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Patterns in clonal traits in semi-dry calcareous grasslands in Slovenia

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Abstract: Due to the widespread importance of clonality in plants, investigating the mechanisms by which clonality-related traits are associated with community organization is crucial for a functional understanding of vegetation. In this study, the patterns in clonality and other life-history traits in a series of species-rich semi-dry grasslands (alliance *Bromion erecti*, order *Brometalia erecti,* class *Festuco-Brometea*) in the central-European region of Slovenia, all assigned to the same EUNIS (Middle European *Bromus erectus* semi-dry grasslands, code R1A32) and Natura 2000 habitat type [Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*), code 6210 (important orchid sites)] were studied. The aims of this research were (i) to assess the diversity of clonal growth organs (CGOs) and other clonal traits in semi-dry grasslands and (ii) determine differences in distribution of clonal growth organs and other clonal traits in three plant communities (associations). Data from 224 vegetation plots (phytosociological relevés) with 247 species and nine plant traits of grassland species were used. This revealed that more than half of the plant species were clonal. Most common clonal growth organs (CGOs) were perennial splitting main root (produced by non-clonal plants), epigeogenous rhizomes and hypogeogenous rhizomes. For each plot, the community weighted mean (CWM) of all plant traits was calculated to determine differences between the three grassland types. Soil moisture and productivity seem to be the key factors associated with differences in clonal growth in the associations studied. Clonal tussock plants with rhizomes, and species with a rich bud bank and a high number of clonal offspring were abundant in grasslands with deep soils and mesic conditions (*Onobrychido-Brometum* association). Grasslands on stony soils over fissured limestone or dolomite and with more xeric conditions were characterized by rosette clonal plants with hypogeogenous rhizomes (*Bromo-Danthonietum calycinae*) and/or non-clonal plants with splitting main root (*Scabioso hladnikianae-Caricetum humilis*). The diversity and characteristics of clonality-related traits indicate that clonal growth is an essential feature of these species-rich grasslands. Importantly, the results of this study indicate that in order to support the characteristic species and functional composition of all types of grassland, management plans for semi-dry grassland habitats in the area studied need to be carried out at a finer scale (e.g. at the level of associations) than the level of EUNIS and Natura 2000 habitat types.

Keywords: biodiversity, CLO–PLA, community assembly, community weighted mean, *Festuco-Brometea*, functional traits, high nature value habitats, species coexistence

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Introduction

The ability to reproduce is important for the survival and ecological success of organisms (Herben et al. 2016). Most plants reproduce sexually, but they often combine reproduction by seeds with vegetative reproduction by clonal growth (Fischer & van Kleunen 2001, Klimešová & Klimeš 2008). Clonal growth organs (CGOs; sensu Klimeš et al. 1997) such as a stolon, rhizome or similar organ, which are capable of forming new functional individuals, are well represented in herbaceous plants (Herben et al. 2012). In addition to providing an alternative mode of reproduction (Aarssen 2008), clonal growth can also enable them to rapidly colonize open areas, store resources for growth and regeneration, and forage for resources in a heterogeneous microhabitat (Wellstein & Kuss 2011, Klimešová et al. 2018).

In recent decades clonality-related traits have been generally recognized as important and relevant in providing a functional understanding of vegetation (Wellstein & Kuss 2011) and there are many studies on this topic (Klimeš et al. 1997, Cornelissen et al. 2003, Klimešová & Klimeš 2007, Kleyer et al. 2008, Klimešová et al. 2017), especially focusing on the functional role of plant traits in determining biodiversity and ecosystem functioning (e.g. Wellstein & Kuss 2011, Janovský & Herben 2020, Martínková et al. 2020, Chelli et al. 2024, Kapás et al. 2024). However, clonality is still a largely underexplored life history trait (Janovský & Herben 2020, Klimešová et al. 2023).

Grassland habitats worldwide are mainly dominated by clonally reproducing graminoids and species with rhizomes (Klimeš et al. 1997), which have an important role in the structure and processes in grassland ecosystems (Canullo et al. 2006). Understanding the abundance and distribution of clonality-related traits is also important from the perspective of maintaining diversity (Klimeš 1999). Therefore, considering the mechanisms by which clonality influences community organization is also essential for determining effective conservation and restoration (Török et al. 2011, Kapás et al. 2024). This is particularly important for species-rich grassland habitats, as their area continues to decline despite their high value in terms of diversity (United Nations 2019, Klinkovská et al. 2024).

Slovenia is a biodiversity hotspot and more than 38% of its territory is included in the Natura 2000 network (Šilc et al. 2020). Its location at the intersection of four major European geographical units (the Alps, karstic Dinaric Alps, Mediterranean and Pannonian Plain) resulted in diverse geological, orographic, pedological, climatic and hydrological features and a high diversity of landscapes (Perko & Ciglič 2015). Permanent grasslands cover more than half of the agricultural area (SURS 2023) and include many species-rich grassland habitats (Kaligarič et al. 2019, Škornik et al. 2023). Most of them are seminatural as they replaced primary forest vegetation and have been maintained as pastures or meadows for centuries (Kaligarič & Ivajnšič 2014). Among them, dry and semi-dry grassland communities (alliance *Bromion erecti*, order *Brometalia erecti*, class *Festuco-Brometea*) in the continental (central-European) part of Slovenia are particularly known for their high floristic diversity at local, regional and global scales (Pipenbaher et al. 2013, Kaligarič et al. 2019). They are classified as Middle European *Bromus erectus* semidry grasslands according to the EUNIS classification system (EUNIS code R1A32) and in the EU Habitat Directive as Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) code 6210 (important orchid sites) (Škornik et al. 2023). Over the course of the 20th century, the area of species-rich Slovenian grasslands has declined rapidly, mainly due to the abandonment of management or intensification of agriculture (Jančar 2014, Kaligarič & Ivajnšič 2014, Šorgo et al. 2016). In order to preserve these very valuable habitats, different conservation management within the scope of the grassland-specific agri-environment measures (AEM) were implemented within the framework of the European Agricultural Fund for Rural Development (EAFRD) (Škornik et al. 2023). However, their effectiveness is rated as very low (Kaligarič et al. 2019).

Studies on the functional structure of Slovenian grasslands are scarce and mainly only consider above-ground plant traits (Pipenbaher et al. 2013, 2014, Batalha et al. 2015, Unuk et al. 2018). Consequently, and given the widespread importance of clonality in plants (Klimešová et al. 2018, Laughlin 2023), the inclusion of clonality-related traits in studies investigating the functional structure of communities is crucial both for a better understanding (Klimešová et al. 2021, Laughlin 2023) of the response of these traits to environmental gradients and their potential effect on ecosystem properties and services (Jackson et al. 2000, Cornelissen et al. 2014).

