs over different parent rocks: Muschelkalk, porphyry, Schieferletten of the Buntsandstein, limestone from the Zechstein, sandstone from the Carboniferous and gypsum from the Keuper (Rauschert, 1978).

pH values of mineral soil (0–10 cm) from different sites revealed pH_{KCl} ranges of 3.84–4.76 over porphyry and 4.46–7.32 over loess.

The habitats of the species outside Central Europe are rocky pastures in Italy (Brilli-Cattarini and Ballelli, 1979), shrubs in Romania (Zahariadi, 1966), steppe, shrubs, edges of woods and fields in Russia (Fedorova, 1979), grassy slopes and shrubs in the Caucasus region (Grossgejm, 1949), pastures, rocky slopes, *Artemisia* steppe, *Pinus nigra* and *Pinus brutia* forests in Turkey (Davis and Stuart, 1980, 1984) and fields and shrubs in Iran (Rechinger, 1990).

Communities

In Central Europe, *M. tenuiflorum* occurs in a number of xerothermic dry grassland types and spatially or successional related communities that often form mosaics depending on small scale soil patterns on outcrops or slopes (Mahn, 1965; Partzsch, 2001). Some of these plant communities are considered to be relicts of early postglacial times (Partzsch and Mahn, 1998).

The analysis of 312 relevés with *M. tenuiflorum* recorded in Central Germany (Weiss, unpublished data) revealed that *M. tenuiflorum* occurs preponderantly together with xerophilous plant species. The 15 species most commonly accompanying *M. tenuiflorum* were (nomenclature follows Jäger and Werner, 2002): *Euphorbia cyparissias* (65% of relevés), *Achillea millefolium* (59), *Koeleria macrantha* (54), *Potentilla incana* (52), *Festuca rupicola* (50), *Festuca valesiaca* (50), *Poa angustifolia* (49), *Allium oleraceum* (45), *Elytrigia repens* (44), *Filipendula vulgaris* (44), *Centaurea stoebe* (36), *Salvia pratensis* (35), *Viola arvensis* (35), *Eryngium campestre* (34).

In Czechia, the 15 most common accompanying species were: *Euphorbia cyparissias* (71% of 144 relevés), *Festuca valesiaca* (67), *Koeleria macrantha* (65), *Potentilla incana* (58), *Teucrium chamaedrys* (48), *Salvia pratensis* (47), *Eryngium campestre* (47), *Stachys recta* (46), *Verbascum lychnitis* (42), *Festuca rupicola* (40), *Carex humilis* (40), *Dianthus carthusianorum* (39) *Centaurea stoebe* (38) *Fragaria viridis* (36) and *Stipa capillata* (35) (Working Group For Vegetation Science, 2002).

In Germany, *M. tenuiflorum* occurs in the pioneer community Thymo-Festucetum cinereae Mahn 65. It occupies extremely shallow, dry, acidic soils on porphyry rocks or gravel and is characterized by a dominant layer of *Festuca cinerea* with a canopy height of 15 cm. Typical accompanying species are *Hieracium pilosella*, *Sedum reflexum* and *Thymus serpyllum*. On deeply weathered acid soils of northern exposure, *M. tenuiflorum* is found in the species rich *Filipendulo vulgaris*-*Helictotrichetum pratensis* Mahn (1965) characterized by *Filipendula vulgaris* and *Helictotrichon pratense*. Where loess overlays the porphyric rocks, the continental dry grassland community Festuco valesiacae-Stipetum capillatae (Libb. 31) Mahn 65 develops on south- and west-facing slopes, where *M. tenuiflorum* occurs together with *Festuca valesiaca* and *Stipa capillata*. An illustration of a vegetation profile of that community was provided by Mahn (1957). On stronger layers of loess with basic to neutral pH-value and balanced soil humidity continental semi-dry grasslands of the Festuco rupicolae-Brachypodietum pinnati Mahn 65 develop where *M. tenuiflorum* accompanies *Festuca rupicola* and *Brachypodium pinnatum*.

Besides these typical xerothermic and semi-dry grassland communities *M. tenuiflorum* is also found in the derived fragmentary communities dominated by single grass species like *Festuca valesiaca*, *Festuca rupicola* or *Helictotrichon pratense*. It can also be found in adjacent semi-ruderal semi-dry grasslands like the Falcario vulgaris-Agropyretum repentis Müller et Görs 69, ruderaly influenced fresh meadow communities such as the Tanaceto vulgaris-Arrhenatheretum elatioris Fischer 85 or in sites dominated by single mesomorphic grass species like *Arrhenatherum elatius*, *Poa angustifolia* or *Bromus inermis*.

