Overview and comparative analysis of *Festuca* species dominant in extremely dry sandy grasslands of the Great Plain and important from a grassland management perspective

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ABSTRACT

Among the narrow-leaved Festuca taxa occurring in the Carpathian Basin, those inhabiting extremely dry lowland habitats are mainly species with a continuous sclerenchyma ring in their leaves, or in which the sclerenchyma becomes ring-shaped by the end of the vegetation period. The most characteristic representative of this group is Festuca vaginata, but recent studies have also confirmed the presence of Festuca pseudovaginata and Festuca tomanii in these habitats.

These species are of high importance for grassland management, as they are dominant components of dry steppe vegetation. In this paper, we provide a comparative and critical review of the three taxa, summarizing previous literature and presenting morphological data aimed at identifying the most reliable diagnostic characters for species delimitation. Our results indicate that the position of the fourth spikelet on both the terminal and the longest panicle branches are among the most informative morphological traits for distinguishing the species. Within the spikelets, the length of the outer glume in the second floret proved to be the most consistent and useful character, which is recommended for practical identification purposes as well.

Keywords*: Festuca vaginata, Festuca psammophila series, sandy vegetation,*

ÖSSZEFOGLALÁS

A Kárpát-medencében is előforduló, keskenylevelű Festuca fajok azon taxonjai közül az extrém száraz alföldi élőhelyeken elsős sorban olyan fajok találhatók meg amelyek gyűrűs szkelrenchimával rendelkeznek vagy gyűrűssé válik a vegetációs időszak végére. Elsősorban ez a Festuca vaginata fajt jelenti. Az utóbbi időszak kutatási eredményei alapján emellett több faj is megtalálható itt, a Festuca pseudovaginata, Festuca tomanii. Ezen fajok gyepgazdálkodási szempontból is fontosak, hiszem gyepalkotók. E fajok összehasonlító elemzését adjuk meg, áttekintő jelleggel a kéziratban. Kritikai áttekintés adunk a fajok eddigi közléseiről. A három faj morfológiai adatait is összehasonítjuk azzal a céllal, hogy megállapítsuk, mely morfológia bélyegek a legalkalmasabbak a fajok elkülönítésére. Megadtuk a 3 faj irodalmi áttekintését is. A három faj elkülönítésére a csúcsi és a leghosszabb bugaág 4. füzérke pozíciónak bizonyultak a legjobb elkülönítő morfológiai paramétereknek. A füzérkékben a külső toklászok hosszának elemzésekor a 2. virág a legmegbízhatóbb, amit a határozásnál is érdemes alkalmazni.

Kulcsszavak: *Festuca vaginata, Festuca psammophila fajcsoport, homoki vegetáció, morfológia*

BEVEZETÉS

Critical analysis of selected taxa within the *Festuca ovina* and *Festuca valesiaca* complexes based on morphological, genetic and coenological data. Taxonomic challenges of the narrow-leaved fescues (*Festuca ovina* agg.) in the Pannonian region. The genus *Festuca* – one of the most species-rich groups within the grass family (Poaceae) – comprises about 700 species worldwide and represents a key component of temperate grasslands (Šmarda et al., 2008). Taxonomic relationships within the genus are highly complex, particularly in the *Festuca ovina* complex, which includes the narrow-leaved fescues and is considered one of the most taxonomically challenging groups in botany (Galli et al., 2006; Penksza et al., 2019).

These taxonomic difficulties arise from several interrelated factors: the high morphological similarity among species, the considerable intraspecific variability and environmental plasticity of quantitative traits (e.g. leaf length, panicle size), and the frequent occurrence of polyploidization and hybridization events. Together, these factors blur the boundaries between taxa (Galli et al., 2006; Šmarda et al., 2008).

Among the narrow-leaved *Festuca* taxa occurring in the Carpathian Basin, those possessing a curved leaf base and basal sheaths have long been uniformly treated by various floristic authors as belonging to the *Festuca ovina* aggregate (Soó, 1955, 1973a, b; Májovszky, 1962; Horánszky et al., 1971; Nyárády and Nyárády, 1964; Adler et al., 1994; Dostal, 1989; Săvulescu, 1972; Pils, 1985; Patzke, 1961, 1968; Schwarzová, 1967). The species with a continuous sclerenchyma ring are classified within the *eu-ovina* group. These taxa can be easily identified based on their characteristic tissue structure and molecular genetic analyses (Galli et al., 2001, 2006; Armonienė et al., 2010; Šmarda et al., 2007, 2008; Stukonis et al., 2015, 2010).

Pawlus (1985) established a new series within the genus *Festuca*, one of which, the *psammophila* series, includes *F. polesica* Zapal., *F. vaginata* W. K., *F. psammophila* Host., and *F. pallens*. Subsequently,

Šmarda et al. (2008) revised and supplemented this group, designating the taxon *F. vaginata* subsp. *dominii* (Krajina) P. Šmarda. Šmarda and colleagues (2007) clarified the taxonomic status of this subspecies and concluded that it represents a subspecies of *F. psammophila* (Čelak.) Fritsch, a taxon currently restricted to pine forests in northern Europe (Bednarska et al., 2017). Therefore, the accepted name is *F. psammophila* subsp. *dominii* (Krajina) P. Šmarda.

Penksza et al. (2019) and Penksza (2019) examined and collected *F. vaginata* individuals from 20 sampling sites in Hungary. Their results confirmed that *F. vaginata* is typically awnless; when an awn is present, it is very short. Anatomical investigations were complemented by cytogenetic data. The ploidy level (chromosome number) was determined using flow cytometry. Different ploidy levels (diploid, tetraploid, hexaploid, etc.) often correlate with morphological characteristics, ecological niches, and reproductive isolation (Šmarda et al., 2008).