In this study, patterns in clonal traits in species-rich semi-dry grassland communities (alliance *Bromion erecti*, order *Brometalia erecti,* class *Festuco-Brometea*) were studied in order to identify previously overlooked aspects of plant ecological strategies and to better understand the mechanisms of species coexistence, diversity levels and dynamic processes in these secondary plant communities. This study had the following aims: (i) to determine the diversity of clonal growth organs (CGOs) and other clonal traits of species-rich semi-dry grasslands in the area studied and (ii) to assess the distribution of clonal growth organs and other clonal traits in three semi-dry grassland plant communities (associations) in the area. It was hypothesized that there are different environments that exert different selection pressures by favouring certain mechanisms of clonal growth, leading to differences in CGO spectra.

Vegetation plots (phytosociological relevés) of dry grasslands from the database of secondary grasslands in the Biology Department, University of Maribor, Slovenia (Kaligarič & Škornik 2002), measurements of plant species traits (Pipenbaher et al. 2013, 2014, Unuk et al. 2018) and the LEDA database (Kleyer et al. 2008) coupled with information on species' clonality from the CLO-PLA database (Klimešová et al. 2017) were used as data sources.

Material and methods

Vegetation and environmental characteristics

The database of secondary grasslands (Kaligarič & Škornik 2002) contains > 1,000 vegetation samples from standard phytosociological relevés of 5 m × 5 m (25 m^2), collected after 1992. To evaluate the spectra of clonal traits for species rich dry and semi-dry calcareous grasslands (class *Festuco-Brometea*) subsamples were taken from the database that included only secondary calcareous grassland plant communities in the continental (central-European) part of Slovenia (habitat type EUNIS code R1A32/Natura 2000 code 6210) (N = 224 relevés). In the area studied in central-European Slovenia (Fig. 1), there are three main plant communities (associations) of this vegetation, i.e. *Bromo-Danthonietum calycinae* Šugar 1973 (86 relevés), *Scabioso hladnikianae-Caricetum humilis* (Horvat

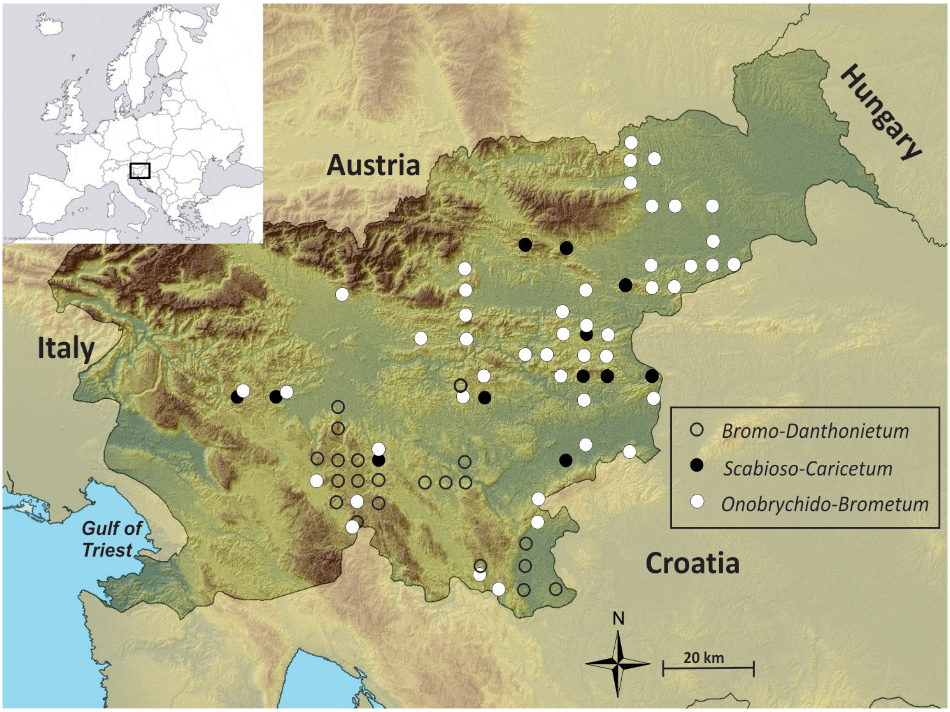

Fig. 1. Map of Slovenia showing the locations of the dry grasslands studied. Source of the orthophoto map: Geologicharka (2012).

1931) Tomažič 1941 (30 relevés) and *Onobrychido-Brometum* T. Müller 1966 (108 relevés) (Škornik et al. 2023). The relevés selected were those from grasslands with favourable conservation status, with characteristic species composition and physiognomy. These extensive grasslands were all subjected to similar management regimes, with mowing at least once a year, often in combination with extensive grazing in early spring and/or late summer. Their productivity was generally low, as they were not fertilized, or only to a very limited extent, and no grass and/or plant species were sown (Škornik et al. 2023). These syntaxa were assigned to alliance *Bromion erecti* Koch 1962, order *Brometalia erecti* Koch 1926, class *Festuco-Brometea* (Kaligarič & Škornik 2002). Vegetation plots were assigned to the three aforementioned associations based on the results of agglomerative hierarchical clustering analysis done using SYN-TAX 5.0 (Podani 1993). There are short descriptions of these types of communities in Table 1. A synoptic table (Supplementary Table S1) showing the calculated frequencies and fidelity of specific species was created in order to compare the differences in species composition in the associations. As a measure of fidelity, the phi coefficient of association for the virtually equalized size of all groups of plots (relevés) representing associations was used (Tichý & Chytrý 2006). The species with a phi coefficient value greater than 0.4 and 0.5 were considered as diagnostic and highly diagnostic, respectively. The calculation of fidelity and the sorting of species were carried out using the programme JUICE 7.0 (Tichý 2002). Taxonomy follows Martinčič et al. (2007) and syntaxonomic scheme follows Šilc & Čarni (2012).

Table 1. The characteristics of secondary dry grassland plant communities (associations) in the central-European part of Slovenia (Kaligarič & Škornik 2002, Škornik et al. 2023) (EUNIS code R1A32/Natura 2000 code 6210).