M. tenuiflorum is sometimes found in the field layer of thermophilous oak forests (Quercion pubescenti-petraeae Br.-Bl. 31), probably as a relict of former use as open coppice forests. These stands are characterized by a quite open tree layer and a well-developed shrub layer. In the field layer *Dictamnus albus*, *Buglossoides purpureocaerulea* and *Viola mirabilis* can be found. *M. tenuiflorum* may occur in *Robinia pseudoacacia* woods and is also mentioned to occur in thermophilic fringe communities of Geranium sanguinei R. Tx. in Th. Müller 61 (Rauschert, 1978).

Exceptionally, *M. tenuiflorum* was observed in a typical weed community (together with e.g. *Chenopodium album*, *C. hybridum*, *Consolida regalis*, *Convolvulus arvensis*, *Descurainia sophia*, *Fumaria officinalis* and *Thlaspi arvense*) at a field margin of wheat crop in the direct neighbourhood of a porphyric outcrop (own observation). Undoubtedly, the bulbs were ploughed into the field from the edge of the porphyric outcrop.

In Bohemia, *M. tenuiflorum* is mentioned in initial phases of vegetation development on rocks and rock

debris (Klika, 1929). With further soil development eventually the Caricetum humilis stipetosum develops where *M. tenuiflorum* is accompanied by *Carex humilis*, *Potentilla incana*, *Festuca valesiaca*, *Koeleria gracilis*, *Stipa capillata*, *S. pulcherrima* and *S. tirsia*. Like in Germany it is often found in the Festuco valesiacae-Stipetum capillatae (Klika, 1929).

In Austria, *M. tenuiflorum* is treated as a diagnostic species of continental dry grasslands (Festucion valesiacae Klika 31; Mucina et al., 1993).

Response to abiotic factors

Although *M. tenuiflorum* is a typical species of dry grasslands, flowering can be prevented by insufficient precipitation in spring. The number of flowering individuals was reduced to 60–80% in the dry year 2000 compared with 1999 when precipitation was higher. Fruit and seed production totally failed at some sites in the dry year. Due to a lack of rainfall in April and the first half of May (precipitation at Halle/Saale, 1m^{-2} : April 1999/2000: 39,2/15,1–May: 47,1/35,9–June: 60,0/50,1; Herrmann, 2003) many inflorescences withered in bud stage. This preponderantly occurred in habitats with shallow soils and southern aspect.

The phenology of *M. tenuiflorum* is influenced by exposure and inclination. In shaded habitats with a northern aspect flowering and dissemination are delayed by nearly 2 weeks.

When *M. tenuiflorum* is growing in the field layer of forests, leaves and inflorescence are elongated. Flower stalks are flexible; flowering is delayed and flower number and seed set is drastically reduced. Leaves stay green much longer than under full light.

If the bulb is removed from soil, e.g. by erosion, wildlife or ploughing, narrow spindle-shaped contractile roots are formed in order to pull the bulb back into the soil. This was observed in a water-worn ravine at the edge of a field in south-eastern Turkey.

Abundance

In Germany, 43 extant local populations are known to the authors. The largest population has about 9000 individuals; however, more than half of the populations are smaller than 500 adult individuals (mean = 932, $n = 32$; Fig. 13). The number of flowering individuals at a location varies among years depending on weather conditions and should not be taken as change in population size. Thus, repeated assessments have to be made before temporal trends in population size can be detected. The total population size of 32 populations where the current population size is known amounts to approximately 45,000 flowering individuals.

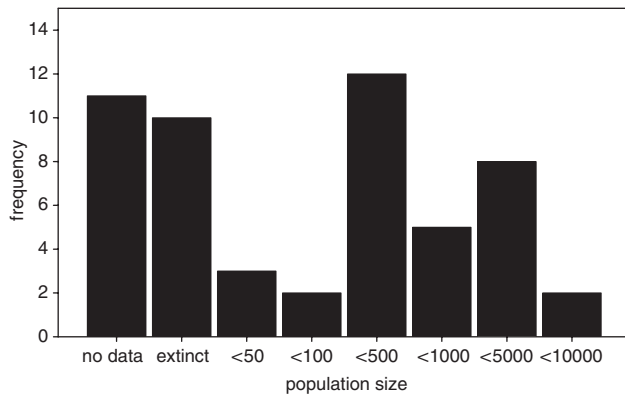


Fig. 13. Frequency distribution of population size of all known 53 local populations of *M. tenuiflorum* in Germany.

In typical habitats the cover of *M. tenuiflorum* is mostly <1% and rarely exceeds 5%. Plants often grow clustered and are missing in large parts of an available habitat. Mean density of *M. tenuiflorum* in 40 analyzed 1 m² plots in various communities was $48.3 \pm 46.7 \text{ SD m}^{-2}$ for the one-leaf stage including seedlings, $26.8 \pm 2.2 \text{ SD m}^{-2}$ for vegetative plants with 2 and more leaves and $12.9 \pm 17.2 \text{ SD m}^{-2}$ for generative plants. Highest densities of 20–50 flowering individuals m⁻² were attained in the dry grassland communities Festuco-Stipetum capillatae, Thymo-Festucetum cineruae and Filipendulo-Helictotrichetum pratensis. The density of adults was significantly reduced in semi-dry grasslands and communities dominated by taller grasses.