Molecular genetic markers, such as the internal transcribed spacer (ITS) region of nuclear ribosomal DNA and the chloroplast *trnL (UAA)* intron, may provide further insight into phylogenetic relationships. However, within the *Festuca ovina* complex, these markers often exhibit extremely low variability, suggesting that diversification within the group is evolutionarily recent. Morphological and cytogenetic differentiation may therefore have preceded divergence in neutral DNA regions (Galli et al., 2006).

The taxonomic uncertainties also have direct coenological (phytosociological) implications. The correct identification, description, and syntaxonomic classification of a plant community fundamentally depend on the precise determination of the dominant *Festuca* species. In the sandy grasslands of the Carpathian Basin, for example, the clarification of the distribution and nomenclature of the *Festuco dominii-Corynephoretum* and *Festuco vaginatae-Corynephoretum* associations has been closely linked to the taxonomic revision of the respective *Festuca* taxa (Penksza et al., 2019).

MATERIAL AND METHODS

All available literature was reviewed, and published data and results were summarized.

We compared collected individuals of 3 taxa. The specimens were transplanted in 2018 in the Experimental Garden of the MATE Genetics Institute, and in 2019, inflorescences were collected from stems grown under the same conditions for assays, leaf tissue analysis, and phytolith assays.

We cut 10-10 leaves of each of the 3 taxa. Cross sections with the blade were made between the lower third and the middle of the deciduous leaves. The air-dry cross-sections were fixed on an aluminum sample holder using a double-sided carbon adhesive and sprayed with a few nm thick gold layers to prevent condensation. A short section (a few mm) was cut from the same side of the leaves and fixed on the sample holder as described above, making the abaxial surface audible. The leaves have not been cleaned beforehand in order to keep the stigma intact. The images were taken with a Hitachi S4300-CFE scanning electron microscope with an accelerating voltage of 15 kV.

For the inflorescence parameter analyzes, 5-5 flowering vessels were collected from each Festuca specimen and their parameters were measured.

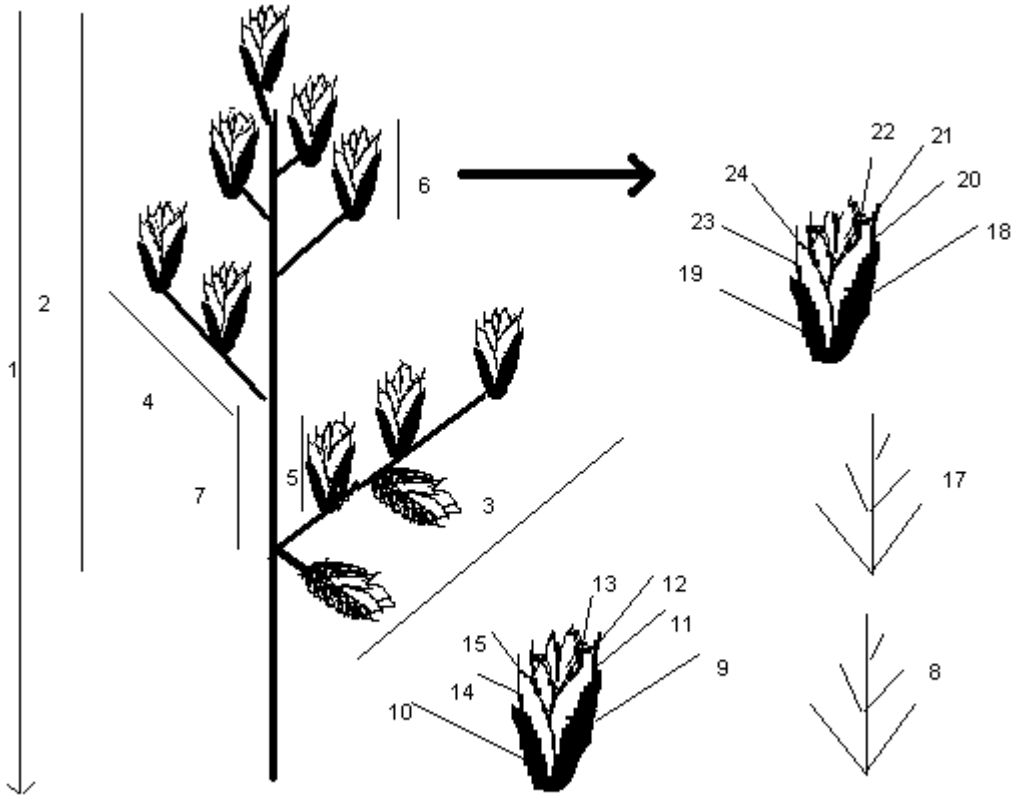
Festuca vaginata individuals: Hungary: Little Hungarian Plain (Győrszentiván), Danube-Tisza Interfluve (Tahitótfalu, Kisoroszi, Homoktövis TT, Tatárszentgyörgy, Imrehegy), Inner Somogy (Böhönye), in South Slovakia (near Ćenkov), Serbia (Deliblato Sands), Romania (Balta Verde: 44°19'43.6"N 22°37'12.9"E).

A total of 140 inflorescence parameters of 28 morphology parameter were measured.

Festuca pseudovaginata individuals: Hungary: Danube-Tisza Interfluve (Kisoroszi, Homoktövis TT, Szigetszentmiklós, Kunpeszér).

Festuca tomanii individuals: Hungary: Danube-Tisza Interfluve (Kisoroszi, Homoktövis TT, Szigetszentmiklós, Tatárszentgyörgy).