Association	Typical species	Habitat description / environmental characteristics	Altitude (m a.s.l.) (mean)	No. of vascular plants (mean no./relevé)	No. of relevés
Bromo-Danthonietum calycinae	*Danthonia alpina*, *Filipendula vulgaris*, *Chamaespartium sagittale*, *Globularia punctata*	Semi-mesic, shallow to medium-deep, neutral to slightly acid soil on limestone and dolomites.	168–880 (548)	181 (53±9)	86
Scabioso hladnikianae-Caricetum humilis	*Acinos alpinus*, *Genista januensis*, *Veronica jacquinii*, *Scabiosa hladnikiana*, *Leontodon incanus*, *Koeleria pyramidata*	Shallow, xeric, neutral to basic, and nutrient-poor soil (rendzinas) on limestone and dolomites.	380–900 (643)	125 (47±7)	30
Onobrychido-Brometum	*Onobrychis viciifolia*, *Poa angustifolia*, *Medicago lupulina*, *Bromopsis erecta*, *Salvia pratensis*	Semi-mesic vegetation on medium-deep eutric cambisols, with neutral to basic pH reaction, on limestone or flysch bedrock.	200–700 (377)	162 (42±7)	108

Plant traits

The species pool contained 247 species of plants (Supplementary Table S1). Data for nine traits were obtained from the literature (Martinčič et al. 2007), from the database (protocol standardized by Hodgson et al. 1999; see Pipenbaher et al. 2013), and from CLO-PLA3, which is a database of clonal growth in plants in central Europe (Klimešová et al. 2017), and LEDA (Kleyer et al. 2008). The following traits were selected: life form, growth form, type of clonal growth organ (CGO), persistence of connections between ramets, number of clonal offspring shoots produced per year, lateral spread by clonal growth, role of CGO in life history of a plant, size of plant bud bank expressed as the total number of buds per shoot, including stem buds at the soil level and root buds at different depths, and CSR strategy (Table 2). Values for persistence of the connections, the number of offspring shoots and lateral spread by clonal growth were estimated based on categories in the CLO-PLA3 database (Klimešová et al. 2017). The mean values of these categories were used as suggested and reported in the Pladias Database of Czech Flora and Vegetation (Chytrý et al. 2021).

For the multivariate analyses, the CSR strategy was expressed in terms of three continuous variables (C, S, R), which reflect the degree to which species are associated with each of the CSR axes. The categorical plant traits (life form, growth form, type of CGO, role of CGO and plant bud bank) were coded as dummy variables before use in the analysis. This resulted in the number of variables in the matrix increasing from nine to 31.

Based on the published list of diagnostic species in phytosociological classes (Kaligarič & Škornik 2002), species were also classified according to their affinity to different types of grassland (syntaxa). Five main species groups were recognized as characteristic of (i) dry and semi-dry grasslands (corresponding to the *Festuco-Brometea* class), (ii) mesotrophic grasslands (*Molinio-Arrhenatheretea*), (iii) dwarf-shrub and mat-grass heaths on acidic

Table 2. Plant traits (N = 9) recorded for 247 species of vascular plants of secondary dry grasslands in the central-European part of Slovenia.

Plant traits	Abbreviation and description (attributes)
Life form	LF_ch = chamaephytes; LF_ge = geophytes; LF_he = hemicryptophytes; LF_th = therophytes;
Growth form	GF_tuss = tussocks; GF_roset = rosette; GF_le_st = leafy stem; GF_ro_le = rosette and leafy stem;
Type of clonal growth organ (CGO)	CGO_no = none; 1_stolon = stolon; 9_epigeo_rhiz = epigeogenous rhizome; 10_hypogeo_rhiz = hypogeogenous rhizome; 12_tuber_bg_st = belowground stem tuber; 13_bulb = bulb; 14_root_splitt = root splitters; 15_adv_buds = root with adventitious buds; 16_root_tuber = root tuber
Persistence of connection in CGO [years]	Persist_CGO (0.5 / 1.5 / 4)
Number of clonal offspring shoots	No_clo_sh (0.5 / 1 / 6 / 15)
Lateral spread by clonal growth [m/year]	Lat_spread (0.005 / 0.13 / 0.5)
Role of clonal growth organs	Role_add = additive; Role_obl = necessary; Role_reg = regenerative; Role_non = none
Bud bank of plant	NoBB_ab_10 = bud bank located on a plant taller than 10 cm (0 / 5 / 15 buds per shoot); NoBB_10 = bud bank on the plant 10 to 0 cm (0 / 5 / 15 buds per shoot); NoBB_0 = bud bank at the soil surface (0 / 5 / 15 buds per shoot); NoBB_010 = bud bank at a depth of 0 to 10 cm (0 / 5 / 15 buds per shoot)
CSR strategy	C = competitors; S = stress-tolerant; R = ruderals

soils (*Calluno-Ulicetea*), (iv) thermophilous woodland fringe and tall-herbaceous vegetation (*Trifolio-Geranietea sanguinei*) and (v) alpine grasslands on base-rich soil (*Elyno-Seslerietea*).

Data analysis

Linear regressions were used to test for significant associations between species richness and CGO diversity. To quantify the variability in CGO diversity among families, the Shannon diversity index H' was calculated for each family using the number of species in each CGO type in each family.

In order to visualize the differences in the flora in the three grassland communities studied, the multivariate data on species composition (matrix 247 species × 224 relevés) were summarized using detrended correspondence analysis (DCA; Hill & Gauch 1980).

To characterize the plant communities based on values of characteristics (plant traits) of their species, the community weighted mean trait values (CWMs) were calculated for all traits. For this, the 247 species × 224 relevés matrix was combined with the corresponding 247 species × 31 traits matrix. Before doing this analysis, the Braun-Blanquet alpha-numerical scale values were converted to a numerical 1–9 scale as proposed by van der Maarel (1979) (r = 1, + = 2, 1 = 3, 2 = 4, 3 = 7; 4 = 8, 5 = 9). The CWM was calculated using the following equation:

$$CWM_{jk} = \sum_{i=j}^{S} p_{ik} \cdot x_{ij}$$

In which CWM_{jk} is the community-weighted mean value of trait *j* at site *k*, p_{ik} is abundance (abundance is equivalent to plant cover in this case) the relative above-ground cover of species *i* (*i* = 1, 2... S) at site *k* and x_{ij} is the value of trait *j* for species *i* (Ricotta & Moretti 2010). This operation resulted in matrix CWM with 31 new traits based on 224 relevés.

Differences in plant characteristics and species richness among the three types of communities were tested using ANOVA for variables with normally distributed data (tested using the Shapiro-Wilk test) and post hoc Bonferroni test. Variables with non-normally distributed data were tested using the Kruskal-Wallis test and a Bonferroni correction. All tests were done using IBM SPSS Statistics for Windows, version 28.0.

Overall differences in trait composition in the three communities were additionally evaluated using principal components analysis (PCA) of CWM values. Only traits with significant differences in their CWM values in three grassland associations (tested with ANOVA and post hoc tests) were used in the PCA. Pearson's correlation coefficients were also calculated for each of the traits (Supplementary Table S2).

The three grassland associations, phytosociological classes and botanical families were used as supplementary variables in the multivariate analysis. The ordination methods (DCA, PCA) and visualization of their results in the form of a biplot ordination diagrams were produced using the programmes Canoco version 4.5 and CanoDraw (ter Braak & Šmilauer 2002).

Results

Clonal trait composition of plants in semi-dry grasslands

The species pool consisted of 247 species of plants (Supplementary Table S1). Most grassland species were perennial hemicryptophytes (76%). The remainder were geophytes (10%), chamaephytes (8%) and therophytes (6%) (Fig. 2A). About 41% were species with a leafy stem, 31% consisted of a rosette and leafy stem, rosette and tussock species made up 14% and 13%, respectively (Fig. 2B).