Life cycle and biology

Life cycle – general notes

M. tenuiflorum is a polycarpic bulbous geophyte with extremely stunted internodes. The stem system is annually renewed at its top by the formation of leaves (cataphylls and foliage leaves), while it gradually withers at its base. While the foliage parts of leaves are short lived, the bases of leaves and cataphylls survive at least a whole year. Adult plants can produce an inflorescence every year if environmental conditions allow.

As in other bulbous geophytes, e.g. *Ornithogalum pyrenaicum* (Hill and Price, 2000), there is no information about the longevity of individuals of *M. tenuiflorum*, but they probably can survive for several decades.

Phenology

Phenology of *M. tenuiflorum*

An overview of the phenology of *M. tenuiflorum* is given in Fig. 14.

Roots: The rhizogenesis of *M. tenuiflorum* is intensive in early autumn, interrupted in winter and is very intensive

again in early spring. During the dry summer the bulb aestivates without any formation of adventitious roots.

The roots of *M. tenuiflorum* are short lived. There are no detailed observations, but the roots probably do not live longer than a few months. Within the genus *Muscari* longer living roots might occur in *M. moschatum* and *M. macrocarpum* (Speta, 1982).

Leaves: First leaf primordia of the next year's generation can be found even during the flowering period in May/June (Fig. 6), and by the end of August all leaf primordia are present.

Typically, leaves grow out from the bulb in early spring and appear aboveground at the beginning of March and reach their final length during May. However, *M. tenuiflorum* is a facultative wintergreen species. By the beginning of autumn leaves grow out from the bulb at some sites. Autumnal leaf growth was mainly observed in sites with shallow soils and a thin or missing litter layer. Similar observations have been made in the bulbous geophyte "*Ornithogalum angustifolium*", and might be connected to different soil temperatures (Herrmann, 2002). Autumnal leaf growth may also be connected to drought and flower abortion, since from 2 adjacent sites only plants in a dry Thymo-Festucetum, that had aborted flowering, showed overwintering leaves, whereas plants from a mesic Brachypodietum had flowered regularly and showed typical leaf emergence in spring.

Leaves that sprouted in autumn often show an undulating form and are not erect but lay on the ground. These overwintering leaves often suffer frost damage in the distal part, but they endure during winter.

Just before the main flowering period, leaves begin to die and by the end of June they are normally completely withered. In moist years or mesic sites lifespan may be elongated up to the end of July.

Flowers: By the end of August a small inflorescence bud can be recognized within the mature bulb, 3 mm high and 1 mm in diameter. This bud enlarges till the end of September to a length of 8 mm (Fig. 15). Single flower initials can be recognized at that time, but the flower components are not differentiated yet. It remains in this stage until April of the following year.

By the beginning of May the inflorescence bud grows out of the bulb by elongation of the scape. The bud

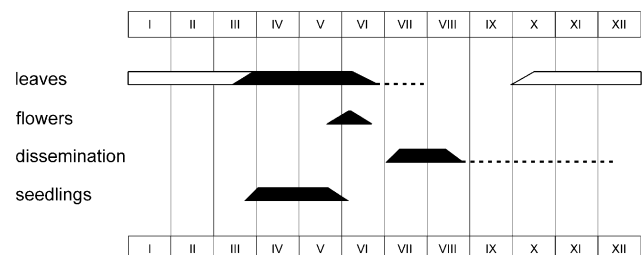


Fig. 14. Phenology of *M. tenuiflorum*.

becomes visible at the soil surface about the middle of May. The main flowering period extends from the end of May to the middle of June. The time span from opening of the flower until opening of the ripe capsule is 45–54 days (mean 49.5 ± 3.4 SD; $n = 8$). The first fruiting plants of *M. tenuiflorum* can be observed in the second half of July.

Co-flowering species of *M. tenuiflorum* in the same or adjacent habitats are e.g. *Salvia pratensis*, *Filipendula vulgaris*, *Ranunculus illyricus*, *Helianthemum nummularium*, *Anthericum liliago*, *Stachys recta*. According to the phenological system of Dierschke (1995) *M. tenuiflorum* flowers in the *Cornus sanguinea*–*Melica uniflora* phase at the beginning of early summer.

Seedlings: Germination commences in the second half of March. In pot cultures and after mild winters seedlings were even observed in the middle of February. The cotyledon withers in the second half of May at which time a small bulb has been produced.