Figure 1: **Inflorescence parameters of investigated Festuca taxa**



Note: 1. Length of generative stem; 2. Length of inflorescence; 3. Length of the longest branch on the 1th node; 4. Length of the longest branch on the 2nd node; 5. Length of the 4th spikelet from the top of branch (1); 6. Length of 4th spikelet from the top of inflorescence; 7. Length of the 1th internode of the inflorescence. 7-15 (1): 4th spikelet from the top of branch (2): 8. Floral number of spikelet, 9. Length of upper glume, 10. Length of lower glume, 11. Length of the 2nd flower's lemma, 12. Length of the 2nd flower's awn, 13. Hair of spikelet, 14. Length of the 1th flower's lemma, 15. Length of the 1th flower's awn, 16. Hair on the lemma (if present, not shown), 17-24. 4th spikelet from the top of inflorescence: 17: Floral number of spikelet, 18. Length of upper glume, 19. Length of lower glume, 20. Length of the 2nd flower's lemma, 21. Length of the 2nd flower's awn, 22. Hair of spikelet 23. Length of the 1th flower's lemma, 24. Length of the 1th flower's awn(1)

1. ábra: A vizsgált virágzati paraméterek

Jelmagyarázat: 1. a virágzó hajtás hossza; 2. a buga hossza; 3. az első nódusz leghosszabb bugaágának hossza; 4. az első internódium hossza; 5. a csúcsi 4. füzérkében a virágok száma; 6. a csúcsi 4. füzérke hossza; 7. a csúcsi 4. füzérke felső pelyvalevelének hossza; 8. a csúcsi 4. füzérke alsó pelyvalevelének hossza; 9. a csúcsi 4. füzérke 4. virágáig mért hossza; 10. a csúcsi 4. füzérke első virágának külső toklász hossza; 11. a csúcsi 4. füzérke első virágának belső toklász hossza; 12. a csúcsi 4. füzérke első virágának külső toklász szálkájának hossza; 13. a csúcsi 4. füzérke második virágának külső toklász hossza; 14. a csúcsi 4. füzérke második virágának belső toklász hossza; 15. a csúcsi 4. füzérke második virágának külső toklász szálkájának hossza;16: szőr a külső toklászon (ha van, nincs ábrázolva); 17. az alsó bugaág füzérke hossza; 18. az alsó bugaág füzérke felső pelyvalevelének hossza; 19. az alsó bugaág füzérke alsó pelyvalevelének a hossza; 20. az alsó bugaág füzérke 4. virágáig mért hossza; 21. az alsó bugaág füzérke első virágának külső toklász hossza; 22. az alsó bugaág füzérke első virágának belső toklász hossza; 23. az alsó bugaág füzérke első virágának külső toklász szálkájának hossza; 24. az alsó bugaág füzérke második virágának külső toklász hossza(1)

RESULTS

Festuca vaginata Waldst. & Kit. ex Willd. – Hungarian fescue

Taxonomic classification and nomenclature

Festuca vaginata Waldst. & Kit. ex Willd., commonly known as Hungarian fescue, is one of the most characteristic and well-known members of the *Festuca ovina* aggregate in the Carpathian Basin. Taxonomically, it belongs to the series *Psammophilae* Pawlus, which comprises sand-dwelling (psammophytic) species (Galli et al., 2006; Penksza, 2009). This species is a key characteristic element of the Pannonian sand steppes and serves as the eponymous and dominant species of the *Festucetum vaginatae* plant association (Soó, 1964; Borhidi et al., 2012). Its taxonomic status and delimitation from closely related taxa have been the subject of long-standing debate, particularly concerning its

relationship with taxa occurring on acidic sandy soils (*Table 1*). In earlier literature, the dominant fescue of acidic sandy grasslands was often identified as *F. vaginata*, or was associated with the morphologically similar taxon *Festuca dominii* Krajina. However, recent studies based on herbarium revisions and extensive field collections have clarified that *F. dominii* does not occur in the Pannonian region, and that the dominant fescue species in the acidic sandy grasslands – specifically within the *Festuco vaginatae-Corynephoretum* association – is indeed *F. vaginata* (Penksza et al., 2019).

Morphological and Anatomical Description

The morphological and anatomical characteristics of *Festuca vaginata* are relatively well-defined and serve as key diagnostic features for both field and laboratory identification.

Habit and vegetative organs: *Festuca vaginata* is a perennial, densely tufted grass forming hard, hemispherical tussocks. Its basal leaves are stiffly erect, wiry, and folded in cross-section. The most important vegetative traits are the color and surface texture of the basal leaves: they are glabrous and distinctly bluish-green, covered with a waxy coating that gives them a glaucous appearance. This characteristic coloration is easily recognizable in the field and clearly distinguishes the species from the closely related, bright-green *F. pseudovaginata* (Penksza, 2003 in Szabó et al., 2017; Penksza and Lisztes-Szabó, 2020). Leaf anatomy: The most reliable method for identifying the species is the examination of the cross-section of basal leaves. *Festuca vaginata* belongs to the so-called *eu-ovina* type, which is characterized by a continuous sclerenchyma ring. In the leaf blade, the sclerenchyma forms a thick, uninterrupted ring beneath the outer epidermis, running evenly along the mesophyll. This feature clearly separates the species from those possessing interrupted sclerenchyma strands, such as *Festuca rupicola* (Galli et al., 2006; Penksza, 2009; Penksza, 2003 in Szabó et al., 2017). Generative organs: The panicle is relatively short and compact, usually measuring (4–)5–7 cm in length (Penksza, 2003 in Szabó et al., 2017). The spikelets consist of 4-5 florets (Penksza et al., 2020). The most important generative diagnostic character is the morphology of the lemma apex. In *Festuca vaginata*, the lemma is awnless or terminates in a very short tip, at most 0.1-0.4 mm long, which cannot be regarded as a true awn (Penksza and Lisztes-Szabó, 2020; Šmarda et al., 2007 in Penksza et al., 2021). This feature clearly distinguishes the species from closely related taxa possessing a well-developed awn, such as *F. pseudovaginata* and *F. tomanii*.