A total of 91% (N = 226) of the plants in the grasslands studied were taxa with CGOs. Excluding annual herbaceous plants (N = 15), the percentage of taxa with clonal growth organs (CGOs) was 97% for those with perennial life cycles (N = 232). In total, eight out of 17 CGOs were recorded in the species pool studied (Fig. 2C). Most plants had CGOs that occur belowground. The most common CGO type in the grassland species pool is a splitting main root (CGO14, 94 species, 38%). Plants having this CGO (for example *Dianthus carthusianorum*, *Globularia punctata*, *Knautia arvensis*, *Peucedanum oreoselinum* etc.), can be regarded as nonclonal, since this belowground organ does not have a clonality function, but is associated with them being perennial and capable of re-sprouting (i.e. a non-clonal organ) (Klimešová & Klimeš 2008). Other common CGOs are two types of rhizomes: epigeogenous (53 species, 21%) and hypogeogenous (45 species, 18%) rhizomes. The least represented types of clonal growth organs are bulbs (6.2%) and stem tubers (three species, 1%) (Fig. 2C). About 9% of the species (N = 20) had more than one CGO, for example *Cruciata laevipes* with a stolon (CGO1) and hypogeogenous rhizome (CGO10) and *Geranium sanguineum* with hypogeogenous rhizome (CGO10) and roots with adventitious buds (CGO15).

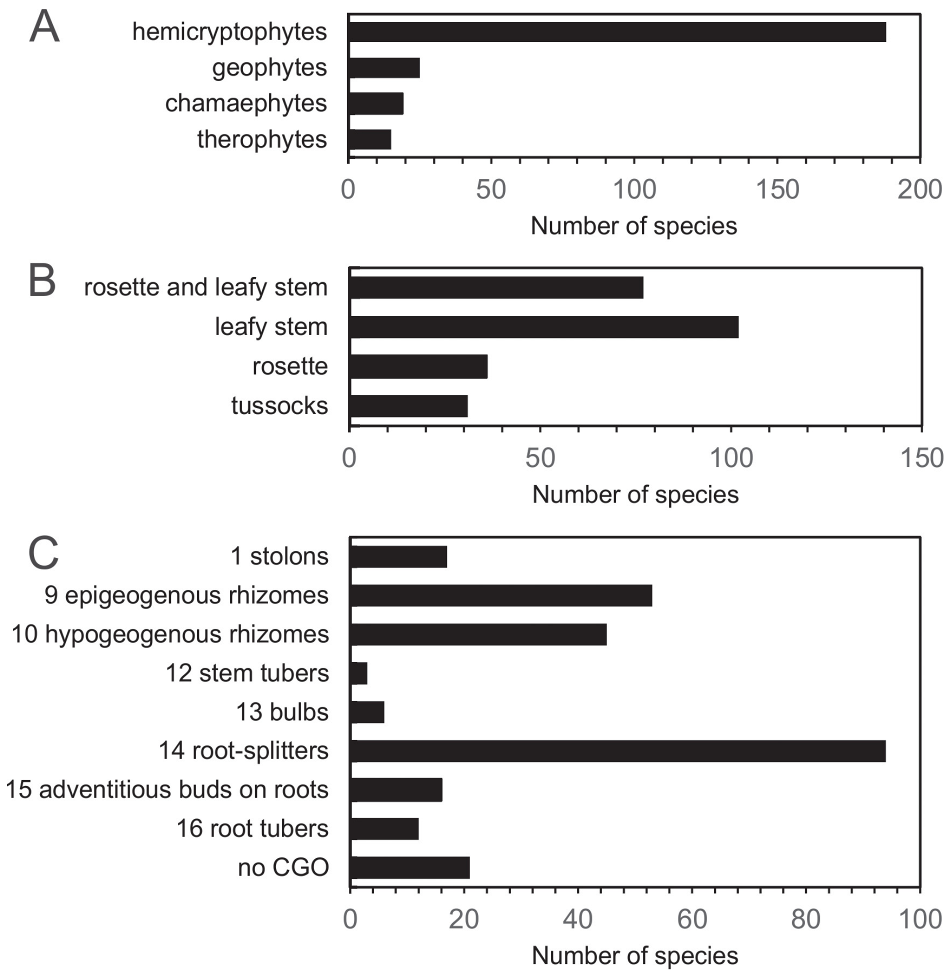

Fig. 2. Classification of (A) life forms (Raunkiaer 1934), (B) growth forms and (C) distribution of the different types of clonal growth organs (CGOs) in 247 species of plants that occur in dry grasslands (Natura 2000 habitat type 6210) in the central-European part of Slovenia. The CGO numbers correspond to the numbers used in the original classification (Klimešová & Klimeš 2008).

The grassland species studied belong to 40 families all of which had at least one species with a CGO (Table 3). The highest number of species with a CGO was recorded in the *Fabaceae* (30), followed by the *Poaceae* (23) and the *Asteraceae* (18 species). Some families had a specific type of clonal growth organ. For instance, all species in the *Liliaceae* were bulbous and 92% of *Orchidaceae* were tuberous, and 90% and 80% of species (including only those with CGO) had a splitting main root were in the *Caryophyllaceae* and *Fabaceae*, respectively (Table 3). As some types of CGOs, such as stolon, splitting main root and roots with adventitious buds were recorded in the eudicot families in the vegetation studied, the Shannon's diversity index indicated that the diversity of clonal growth organs was higher in the eudicot clade than the monocot clade. The *Ranunculaceae* had the highest belowground organ diversity (H' = 1.47), as five

Table 3. Distribution of taxa with different clonal growth organs (CGOs) in major clades and plant families in Slovenian central-European dry grasslands. The numbers presented are those of taxa and CGO type per family. N is the total number of species in each family, n is the number of species with a CGO, and CGO (%) is the percentage of the number of taxa with CGOs in each family. H' is the Shannon diversity index, with values of H' > 1.2 indicated in bold. CGO abbreviations are defined as follows: CGO_no – none; 1_stolon – stolon; 9_epigeo_rhiz – epigeogenous rhizome; 10_hypogeo_rhiz– hypogeogenous rhizome; 12_tuber_bg_st – belowground stem tuber; 13_bulb – bulb; 14_root_splitt – root splitter; 15_adv_buds – root with adventitious buds; 16_root_tuber – root tuber.