Ecogeographical interpretation of the phenology

M. tenuiflorum differs phenologically from other bulbous spring flowering plants occurring in Central Europe in that the development of the inflorescence bud within the bulb lasts remarkably long. As mentioned above, the flowers of *M. tenuiflorum* are not differentiated before April in the year of flowering. In

contrast to that the flowers in other bulbous geophytes are already completely differentiated in the autumn before flowering, e.g. *Ornithogalum umbellatum* (Irmsch, 1850), *Galanthus nivalis* (Hoffmann, 1875), *Tulipa sylvestris* (Jäger, 1973) and “*Ornithogalum angustifolium*” (Herrmann, 2002). In Western Europe the same was observed in the bulbous plants *Hya-cinthoides non-scripta* (Blackman and Rutter, 1954), *Narcissus pseudonarcissus* (Caldwell and Wallace, 1955) and *Ornithogalum pyrenaicum* (Hill and Price, 2000).

Most of these species are mainly distributed in oceanic and/or suboceanic areas with moderate mean temperatures and humid summers (oceanity value according to Jäger and Werner (2002): *H. non-scripta*: 1, *N. pseudonarcissus*: 1–2, *T. sylvestris*: 1–4, *O. umbellatum*: 2–4, *G. nivalis*: 2–5, *O. pyrenaicum*: 1–5). On the other hand *M. tenuiflorum* is restricted to subcontinental/continental areas with oceanity values of 4–6 (Jäger and Werner, 2002). These are areas with cold winters with low precipitation, warm humid springs and hot and dry summers. The observed phenology of *M. tenuiflorum* might be interpreted as an adaptation to these climatic conditions. The flowers are differentiated within the bulbs in April, nearly coinciding with the peak of annual precipitation in the range centre of the species. An earlier differentiation might be hindered by unfavourable climatic conditions in autumn and low temperatures in winter typical for the continental climate. The late development of the flowers might cause the late flowering period in May and June relative to the bulbous geophytes mentioned above.

Reproduction

Floral biology

As already remarked by Kirchner et al. (1934) flowers of *M. tenuiflorum* are protogynous. In early flowering stage, nearly a day after the circular mouth of the flower has opened by back-rolling of its perianth lobes, the receptive stigma is positioned behind the closed anthers. Then the style elongates to a length of 4 mm, placing the stigma between the anthers. This process coincides with the introrse dehiscence of the anthers, which occurs at first in the outer whorl of stamens, then in the inner one. Thus, self-pollination becomes possible.

The showy structure of sterile flowers at the top of inflorescence seems to play an important role in attracting pollinators. It might serve as long-distance orientation for pollinators (as described by Troll (1957) in *M. comosum*), although insects in most cases fly straight towards the fertile flowers. They are probably attracted by the slight scent of the fertile flowers which offer pollen and nectar as reward.

M. tenuiflorum is visited mainly by bumble bees of varying tongue length that gather nectar and pollen. The

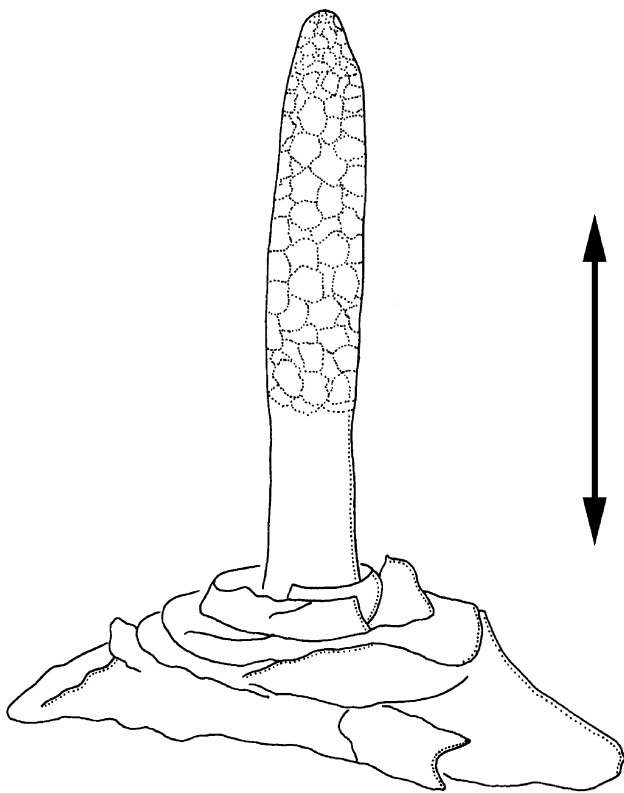


Fig. 15. Inflorescence bud of *M. tenuiflorum* at the end of September. Scale bar: 5 mm.

following species were detected in 2 sites near Halle/Saale, Germany: *Anthophora aestivalis* Panzer, *Bombus sylvarum* L., *B. hortorum* L., *B. ruderarius* Müller, *Psithyrus rupestris* Fabricius. An interesting behaviour was observed when a *Bombus pascuorum* L. bumble bee collected pollen by changing its wing beat frequency (*buzzing* behaviour, Herrmann, 2003). Pollinating bumble bees showed flower constancy visiting exclusively *M. tenuiflorum* in up to 48 consecutive visits.