Genetic characteristics

The genetic characteristics of *Festuca vaginata*, particularly its ploidy level, have been at the center of long-standing taxonomic debates, highlighting the potential intraspecific complexity of this taxon. Ploidy level: Conflicting data exist in the literature regarding the chromosome number of the species. Based on flow cytometric analyses of Romanian and Hungarian populations, Šmarda et al. (2008) clearly identified the species as diploid ($2n \approx 2\times$). In contrast, later publications citing the original description and work of Penksza (2003) (e.g. Szabó et al., 2017) reported *F. vaginata* as tetraploid ($2n = 4\times = 28$). This considerable discrepancy suggests that the name *Festuca vaginata* may in fact encompass a cryptic species complex or, at the very least, a series of cytotypes differing in ploidy level. When cytogenetic evidence is taken into account, the taxonomic stability of the species becomes questionable. Although *F. vaginata* appears to be morphologically and coenologically well defined, the contradictory data on ploidy levels indicate that it may represent a hidden complex of cytotypes rather than a single, homogeneous species. Such uncertainty has major implications for the interpretation of comparisons with related taxa, such as *F. pseudovaginata*, since it is often unclear which cytotype is being compared. Taxonomy is founded on the clear delimitation of well-defined units, and *F. vaginata* has traditionally been considered such an "anchor species" within the Pannonian sand grasslands. The difference between diploid and tetraploid cytotypes is far from trivial: polyploidy is frequently associated with morphological and ecological shifts and may represent an early stage of reproductive isolation. Until the potential differences in distribution, morphology, and ecology between the 2× and 4× cytotypes are clarified, any taxonomic or coenological conclusions concerning this species must be regarded as provisional.

Molecular data: Galli et al. (2006) conducted molecular analyses on ten taxonomically problematic species within the *Festuca ovina* aggregate, including *F. vaginata*. Their results showed that both the nuclear ribosomal DNA ITS region and the chloroplast *trnL (UAA)* intron exhibited extremely low variability among the studied taxa. In the case of *F. vaginata*, no intraspecific variation was detected, and its sequences did not differ significantly from those of the other examined species. These molecular data alone do not support the independent species status of taxa described on the basis of morphological and ploidy-level differences. Instead, they may indicate a common maternal origin within the group or an evolutionarily very recent, rapid adaptive radiation, in which morphological differentiation preceded divergence in neutral DNA markers (Galli et al., 2006).

Ecology and coenology

Habitat: Festuca vaginata is a strictly psammophytic (sand-dwelling) species that plays a key role in the pioneer vegetation of the calcareous, carbonate-rich sandy areas of the Danube-Tisza Interfluve. It typically occurs in open, extremely dry habitats with low organic matter and nutrient content, where competition among plant species is weak (Penksza et al., 2019; Penksza and Lisztes-Szabó, 2020). Most of its root system is concentrated within the upper 20 cm of the soil, which is highly susceptible

to rapid desiccation (Fekete et al., 1976 in Szabó et al., 2017).

Phytosociological role

The species is the name-giving and dominant element of the *Festucetum vaginatae* Rapaics ex Soó 1929 em. Borhidi 1996 (Hungarian fescue sand steppe) association, which is endemic to the Pannonian Basin. This association belongs to the alliance *Festucion vaginatae* Soó 1929 (Pontic–Pannonian perennial sand steppes) and to the order *Festucetalia vaginatae* Soó 1957 (Borhidi et al., 2012; Penksza et al., 2021). The *Festucetum vaginatae* grasslands are naturally open communities with low overall cover (40-50%), and their soil surface is characterized by a well-developed cryptogamic (moss–lichen) synusia. This cryptogamic layer plays an important role in stabilizing the soil surface and maintaining the water balance (Borhidi et al., 2012; Szabó et al., 2017).

Festuca pseudovaginata Penksza – Tece fescue

Taxonomic classification and nomenclature

Festuca pseudovaginata Penksza is a relatively recently described species, first recognized by science in 2003, and it is endemic to the Carpathian Basin (Penksza, 2003). The species belongs to the *Festuca ovina* aggregate, and its name reflects both its striking morphological similarity to *F. vaginata* and the distinct differences that separate the two. The type specimens (locus classicus) used for the formal description originate from the Kis-Tece pasture near Vácrátót, which also inspired the Hungarian common name of the species (Penksza, 2003; Penksza et al., 2021). The discovery and description of this taxon represented an important advance in understanding the taxonomy and coenological relationships of Pannonian sandy grasslands, as it drew attention to a previously unrecognized element of hidden diversity (Penksza, 2003; Penksza et al., 2017) (*Table 1*).

Morphological and Anatomical Description

Festuca pseudovaginata is morphologically and anatomically well distinguished from its close relative *F. vaginata*, with differences evident in both vegetative and generative organs.

Habit and vegetative organs: Like *F. vaginata*, it is a perennial species forming dense, turf-like tussocks. The most conspicuous and field-relevant distinguishing feature is the color of the basal leaves. In contrast to the glaucous, bluish-green leaves of *F. vaginata*, the basal leaves of *F. pseudovaginata* are bright or light green and lack any waxy coating (Penksza, 2003 in Szabó et al., 2017; Penksza et al., 2021). Leaf anatomy: Leaf cross-section analysis confirms the species' distinctiveness. Although the sclerenchyma tissue also forms a continuous ring in this species, its structure differs from that of *F. vaginata*. The sclerenchyma ring is markedly thick and uneven in width along the mesophyll, which represents a key anatomical diagnostic character. In young leaves, the ring may even appear partially interrupted, providing an additional distinguishing feature (Penksza, 2003; Penksza et al., 2021). Generative organs: The panicle is 5-8.5 cm long, thus generally longer than in *F. vaginata*. Spikelets frequently contain a sterile floret at the apex (Penksza and Lisztes-Szabó, 2020). The most important generative diagnostic trait is the well-developed awn (1.2-1.8 mm long) present on the lemma, which clearly differentiates this species from the awnless *F. vaginata* (Penksza, 2003 in Szabó et al., 2017; Penksza and Lisztes-Szabó, 2020). The glumes are also longer: the lower glume measures 2.9-3.2 mm, and the upper one 3.9-4.1 mm (Szabó et al., 2017).