Clade / Family	CGO_no	1_stolon	9_epigeo_rhiz	10_hypogeo_rhiz	12_tuber_bg_st	13_bulb	14_root_splitt	15_adv_buds	16_root_tuber	N	n	CGO (%)	H'
All species	21	17	53	45	3	6	94	16	12	247	226	91.5	1.66
Monocots	0	0	22	16	2	6	0	0	11	57	57	100.0	**1.40**
Eudicots	21	17	31	29	1	0	94	16	1	190	169	88.9	**1.65**
Tofieldiaceae	0	0	1	0	0	0	0	0	0	1	1	100.0	0
Colchicaceae	0	0	0	0	1	0	0	0	0	1	1	100.0	0
Liliaceae	0	0	0	0	0	3	0	0	0	3	3	100.0	0
Orchidaceae	0	0	0	1	0	0	0	0	11	12	12	100.0	0.29
Iridaceae	0	0	0	0	1	0	0	0	0	1	1	100.0	0
Amaryllidaceae	0	0	0	0	0	1	0	0	0	1	1	100.0	0
Aspergaceae	0	0	1	1	0	2	0	0	0	4	4	100.0	0.71
Juncaceae	0	0	0	1	0	0	0	0	0	1	1	100.0	0
Cyperaceae	0	0	6	4	0	0	0	0	0	10	10	100.0	0.67
Poaceae	0	0	14	9	0	0	0	0	0	23	23	100.0	0.67
Ranunculaceae	0	1	2	2	1	0	4	0	0	9	9	100.0	**1.47**
Saxifragaceae	0	1	0	0	0	0	0	0	0	1	1	100.0	0
Hypericaceae	0	0	0	0	0	0	1	1	0	1	1	100.0	0.69
Violaceae	0	0	1	0	0	0	1	0	0	2	2	100.0	0.69
Euphorbiaceae	0	0	0	2	0	0	0	1	0	2	2	100.0	0.64
Linaceae	1	0	0	0	0	0	3	0	0	4	3	75.0	0
Fabaceae	4	1	0	4	0	0	24	2	1	34	30	88.2	0.87
Polygalaceae	0	1	0	0	0	0	3	0	0	3	3	100.0	0.56
Rosaceae	0	2	6	1	0	0	3	1	0	10	10	100.0	**1.38**
Geraniaceae	0	0	0	1	0	0	0	1	0	1	1	100.0	0.69
Cistaceae	0	0	0	0	0	0	1	0	0	1	1	100.0	0
Brassicaceae	1	0	0	0	0	0	1	0	0	2	1	50.0	0
Santalaceae	0	0	0	0	0	0	2	2	0	2	2	100.0	0.69
Polygonaceae	0	0	1	0	0	0	0	0	0	1	1	100.0	0
Caryophyllaceae	1	1	0	1	0	0	8	0	0	10	9	90.0	0.64
Primulacea	0	0	1	0	0	0	0	0	0	1	1	100.0	0
Ericaceae	0	0	1	0	0	0	1	0	0	2	2	100.0	0.69
Rubiaceae	0	3	0	4	0	0	2	0	0	6	6	100.0	1.06
Gentianaceae	2	0	0	3	0	0	0	1	0	5	3	60.0	0.56
Convolvulaceae	1	0	0	0	0	0	0	1	0	2	1	50.0	0
Boraginaceae	2	0	0	0	0	0	1	0	0	3	1	33.3	0
Plantaginaceae	1	3	1	2	0	0	6	0	0	12	11	91.7	1.20
Scrophulariaceae	0	0	0	0	0	0	1	0	0	1	1	100.0	0
Lamiaceae	0	2	3	3	0	0	8	1	0	17	17	100.0	**1.39**
Orobanchaceae	4	0	0	0	0	0	0	1	0	5	1	20.0	0
Campanulaceae	1	0	0	0	0	0	2	0	0	3	2	66.7	0
Asteraceae	1	0	8	6	0	0	4	1	0	19	18	94.7	**1.21**
Cichoriaceae	1	2	5	0	0	0	7	1	0	15	14	93.3	1.17
Apiaceae	1	0	1	0	0	0	5	2	0	9	8	88.9	0.90
Dipsacaceae	0	0	1	0	0	0	6	0	0	7	7	100.0	0.41

types of CGOs were recorded in this family. A similar pattern was also recorded for the *Rosaceae*, *Lamiaceae* and *Asteraceae* (Table 3).

Plant species composition and characteristics in different communities

Species richness in 25 m^2 relevé (N = 224) ranged from 25 to 76 with an average of 47. A mean of 6.4 CGOs were recorded per relevé (min: 4, max: 8) (Supplementary Fig. S1). The ANOVA revealed significant differences in the mean number of species ($P < 0.001$), and CGOs ($P < 0.01$) among the three grassland communities, with the highest value in *Bromo-Danthonietum calycinae* (species richness: 53±9, CGO diversity: 6.7±0.8), middle values in *Scabioso hladnikianae-Caricetum humilis* (species richness: 47±7; CGO diversity: 6.3±0.8) and lowest in *Onobrychido-Brometum* (species richness: 42±7; CGO diversity: 6.2±0.9). CGO diversity within a sample increased significantly with species number ($R^2 = 0.15$, $P < 0.001$) (Supplementary Fig. S2).

The three dry grassland communities differed significantly in their species composition, as the plots (relevés) formed separate groups in ordination space (Supplementary Fig. S3 A). There were 80 species (32%) that occurred in all three associations (Supplementary Table S1). These were mainly species characteristic of the *Festuco-Brometea* class of dry and semi-dry grasslands, e.g. *Bromopsis erecta*, *Briza media*, *Buphthalmum salicifolium*, *Carex caryophyllea*, *Carlina acaulis*, *Galium verum*, etc. (Supplementary Table S1, Supplementary Fig. S3). Overall, there were more species exclusively in the *Onobrychido-Brometum* association, while the *Bromo-Danthonietum calycinae* and *Scabioso hladnikianae-Caricetum humilis* relevés were more similar in species composition. The *Onobrychido-Brometum* plots had the highest percentage of species typical of mesotrophic grasslands (*Molinio-Arrhenatheretea*), e.g. *Festuca pratensis*, *Pastinaca sativa, Trisetum flavescens* and *Lathyrus pratensis*. The *Bromo-Danthonietum calycinae* relevés contained species typical of dwarf shrub and mat-grass heaths on acidic soils (*Calluno-Ulicetea*), such as *Agrostis capillaris*, *Danthonia decumbens*, *Chamaespartium sagittale* and *Polygala vulgaris* (Supplementary Figs S3, S4). There was also a characteristic group of species in *Scabioso hladnikianae-Caricetum humilis*, namely species of alpine grasslands on base-rich soil (class *Elyno-Seslerietea*), e.g. *Acinos alpinus, Phyteuma orbiculare* and *Gentiana verna*, and species of the class *Trifolio-Geranietea*, the class of thermophilous woodland fringe and tall-herbaceous vegetation (species *Geranium sanguineum*, *Veronica jacquinii*, *Thesium bavarum*) (Supplementary Table S1, Supplementary Figs S3, S4).