Breeding system

The pollen-ovule ratio of *M. tenuiflorum* was 2257 ± 214 (SD, $n = 3$), indicative for xenogamy or facultative xenogamy (Cruden, 1977). Seed set in open pollinated plants was 3.81 ± 1.76 (SD, $n = 7242$) seeds per flower, thus the seed/ovule ratio was 0.635. Seed set in caged flowers or with additional hand self pollination showed only minor reductions in seed set (ISI-index = 0.77). This indicates that *M. tenuiflorum* is fully self-compatible. Pollen supplementation experiments had no significant effect on seed set. Neither did pollinator exclusion decrease, nor did pollen supplementation increase seed set. Allozyme analyses revealed a mean fixation index for adult plants at population level of $F = 0.166$ from which a mean population outcrossing rate of $t = 0.715$ can be deduced (Durka and Weiss, in preparation). Thus, *M. tenuiflorum* is characterized by a facultative xenogamous breeding system being largely outcrossed in the presence of pollinating insects and selfing in the absence of pollinators.

Development of seeds

Individual plants can produce up to 430 seeds. The mean number of seeds per plant ranged from 55 to 106 among populations (mean 77.0 ± 15.6 SD, $n = 20$ individuals from 15 populations each; data from 1995). The number of seeds per capsule ranged from 2.2 to 4.3 among populations (mean 3.7 ± 0.7 SD) and was correlated to population size (Fig. 16; Weiss and Mahn, 1996). Whether the low seed production in small populations is due to inbreeding depression, pollinator limitation or to site conditions is unknown.

Dissemination and dispersal

The capsule of *M. tenuiflorum* dehisces loculicidally by 3 longitudinal slits. The dehiscence starts at the top and continues approximately down to the middle of the carpels. During seed-shedding the open capsules have a funnel-like form, and the pedicels are orientated horizontally or slightly slanted downwards (Fig. 8e).

Generally the diaspores are seeds, only exceptionally fruits or infructescences. The seeds fall from the capsule close to the plants. The terminal velocity of falling seeds is very high (3.5 m s^{-1} according to Tackenberg, 2001)

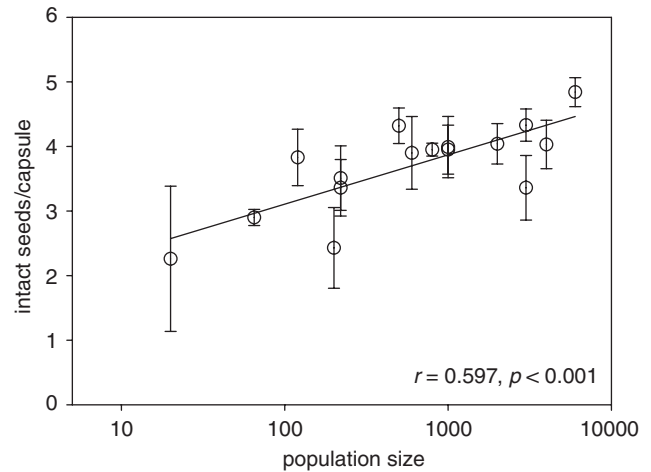


Fig. 16. Correlation of population size and seed production per flower (error bars represent 95% confidence intervals; Weiss and Mahn, 1996).

preventing any dispersal by wind. The diaspores are dispersed by swaying movements of the infructescence (semachory) or by rain drops hitting the capsules (ombrochory) which was also observed in *M. comosum* by Müller-Schneider (1986).

The diaspores of *M. tenuiflorum* are spherical and have no morphological or anatomical adaptations to long distance dispersal, for instance by wind or animals. However, epizoochorous dispersal across longer distances is possible (Dannemann et al., 1999). Experiments showed that seeds can be taken up and transported in the fur of sheep (Bockelmann, 1997). Sometimes seeds are not shed completely out of the fruits and overwintering infructescences still contain some seeds. Thus, the potential for dispersal may be prolonged in time and the possibility for long distance dispersal increased by adhesion of diaspores to larger herbivores.

However, in Central Germany sheep pasturing strongly declined since 1989. For that reason dispersal by sheep seems to be very unlikely nowadays (Dannemann et al., 1999).

Vegetative propagation

Vegetative propagation by bulbils does not occur in *M. tenuiflorum*. In contrast, in *M. comosum* 3–4 bulbils are formed (Wehsarg, 1954). The bulbs of adult plants of *M. comosum* are usually found in deeper soil layers than those of *M. tenuiflorum* (Speta and Adler, 1994; own measurements in Bohemia, Czech Republic: 25–30 cm). Both characters, depth of bulbs and formation of bulbils, might enable *M. comosum* to occur in extensively used fields and vineyards (Kästner et al., 2001; Oberdorfer, 1994; Rosenbauer, 1998).