Genetic Characteristics

The genetic features of *Festuca pseudovaginata* are consistent and support its taxonomic distinctness. Cytogenetic studies conducted since its description have uniformly identified the species as diploid ($2n = 2\times = 14$) (Penksza, 2003 in Szabó et al., 2017; Šmarda et al., 2008). This stable diploid level corresponds to one of the reported cytotypes of *F. vaginata*, but differs from its tetraploid form, further confirming the genetic separation between the two taxa. Molecular data: Since the species was described only in 2003, earlier large-scale molecular taxonomic studies (e.g. Galli et al., 2006) did not include it. However, subsequent investigations based on morphology, anatomy, ploidy, and ecology have all confirmed its independent species status. A phytolith analysis conducted by Penksza and Lisztes-Szabó (2020) yielded particularly interesting results: based on phytolith composition – especially the frequency of ELONGATE SINUATE-type phytoliths – *F. pseudovaginata* appears to be more closely related to *F. tomanii* than to the morphologically more similar *F. vaginata*. This finding suggests more complex phylogenetic relationships among the sandy fescues.

Ecology and Coenology

The ecological and coenological characteristics of *Festuca pseudovaginata* differ markedly from those of *F. vaginata*, and the species' presence reflects specific landscape-historical and successional processes. Habitat: This species does not inhabit the stable, primary sand steppes typical of *F. vaginata*. Instead, it usually occurs in disturbed, secondary habitats – often in regenerating grasslands that have developed on abandoned arable fields, former military areas, or clear-cut forest sites (Penksza et al., 2019; Szabó et al., 2017). Compared to the habitats of *F. vaginata*, its soils are more developed, frequently formed on remnants of former brown forest soils with higher organic matter content, but potentially lower pH and nutrient levels (Péter, 2021; Szabó et al., 2017). Phenologically, it also differs, flowering 2-3 weeks earlier than *F. vaginata*, which may represent a strategy to avoid competition in denser and more species-rich vegetation (Szabó et al., 2017). *Festuca pseudovaginata* is not merely a morphologically distinct species but an ecological specialist that thrives in "landscape scars" created by human activity – disturbed habitats with more developed soils than

those of pioneer sand steppes. Its presence in a given area indicates past deforestation and subsequent secondary succession. Whereas *F. vaginata* characterizes natural, long-term stable, and extremely harsh pioneer sand steppes, *F. pseudovaginata* occupies "disturbed sites" and "former forest soils." Its associated community, *Festucetum pseudovaginatae*, is species-rich and includes elements typical of more closed grasslands, suggesting that it represents a more advanced stage within a successional gradient. The existence and distribution of *F. pseudovaginata* thus constitute a biological imprint of the anthropogenic transformation of the Pannonian landscape, representing a species of dynamically changing, regenerating environments. Consequently, it has high coenological and conservation indicator value: its occurrence signals both the degree of past disturbance and the present regenerative potential of a habitat.

Phytosociological role

Festuca pseudovaginata forms its own distinct plant association, *Festucetum pseudovaginatae*, which is endemic to the Pannonian Basin (Penksza et al., 2021). This association differs significantly from *Festucetum vaginatae*: it has a richer species composition, denser vegetation cover, and a markedly higher proportion of *Festuco-Brometea* elements typical of more closed and mesophilous grasslands. Its diagnostic species include *Colchicum arenarium*, *Ephedra distachya*, *Koeleria majoriflora*, and *Astragalus onobrychis*, while the disturbance indicator *Cynodon dactylon* is also frequently present (Penksza et al., 2021).

Festuca tomanii Korneck & T. Gregor

Taxonomic classification and nomenclature

Festuca tomanii Korneck & T. Gregor is a relatively recently recognized and studied member of the *Festuca ovina* aggregate, occurring in the sandy grasslands along the Danube, alongside *F. vaginata* and *F. pseudovaginata* (Penksza and Lisztes-Szabó, 2020). Its taxonomic position and phylogenetic relationships are still under active investigation, but morphological and micromorphological analyses clearly distinguish it from the related psammophilous species. Within the flora of Hungary, it is regarded as a newly recorded species (Péter et al., 2021).

Morphological and Anatomical Description

Festuca tomanii can be distinguished from other psammophilous fescues by its most striking morphological and anatomical features. Habit and vegetative organs: The most conspicuous and easily recognizable trait of the species is its silvery-grey leaf color. This coloration is caused by the dense and relatively long trichomes (hairs) on the abaxial (outer) epidermis, combined with the high silica content incorporated into the cell walls. This feature not only facilitates species identification but also represents an important ecological adaptation (Penksza and Lisztes-Szabó, 2020). Leaf anatomy: In leaf cross-section, the sclerenchyma ring is continuous, placing the species within the *F. vaginata* group. However, the structure of the ring is unique: near the midrib, one to three intercalated epidermal cells often interrupt the continuity of the strengthening tissue. This subtle anatomical trait differs both from the uniformly thick sclerenchyma ring of *F. vaginata* and from the unevenly thickened ring of *F. pseudovaginata*, and serves as an important microscopic diagnostic character (Penksza and Lisztes-Szabó, 2020). Generative organs: Among the three studied psammophilous species (*F. vaginata*, *F. pseudovaginata*, *F. tomanii*), *F. tomanii* has the largest and loosest panicle. The spikelets consist of 5-6 florets. The most significant quantitative difference lies in the length of the lemma awn: in *F. tomanii* the awn is the longest, typically exceeding 2 mm, which is considerably longer than in *F. pseudovaginata* (~1.5 mm) and the nearly awnless *F. vaginata* (Penksza and Lisztes-Szabó, 2020) (*Table 1*).