When grassland communities were compared in terms of trait composition using ANOVA (Table 4), there were significant differences for most of the plant traits analysed. There was no significant difference in the persistence of connections between ramets. Clonal semi-dry grassland species had in general perennial long-lasting connections between ramets (with a mean value > 3 years) (Table 4). In addition, post hoc tests indicated that CWM values for geophytes, leafy stem, root tubers (CGO16) and CGO with a regenerative role in clonal growth organs did not differ between the three groups (Table 4). The association *Bromo-Danthonietum calycinae* was characterized by the highest CWM values for epigeogenous rhizomes (e.g. species *Cirsium acaule*, *Danthonia alpina*, *Festuca filiformis*, *Potentilla alba*, *Succisa pratensis*), lowest percentage of therophytes and ruderals (R-strategy). Plants with a splitting main root (CGO14), which was the most

Table 4. Results of a one-way ANOVA for aggregated trait (CWM, community-weighted means) values for three dry grassland associations. CWM values for categorical plant traits are in percentages; values bearing the same letters row-wise are not significantly different. BrDa: *Bromo-Danthonietum calycinae*; ScCa: *Scabioso hladnikianae-Caricetum humilis;* OnBr: *Onobrychido-Brometum*. Abbreviations of plant traits are listed in Table 2. Stars indicate significant results: ** < 0.01 and *** < 0.001.

Plant traits	Abbreviation (factor)	CWM			
		BrDa	ScCa	OnBr	Sig.
Life form	LF_ch	9.5[a]	9.2 [a]	6.3 [b]	***
	LF_ge	4.7	4.6	4.2	n.s.
	LF_he	81.7 [ab]	80.1 [a]	83.3 [b]	***
	LF_th	4.2 [a]	6.0 [b]	6.3 [b]	***
Growth form	GF_tuss	21.8 [a]	19.1 [a]	26.0 [b]	***
	GF_roset	15.8 [a]	15.8 [a]	10.0 [b]	***
	GF_le_st	38.6	37.4	36.4	n.s.
	GF_ro_le	23.8 [a]	27.5 [b]	27.0 [b]	***
Type of clonal growth organ (CGO)	CGO_no	3.5 [a]	5.4 [b]	4.0 [ab]	**
	1_stolon	3.7 [ab]	2.8 [a]	4.3 [b]	**
	9_epigeo_rhiz	26.1 [a]	20.6 [b]	21.5 [b]	***
	10_hypogeo_rhiz	21.9 [a]	18.4 [b]	23.6 [a]	***
	12_tuber_bg_st	0.7 [a]	0.8 [ab]	1.4 [b]	***
	13_bulb	0.8 [a]	0.3 [ab]	0.5 [b]	**
	14_root_splitt	37.5 [a]	45.3 [b]	38.3 [a]	***
	15_adv_buds	3.5 [a]	3.8 [ab]	4.7 [b]	***
	16_root_tuber	2.3	2.6	1.7	n.s.
Persistence of connection in CGO	Persist_CGO	3.5	3.5	3.4	n.s.
Number of clonal offspring shoots	No_clo_sh	2.2 [a]	2.2 [a]	2.4 [b]	***
Lateral spread by clonal growth	Lat_spread	0.04 [a]	0.05 [a]	0.06 [b]	***
Role of clonal growth organs	Role_add	0.48 [a]	1.02 [b]	0.63 [a]	**
	Role_obl	55.5 [a]	45.4 [b]	53.9 [a]	***
	Role_reg	2.9	2.4	3.0	n.s.
	Role_non	39.6 [a]	49.1 [b]	39.5 [a]	***
Bud bank	NoBB_ab_10	3.4 [a]	3.4 [a]	4.3 [b]	***
	NoBB_10	4.3 [a]	4.3 [a]	4.7 [b]	***
	NoBB_0	5.7 [a]	5.5 [ab]	5.5 [b]	**
	NoBB_010	11.1 [a]	11.2 [a]	11.9 [b]	***
CSR strategy	C	45.2 [a]	43.8 [a]	46.6 [b]	***
	S	33.6 [a]	32.8 [a]	27.4 [b]	***
	R	21.0 [a]	23.2 [b]	25.8 [c]	***

common CGO type in the grassland species pool, were most abundant in *Scabioso hladnikianae-Caricetum humilis* association (*Acinos alpinus*, *Asperula cynanchica*, *Phyteuma orbiculare*, *Pulsatilla grandis*). In addition, species with high CWM values in this community were plants with a rosette and leafy stem. Differences in individual clonal traits, growth forms, and life forms were in general less pronounced in *Bromo-Danthonietum calycinae* and *Scabioso hladnikianae-Caricetum humilis.* While the most significant differences were recorded for the *Onobrychido-Brometum* association (Table 4, Fig. 3), where tussock plants (GF_tuss) (e.g. *Brachypodium pinnatum*, *Bromopsis erecta*, *Carex flacca*, *Poa angustifolia, Trisetum flavescens*) and species with a hypogeogenous rhizome (CGO10), e.g. *Arrhenatherum elatius*, *Avenula pubescens*, *Agrimonia eupatoria*, *Clinopodium vulgare*, *Lathyrus pratensis*, *Vicia cracca*, were more common.