Germination

Seeds of *M. tenuiflorum* display morphophysiological dormancy with a dormancy period of about 7–8 months. The seeds are shed in July and germinate in February/March of the following year. Dormancy must be broken by prolonged cold stratification under moist conditions. Germination is insensitive to light or darkness. Seeds kept in a greenhouse at 10 °C did not germinate at all. Germination of seeds kept under outdoor conditions during winter was 100% by middle of February both when buried in the soil and on the surface when moistened. Seeds applied onto the soil surface in the natural habitat did not germinate completely, most of the ungerminated seeds remaining germinable according to the tetrazolium test. However, *M. tenuiflorum* does not form a persistent seed bank.

Seed germination of other *Muscari* species (i.e. *M. comosum*, *M. neglectum*, *M. commutatum*, *M. weissii*) was recently studied by Doussi and Thanos (2002). In all these species no primary dormancy exists, and germination occurs in autumn/winter at a temperature optimum of 10 or 15 °C. Doussi and Thanos (2002) interpreted this as an adaptation to the mild and humid winters in the Mediterranean area, the range centre of these *Muscari* species. The dormancy of *M. tenuiflorum* might be interpreted as an adaptation to a continental climate.

Response to competition and management

M. tenuiflorum is a weak competitor due to low stature, small leaf area and short vegetative phase. Consequently, the density of *M. tenuiflorum* is higher in xerothermic grassland communities than in semi-dry grasslands or other communities dominated by taller grasses. This may be both a consequence of shading and of the failure of seedling establishment due to a dense litter layer.

If the leaves are damaged or destroyed, no further leaves are produced in that year. The same applies to the inflorescence. Consequently trampling has an adverse effect on populations of *M. tenuiflorum*, as by leaf destruction the storage of assimilates in the bulb is reduced or completely prevented. By destruction of the inflorescence no diaspores are produced in that year.

Historical causes for a decline of *M. tenuiflorum* in Central Germany in the past centuries due to human activities were mentioned by Rauschert (1978) and are mainly connected to habitat destruction. Many occurrences of *M. tenuiflorum* in open coppice forests were extinguished in the 18th and 19th century due to abandoning the use of these coppices and the resulting succession. The photophilic species was not able to survive under conditions of increased tree shading. However, a number of extant populations do occur

within forests. They show almost complete failure of seed set despite vigorous vegetative growth, probably due to pronounced shading. This indicates that *M. tenuiflorum* is highly persistent which also offers the possibility to rejuvenate such populations by opening the forest thus allowing for successful seed production. Other reasons for the historical decline of *M. tenuiflorum* were clearing of coppice forests, mining activities and trampling (Große, 1985; Rauschert, 1978).

Most populations of *M. tenuiflorum* in Germany are in dry grasslands that traditionally have been used for sheep grazing for centuries (Dannemann et al., 1999). Thus, *M. tenuiflorum* is tolerant to grazing and might be promoted by grazing of sheep and goats, as it reduces or prevents shrub encroachment, a recent cause of threat for *M. tenuiflorum* in semi-dry grasslands (Frank and Neumann, 1999). Furthermore grazing creates open sites which are essential for seedling establishment. Another positive effect of grazing by sheep could be enhancement of gene flow among genetically strongly isolated populations by epizoochorous dispersal of diaspores. However, since *M. tenuiflorum* is very sensitive to trampling, grazing should not be performed regularly during the vegetative phase, but preferably after mid of July.

As reported by Klika (1929) continental grasslands in Bohemia were managed by annual burning, obviously without negative effects on *M. tenuiflorum*. However, the effect of regular burning to the conservation of steppe flora was judged by Klika (1929) in general as disadvantageous, as rare continental plant species are driven out.

Bulbs ploughed under might be found in deeper layers of soils (up to 20 cm) than in natural habitats. Measurements of the depth of bulbs at the edge of a field revealed that flowering is the more delayed, the deeper the bulb is buried. All individuals occurring in that agricultural field were exceptionally tall and had more flowers than in the adjacent dry grassland habitat.

In the C-S-R classification of plant functional types *M. tenuiflorum* is classified as a stress-tolerant competitor in undisturbed conditions without ruderal tendency (SC) using the approach of Hodgson et al. (1999).

Herbivores and pathogens

Although there are no direct observations, occasionally mammalian herbivores seem to feed on *M. tenuiflorum*. In spring overwintering leaves were found to be bitten off probably by rabbits. During the flowering period inflorescences were found to be bitten off probably by roe deer. The only invertebrate phytophages that have been found on *M. tenuiflorum* was a spittlebug (cf. *Philaenus spumarius*, Cercopidae). However, other phytophages must feed on *M. tenuiflorum* since feeding

traces (holes up to 1 cm wide) have occasionally been found on leaves.