Genetic Characteristics

Ploidy level: Based on morphological and phytolith analyses, *Festuca tomanii* shows a closer affinity to *F. pseudovaginata* (Penksza and Lisztes-Szabó, 2020). Flow cytometric measurements revealed that the species is diploid, which complicates its differentiation from *Festuca wagneri* solely on the basis of chromosome number (Balogh et al., 2023). Molecular data: Phytolith analysis – which examines the morphology of silica bodies accumulated in plant tissues – has provided new insights into phylogenetic relationships. The phytolith composition of *F. tomanii*, particularly the higher proportion of ELONGATE SINUATE phytolith types, shows a strong resemblance to that of *F. pseudovaginata*. The phytolith assemblages of both species differ markedly from that of *F. vaginata*, suggesting that these two awned taxa may be more closely related to each other than to the nearly awnless *F. vaginata* (Penksza and Lisztes-Szabó, 2020). The high silica content in the epidermis was also confirmed by energy-dispersive X-ray spectroscopy (EDX) measurements, supporting the biochemical basis of this micromorphological adaptation (Penksza and Lisztes-Szabó, 2020). The case of *Festuca tomanii* clearly demonstrates that behind apparent macromorphological similarities, there may lie subtle yet ecologically and evolutionarily significant differences at the microscopic level. The silvery leaf color, caused by dense pubescence and silica deposition, is not merely an external feature but part of a complex adaptive strategy. Silica accumulation in plants is a well-known defense mechanism against drought (by reducing transpiration) and herbivory (through the increased abrasiveness and toughness of leaves). *Festuca tomanii* may represent an evolutionary pathway in which speciation was driven by a specific micromorphological–biochemical adaptation. This "silica armor" may have enabled the species to successfully colonize disturbed, dry sandy habitats alongside or in place of *F. pseudovaginata*.

This highlights that the future of *Festuca* taxonomy lies not only in classical morphology but also in the study of such functional and adaptive traits.

Ecology and Phytosociology

The ecological niche of *Festuca tomanii* closely resembles that of *F. pseudovaginata*. It typically occurs in disturbed habitats, such as secondary grasslands, forest edges, and abandoned areas, where soil conditions differ from those of the primary, pioneer sandy grasslands (Penksza and Lisztes-Szabó, 2020; Péter, 2021).

Phytosociological role

The phytosociological role of *F. tomanii* still requires further investigation, but the species often co-occurs with *F. pseudovaginata* in habitats that may represent potential speciation hotspots (Penksza and Lisztes-Szabó, 2020). Due to its aesthetically appealing silvery appearance and presumed drought tolerance, its potential use in horticulture and grassland restoration is under active study. Germination experiments have shown that its seeds germinate better on peat- or coir-based substrates than on natural sandy soil, suggesting that organic matter accumulation is a key factor for its establishment (Péter et al., 2021).

Table 1

Comparison of three related Festuca species in the sandy grasslands along the Danube

Characteristic(1)	*Festuca vaginata*	*Festuca pseudovaginata*	*Festuca tomanii*	Reference(s)(2)
Leaf colour(3)	Glaucous, bluish-green(10)	Bright green(11)	Silvery-grey(12)	Penksza and Lisztes-Szabó (2020)
Leaf surface(4)	Smooth, glabrous(13)	Smooth, glabrous(13)	Densely and long-hairy(14)	Penksza and Lisztes-Szabó (2020)
Awn length(5)	< 0.4 mm (practically awnless)(15)	1.2-1.8 mm	> 2.0 mm	Penksza and Lisztes-Szabó (2020)
Sclerenchyma ring(6)	Continuous, uniform(16)	Continuous, unevenly thickened(17)	Continuous but interrupted(18)	Penksza and Lisztes-Szabó (2020)
Ploidy level(7)	2× or 4×	2×	Unknown(19)	Šmarda et al. (2008); Penksza (2003)
Phytolith composition(8)	Distinct(20)	Similar to *F. tomanii*(21)	Similar to *F. pseudovaginata*(22)	
Typical habitat(9)	Stable, pioneer calcareous sand(23)	Disturbed, secondary sand grasslands(24)	Disturbed, secondary sand grasslands(25)	Penksza et al. (2019); Penksza and Lisztes-Szabó (2020)

1. táblázat: A Duna-menti homoki gyepek három rokon Festuca fajának összehasonlítása

Jelmagyarázat: tulajdonság(1), hivatkozások(2), 3: levélszín(3), levélfelület(4), szálka hossza(5), szklerenchima gyűrű(6), ploiditási szint(7), fitolitszerkezet(8), élőhely típusa(9), kékes, kékes-zöld(10), világos zöld(11), sima, kopasz(12), sima, csupasz(13), sűrű és hosszú szőrű(14), gyakorlatilag szálmentes(15), folyamatos, egyenletes(16), folyamatos, egyenetlenül megvastagodott(17), folyamatos, de megszakított(18), ismeretlen(19), elkülönülő(20), Hasonló a F. tomaniihoz(21), Hasonló a F. pseudovaginatahoz(22), stabil, pionír meszes homokon(23), zavart, másodlagos homoki gyepek(24), zavart, másodlagos homoki gyepek(25)