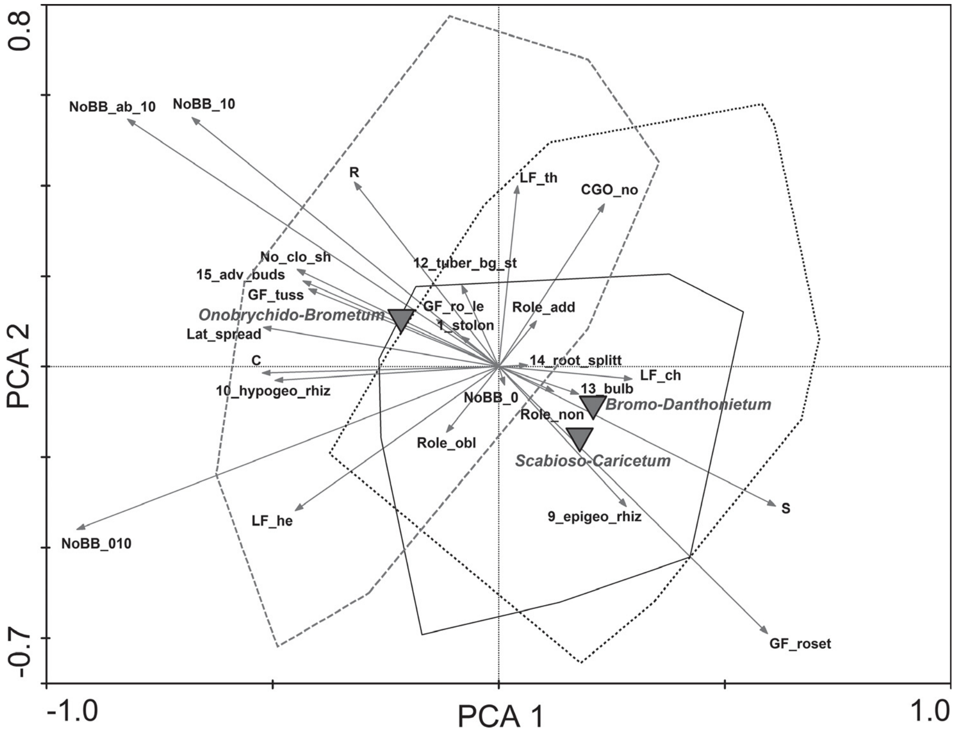

Fig. 3. Principal component analysis (PCA) of CWM matrix (224 relevés × 31 traits). Diagram of plant life-history traits in three dry grassland communities. Only traits (N = 26) with significant differences in their CWM values in the different communities (ANOVA test) are shown. Eigenvalues: axis 1 = 0.66, axis 2 = 0.16. The relevés of three plant communities are emphasized by the convex hulls: *Onobrychido-Brometum* (dashed line), *Bromo-Danthonietum calycinae* (dotted line) and *Scabioso hladnikianae-Caricetum humilis* associations (solid line) and represented by centroids (triangles). Abbreviations of plant traits are listed in Table 2.

In *Onobrychido-Brometum* the highest CWM values were recorded for competitors (C-strategy), number of offspring shoots (No_clo_sh), lateral spread by clonal growth (in meters) (Lat_spread) and for size of plant bud bank located on a plant higher than 10 cm (NoBB_ab_10), on a plant 10 to 0 cm (NoBB_10) and at a depth of 0 to 10 cm (NoBB_010) (Table 4).

The ordination diagrams (Fig. 3 and Supplementary Fig. S5) of the principal component analysis (PCA), summarizing the variation in the composition of plant traits among relevés, indicate clear differences in the habitat preferences of species with different traits. The first two PCA axes accounted for 81.8% of the variance, with 65.8% and 16% for axes 1 and 2, respectively. Relevés were divided into two main groups with similar patterns for *Bromo-Danthonietum calycinae* and *Scabioso hladnikianae-Caricetum humilis*. The *Onobrychido-Brometum* relevés were associated with high values for number of bud banks on plants above the soil level (NoBB_10 and NoBB_ab_10) as well as high values for the number of clonal offspring shoots (No_clo_sh) and lateral spread (Lat_spread). All of these traits were significantly positively correlated (Supplementary Table S2), and increased from plots with species with little clonal multiplication (associations *Bromo-Danthonietum calycinae* and *Scabioso hladnikianae-Caricetum humilis*) to plots with a high incidence of clonal reproduction (*Onobrychido-Brometum*). Among other characteristics, a high number of ruderals (R) and competitors (C), tussock plants (GF_tuss) and plants with CGO15 (root with adventitious buds) were typical for *Onobrychido-Brometum*. In contrast, the associations *Bromo-Danthonietum calycinae* and *Scabioso hladnikianae-Caricetum humilis* were characterized by high abundances of chamaephytes (LF_ch), rosette plants (GF_roset), species with epigeogenous rhizomes (CGO9) and stress tolerant species (S) (Fig. 3). Projection of CWM values for families in PCA space (Supplementary Fig. S6) indicate that *Fabaceae* and *Poaceae,* in particular, were associated with *Onobrychido-Brometum* and had traits characteristic of this association (Fig. 3)*,* whereas *Cyperaceae*, *Cichoriaceae*, *Plantaginaceae* and *Gentianaceae*, for example, were characteristic of the other two grassland communities.

Discussion

The analysis of 247 plant species and their clonal traits in semi-dry calcareous grasslands, which are habitats with high conservation values whose cover is rapidly declining in Europe and worldwide (Chytrý et al. 2015, Biurrun et al. 2021), yielded new insights into plant strategies and their role in the spatial patterns and processes in plant communities.

Most plants were perennial (i.e. hemicryptophytes, geophytes and chamaephytes), and more than half were clonal. These findings are consistent with data from a previous study, which report a percentage of less than 60% clonally growing plants in temperate dry grasslands (Klimešová & Herben 2014). However, clonal growth organs were present in most (97%) of the perennial plants. The discrepancy between the two statements is due to the fact that the presence of a CGO does not mean that the plant grows clonally, but indicates a morphological type of iterative growth (Klimešová & Klimeš 2008). In the grasslands studied, the most common type of CGO was a splitting main root (CGO14). Since this belowground organ has no clonality function, but supports perennial growth and resprouting (i.e. it is a non-clonal organ), plants with this CGO can be considered non-clonal (Klimešová & Klimeš 2008). Previous studies have shown that perennial main roots enable plants to explore deep and more stable and wetter soil layers, for example, in habitats with steep slopes and stony substrates (Hess 1909, Klimešová et al. 2012). In the area studied, semi-dry grasslands include similar habitats, namely steep slopes in hilly regions (Supplementary Fig. S7) and karst areas (Supplementary Fig. S8) in central Slovenia (Kaligarič & Škornik 2002, Škornik et al. 2023). The latter are characterized by stony surfaces and limestone with fissures of varying depths, which are spatially heterogeneous with different microhabitats. A similar situation to sheep pastures in the UK (Sydes & Grime 1984), where species with long taproots tend to forage in narrow deep fissures (Grime 2001). Species with taproots may also be favoured due to lower intraspecific competition during dry conditions (Wellstein & Kuss 2011). The non-clonal nature of a splitting main root (CGO14) was confirmed by the high value recorded for the clonal trait "no role of CGO", as a first approximation to clonal growth is the role that a CGO plays in a plant's life (Klimešová & Klimeš 2008). However, even in these species there are examples of clonal dispersal in certain situations (Klimešová & Klimeš 2008), which can be very important, e.g. for the persistence of very rare and endangered plants.

One such example in the habitats studied is *Pulsatilla grandis*, Natura 2000 species with only two small populations in Slovenian semi-dry calcareous grasslands and a very low germination success (Kaligarič et al. 2006). Its persistence is probably supported by a long-lived, splitting main root. Therefore, preventing the few remaining plants from being dug up is one of the greatest challenges for its conservation (Jogan 2020).