M. tenuiflorum is attacked by several pathogenic parasitic fungi. The smut fungus *Ustilago vaillantii* Tul & C. Tul., which also attacks other *Muscari* and *Scilla* species, has been found on *M. tenuiflorum* in many parts of its range including Germany (Scholz and Scholz, 1988, 2000), Poland (cultivated host, Kochman and Majewski, 1973), Austria (Scheuer and Poelt, 1997), Romania (Savulescu, 1957) and the “Carpathian region” (Vánky, 1985). Infections by *U. vaillantii* are systemic. Infected plants produce enormous amounts of spores in the filaments that fill the whole flower tube of all fertile flowers. Spores are shed at the same time or shortly before uninfected plants flower. Infected plants are sterilized and do not produce any seed. The rust fungus *Uromyces muscari* (Duby) L. Graves is a common parasite on *Muscari* species forming oval rust spots on the leaves and also has been found on *M. tenuiflorum* in Germany (Braun, 1982), Bohemia (Jage, pers. commun.), Austria (Scheuer and Poelt, 1997) and Poland (Kochman and Majewski, 1973). From South Russia the rust fungus *Puccinia festucina* Syd & P. Syd has been described (Gäumann, 1959), which according to Tranzschel (1939, cit. in Gäumann, 1959) obligately uses both *M. tenuiflorum* (and other *Muscari* spp.) and *Festuca ovina* L. with host shift.

Mycorrhiza

Harley and Harley (1987) stated VAM in *M. comosum*. By using the staining technique described in Vierheilig et al. (1998) the presence of mycorrhiza was also detected in *M. tenuiflorum*.

Physiological data

No information available.

Biochemical data

There are no published records on the phytochemistry of *M. tenuiflorum*. However, given the general wide occurrence of many important secondary compounds both within the genus and the family it can be assumed that substances found in other *Muscari* species can be expected in *M. tenuiflorum* also. Chelidonic acid, an acrid irritant, is an important constituent in many plant parts of the Liliaceae s.l. and has also been found in 2 *Muscari* species. Hemolytically acting saponines have been detected in 5 *Muscari* species (Hegnauer, 1963). In *M. comosum* homoisoflavonoides have been detected which are widely distributed in the Liliaceae s.l. In *M. comosum* tetracyclic triterpenes (e.g. Eucosterol) and

their saponinic glycosides (e.g. Muscarosid, Hegnauer, 1983) have been found.

Genetic data

Karyological data

Chromosome counts in different populations of *M. tenuiflorum* in Central Germany revealed a bimodal karyotype with the diploid chromosome number of $2n = 18$. A metaphase plate and corresponding karyogram of an individual collected at “Schiedsberg” near Löbejün (Saxony-Anhalt) is presented in Figs. 17 and 18. A diploid set of chromosomes consists of 4 metacentric, 4 satellited metacentric, 6 submetacentric, 2 subtelocentric and 2 telocentric chromosomes (chromosome formula: $4m + 4m\text{-sat} + 6sm + 2st + 2t$; nomenclature for centromeric position according to Levan et al., 1964). The total length of chromosomes is $71.2 \mu\text{m}$.

Our results corroborate the information about the karyotype structure of *M. tenuiflorum* presented by Delaunay (1922, 1927), Kachidze (1928), Garbari (1966), Šopova et al. (1983), Dalgiç (1991), Garbari et al. (1996), Johnson et al. (1996), Nersesian (2001) and Krahulcová (2003). These authors provided karyotype drawings or photographs of somatic metaphase chromosomes of *M. tenuiflorum*, while Pogosjan (1965), Stuart (1970), Garbari (1973) and Johnson and Brandham (1997) only mentioned the diploid chromosome number of $2n = 18$.

According to Garbari (1966) there should be 2 pairs of telocentric chromosomes, one of them with satellites at the long arms. Šopova et al. (1983) found 3 pairs of telocentric chromosomes; in one of them they mentioned satellites at the short chromosome arms. However, we found only 1 pair of telocentric chromosomes. In agreement with Delaunay (1927) we observed satellites exclusively in metacentric chromosomes. While Delaunay (1927) found 3 pairs of metacentric chromosome with satellites, we observed only 2 of them. Our result of the total length of chromosomes nearly coincides with the values of Delaunay (1927), who



Fig. 17. Metaphase plate of *M. tenuiflorum*. Scale bar: $10 \mu\text{m}$.