COMPARATIVE OVERVIEW OF THE EXAMINED SPECIES

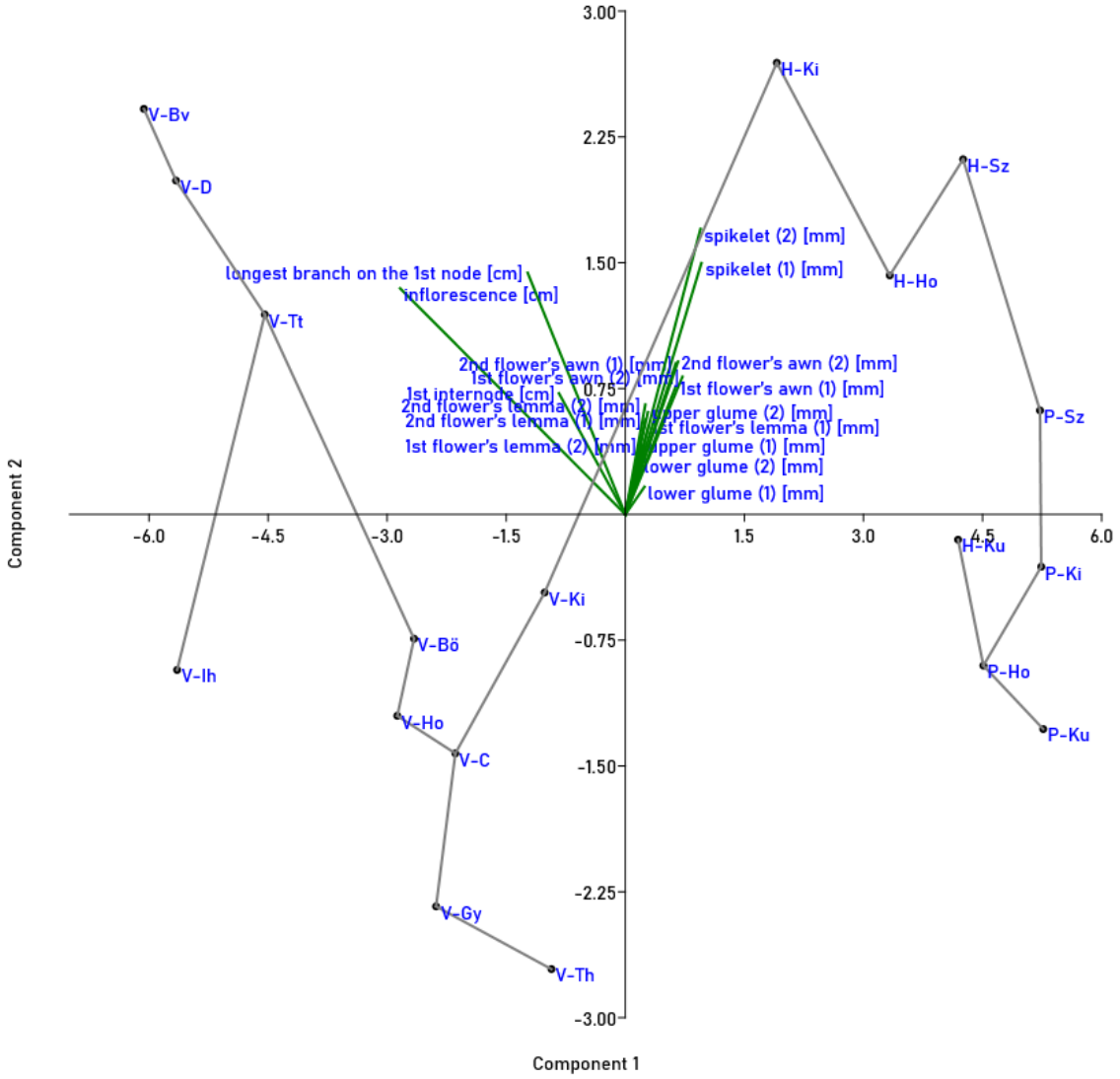
The minimum spanning tree figure clearly highlights the morphological features most responsible for species differences (*Figure 1*). The separation of Festuca vaginata is represented by the following stamps: the other 2 species have a much longer inflorescence (13.47 cm), the longest branch on the 1st node (Figure 1: 3) and the short awn of lemma (Figure 1: 12, 15, 21, 24).

The figure also highlights the morphological parameters by which *F. pseudovaginata* and *F. horanszkyi* differ. The spicelet is also a distinctive feature of *Festuca vaginata* and *F. pseudovaginata* of the 4th spikelet from the top of the branch (Figure 1: 6). as the 4th spikelet from the top of the branch (Figure 1: 7, 15). In the case of *F. horanszkyi*, this length is reversed and the 4th spikelet from the top of the branch is shorter. In these cases, similarly to *Festuca vaginata*, there is a difference with the geographical distribution, the size of the specimens (Ku: Kunpeszér, Kunadacs) from the southern part of the studied areas, the central Kiskunság was smaller.

Differences between F. pseudovaginata and F. tomanii: length of the 2nd flower's awn (cm), length of the 2nd flower's lemma (Figure 1: 11), the length of the lemma awn were as follows: 1: 12, 14), length of upper glume (18), length of 1st flower's lemma (23), length of 1st flower's awn (24). The differences between *F. pseudovaginata* and *F. horanszkyi*: longest branch on the 1st node, length of the 2nd flower's lemma (Figure 1: 11), length of lemma awn: length of the 2nd flower's awn (Figure 1: 12, 14), length of upper glume (18), length of the 1st flower's lemma (23), length of the 1st flower's awn (24).