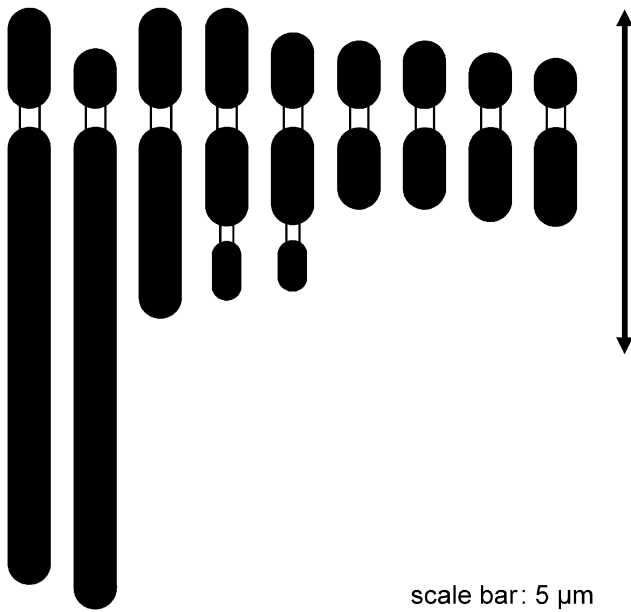


Fig. 18. Karyogram of *M. tenuiflorum*.

measured 70.0 μm and Šopova et al. (1983), who measured 71.84 μm .

From a historical point of view it is remarkable that *M. tenuiflorum* is the second species (after *Galtonia candicans*), where satellite chromosomes were discovered (Delaunay, 1927).

Genetic variation within and among populations

Genetic variability was analysed at allozyme loci in 26 local populations in Germany (Durka and Weiss, unpublished results). Measures of genetic diversity (percent polymorphic loci at population level $P_p = 0.367$, mean number of alleles $A_p = 1.52$) were typical for animal pollinated species with mixed mating system and regional geographic range. Allozyme variability was correlated to population size so that in small populations (<100 flowering individuals) genetic diversity was greatly reduced.

Local populations were considerably differentiated genetically since allozyme analyses revealed an $F_{ST} = 0.215$ among local populations, all of which were less than 40 km apart. Thus 21.5% of total variability resided among populations. Genetic distances among populations were not correlated to geographic distances. This indicates that the loss of diversity due to genetic drift and/or inbreeding is much larger than gene flow through seed or pollen among sites. The spatially isolated populations are also effectively isolated genetically. Consequently, gene exchange should be enhanced to both reduce genetic drift in small populations and to prevent further genetic differentiation. This may be accomplished by site management like sheep herding

that might promote seed dispersal among populations (Eichberg et al., 2005).

Hybrids

In the literature no hybrids with *M. tenuiflorum* are mentioned.

Experimentally performed crosses between *M. tenuiflorum* (female) and *M. comosum* (male) failed. Ovaries of emasculated *M. tenuiflorum* flowers pollinated with *M. comosum* enlarged, but started to wither without seed set 3 weeks after pollination (Figs. 8f and g). In contrast *M. tenuiflorum* ovaries pollinated with *M. tenuiflorum* pollen developed normally until dissemination.

Status of the species

There is no information about an economical use of *M. tenuiflorum*. In contrast to tassel hyacinth (*M. comosum*), that is used as ornamental plant in gardens (Phillips and Rix, 1989), *M. tenuiflorum* has no importance as ornamental plant.

The species is indigenous to Central Europe. According to Korneck et al. (1996) *M. tenuiflorum* is a vulnerable plant species in Germany (red list-category 3), and is additionally protected by law. The threat status of *M. tenuiflorum* for whole Central Europe was rated vulnerable (Schnittler and Günther, 1999) and varies across Europe from unthreatened in Hungary, rare in Austria and Italy, vulnerable in Slovakia and endangered in Czechia (Holub and Prochazka, 2000; Schnittler and Günther, 1999).

M. tenuiflorum is restricted within Germany to the federal states of Saxony-Anhalt and Thuringia. In Saxony-Anhalt, where more than 75% of the sites in Germany are to be found (Frank and Neumann, 1999), *M. tenuiflorum* is considered as vulnerable (red list-category 3; in Frank et al., 1992). Frank and Neumann (1999) stated a decline of the species in Saxony-Anhalt. Dannemann et al. (1999) stated that especially small populations are declining, while larger populations (> 500 individuals) are nearly constant.

In Thuringia the species was formerly treated as vulnerable (Westhus and Zündorf, 1993), while it is now considered as endangered (red list-category 2; Korsch and Westhus, 2001). Although the few occurrences of *M. tenuiflorum* in Thuringia are nearly constant, the new threat-classification was carried out because even an extinction of only few occurrences would result in a high percentage of decline (Korsch, pers. commun.).

Because of the numerous occurrences there, the federal state of Saxony-Anhalt has got the highest responsibility for the conservation of this species in Germany, but in consideration of the total range of the

species Welk (2002) judged the international responsibility of Germany for the conservation of *M. tenuiflorum* as rather low. However, it has to be taken into account that the relictic outposts of the species might have diverged genetically from the range centre due to long lasting isolation and thus might deserve special conservation measures.

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