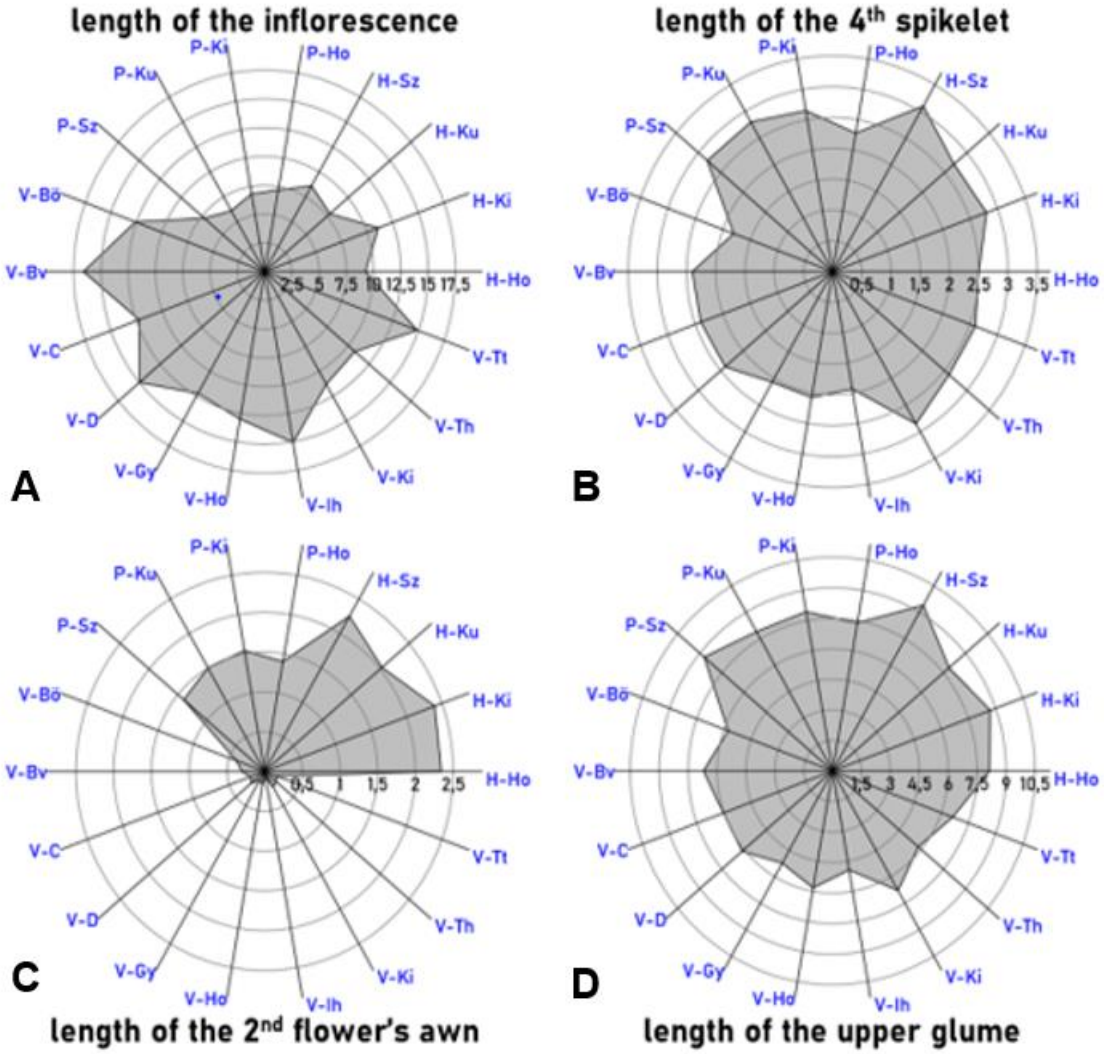
The *Figure 3.* illustrates the differences in the taxa studied in a very illustrative way. 4 morphological parameters were highlighted the length of inflorescence; length of the 4th spikelet from the top of branch; the length of the outer sheath fiber and length of upper glume.

Figure 2: **Classification inflorescence parameters of investigated Festuca taxa**
(D: Deliblato, Ih: Imrehegy, Ku: Kunpeszér, Kunadacs, Sz: Szigetszentmiklós)



2. ábra: A vizsgált fajok virágzati paramétereinek a klaszifikációja

Figure 3: **The most important flowering parameters of the three species studied**



Note: Legend: V: F. vaginata, P: F. pseudovaginata, H: F. tomanii, Bö: Böhönye, Ho: Homoktövis TT, C: Cenkov, Gy: Győrszentiván, Ki: Kisoroszi, Th: Tahitótfalu, Vv: Balta Verde, Tt: Tatárszentgyörgy, D. Deliblato, Ih: Imrehegy, Ku: Kunpeszér, Kunadacs, Sz: Szigetszentmiklós, A: flower cluster length; B: length of the 4th spikelet; C: length of the outer glume of the 2nd flower; D: length of the upper glume

3. ábra: A vizsgált 3 faj legfontosabb virágzati paraméterei
Jelmagyarázat: A: a virágzati hossz; B: a 4. füzérke hossza; C: a 2. virág külső toklászának a hossza D: a felső pelyva hossza

DISCUSSION

Among the panicle parameters, certain traits proved unsuitable for distinguishing the three examined species, namely the floral number of spikelets and the degree of pubescence. Beyond these traits, *Festuca vaginata* could be clearly separated based on the remaining diagnostic parameters. *F. pseudovaginata* and *F. horanszkyi* were not differentiated by spikelet length, although individuals of *F. horanszkyi* from the central part of the Kiskunság region tend to be smaller, which may reflect adaptation to drier and warmer habitats.

In the analysis of spikelets, both the terminal spikelet and the fourth spikelet of the longest panicle branch proved to be reliable positions for comparative examination in these taxa, confirming Horánszky's (1971) earlier observations. Within the spikelet, the second lemma was found to be longer and showed the greatest interspecific variation, supporting the conclusions of Šmarda and Kočí (2003), Šmarda et al. (2007), who identified this character as one of the most informative diagnostic traits for species delimitation.

The lengths of both the lower and upper glumes also proved to be effective morphological parameters for distinguishing *F. vaginata* from the other two taxa, *F. pseudovaginata* and *F. tomanii*.

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