Other common types of CGOs are epigeogenous and hypogeogenous rhizomes, for which a similar pattern occurs in central Europe, where the same clonal classification is used (Klimešová & Klimeš 2008, Klimešová et al. 2017), with the difference that there these two types of rhizomes are the most common CGOs. As for most grassland habitats worldwide (Klimeš et al. 1997), the dominance of clonal tussock grasses with rhizomes is typical. Rhizomatous plants (CGO9 and CGO10) together make up almost the same percentage as perennial plants with a splitting main root. The abundance of rhizomatous species indicates that conditions are less extreme in grasslands, as lack of resources, very dry and/or cold sites, unstable and coarse soils limit rhizome growth (Klimešová et al. 2012, 2023). However, there are differences in the habitat preference of species with epigeogenous and hypogeogenous rhizomes. Species with epigeogenous rhizomes (vegetative shoots close to the mother plant) are more common at cold sites, due to their high ability for regrowth after frost (Klimeš 1999, Wellstein & Kuss 2011) and are less sensitive to poor quality soils than those with hypogeogenous rhizomes (Klimešová et al. 2011). Species with laterally spreading rhizomes, on the other hand, are more common at sites with mesic conditions (Wellstein & Kuss 2011) and deep soils, as they develop below ground (Klimešová et al. 2021).

The taxonomic distribution was quite broad, as 40 families contained at least one species with a CGO. A similar result (44 families) is reported in a study of belowground organs of plants in the Anatolia steppes (Ülgen & Tavţanođlu 2024), although the species pool in the current study is only 7% of the size of that of the Anatolia steppes. In this study, there is a positive relationship between CGO diversity and species-richness in relevés. Samples with the highest number of species in the dataset were collected in more humid climatic conditions at high altitudes in the Dinaric Alps (Fig. 1). An additional analysis, with data on the altitude of the sites revealed a positive relationship ($R^2 = 0.29$, $P < 0.001$) with species richness. The abiotic conditions at these sites seem to favour a rich flora and a high diversity of clonal-traits, which indicates an intermediate intensity of factors limiting productivity, stress and disturbance (Grime 2001). A positive relationship between CGO diversity and species richness as well as an increase in clonal diversity at less stressful sites is also reported by Wellstein & Kuss (2011) in their study on grasslands in the Swiss Alps. The occurrence of clonal species at sites with medium disturbance is also predicted by Bellingham & Sparrow (2000) and confirmed by Janovský & Herben (2020). These species-rich meadows are subject to regular, but moderate disturbance, as they are maintained by traditional agricultural practices of mowing once or twice a year, often in combination with grazing in early spring and/or late summer (Škornik et al. 2023).

The semi-dry grasslands studied were characterized by high local persistence (i.e. little lateral spread and long-term connections between parent and offspring ramets), which confirms the patterns reported in previous studies of temperate dry grasslands (Klimešová et al. 2012, 2023, Klimešová & Herben 2014). Two reasons are suggested for this – in habitats with a low productivity, offspring may require longer maternal support in order to survive environmental fluctuations over long periods of time (Klimeš 2008), and such connections are also better protected against desiccation in dry habitats (Sperry 2003).

Bud banks are typical of perennial herbaceous plants in temperate grasslands and are the most likely source of aboveground shoots than the seed bank (Benson & Hartnett 2006, Vítová et al. 2017). In this study, a relatively high number of buds was recorded, indicating a high capacity for clonal growth in the vegetation studied, as bud bank traits are strongly correlated with the capacity for clonal growth (Klimešová & Herben 2014). Position of bud bank and bud bank depth in the soil can be used as a measure of its protection from disturbance and it is also affected by plant size (Klimešová & Herben 2014). Bud banks were richer in the soil than on parts of plants above the soil surface where they were located shallowly in the soil. In grasslands, the pool of dormant meristems is usually located very close to the soil surface or below ground, where it is protected by litter, snow or soil and is not affected by disturbances such as mowing, grazing or fire (Lubbe et al. 2021, Klimešová et al. 2023). However, shallow bud banks in grasslands make these habitats rather vulnerable to more severe soil disturbance (Dalgleish & Hartnett 2009).

Most semi-dry grassland species produce more than two offsprings per year. As the number of off-spring is considered to be a measure of the intensity of clonal multiplication, values >1 indicate successful multiplication and support the view that clonal growth is an essential characteristic of dry grassland species (Grace 1993, Combroux & Bornette 2004, Sosnová et al. 2011).

Although the three semi-dry grasslands studied have similar floras, they are clearly different in terms of the composition of plant species, which supports their classification in different phytosociological associations (Škornik et al. 2023). Based on their affinity to the different classes, these differences could be interpreted along with specific environmental conditions at the level of associations. The differences were most pronounced in the *Onobrychido-Brometum* stands, where a high percentage of mesotrophic grassland species (class *Molinio-Arrhenatheretea*) indicates that the environment in these habitats is more mesic. While the occurrence of *Calluno-Ulicetea* species in the *Bromo-Danthonietum calycinae* community could be associated with moderately acidic soils (Kaligarič & Škornik 2002), the occurrence of alpine grassland species (*Elyno-Seslerietea*) in the *Scabioso hladnikianae-Caricetum humilis* is due to the high altitude of some of the sites sampled (Table 1). Thermophilus species growing at the fringes of woodland and tall-herbaceous vegetation (class *Trifolio-Geranietea*) were common in all three grassland communities. They can be considered as part of the regular inventory of the secondary grasslands studied, but were especially associated with *Scabioso hladnikianae-Caricetum humilis,* as this type of grassland most often occurs on the border between the edge of forest and more productive agricultural areas (e.g. mesotrophic meadows, orchards; Škornik 2001).

Plant traits also differed considerably in vegetation samples (relevés), which supports the prediction that there are different environments at the association level that exert different selection pressures that each favour different types of clonal growth. The *Onobrychido-Brometum* association differs the most, both floristically and functionally. In this grassland community, tussock plants were more abundant (e.g. *Poaceae*), especially those with hypogeogenous rhizomes. *Onobrychido-Brometum* stands occur on mesic, mid-depth cambisols that develop on carbonate flysch (Kaligarič & Škornik 2002, Pipenbaher et al. 2013), where the conditions for horizontal growth are more favourable than in stony soils (Klimeš 2008, Klimešová et al. 2011), which are more typical of *Bromo-Danthonietum calycinae* and *Scabioso hladnikianae-Caricetum humilis* associations (Škornik et al. 2023). Furthermore, the occurrence of plants with hypogeogenous rhizomes in these grasslands might be that this type of rhizome is an adaptation to growing on steep slopes, with medium-depth brown soil on carbonate flysch, which is prone to erosion (Pipenbaher et al. 2013). The horizontal growth of rhizomes versus the vertical growth of the main roots of perennial plants (e.g. CGO14) determines the distribution of fine roots in the soil and thus the resistance to soil erosion (Yu et al. 2008, Vannoppen et al. 2017). More favourable conditions compared to the other two grassland communities also indicate a greater value for competitors (C) and other traits that may be associated with competition, such as the size of the bud bank and level of clonal multiplication (number of clonal offspring) (Klimešová & Herben 2014). The bud bank of *Onobrychido-Brometum* plants is richer because in competition with other plants it is easier to re-establish an individual with a bud-bearing organ than plants from seed (Klimešová et al. 2023). This study also confirmed the results of a previous study, which reports that ruderal plants are present in *Onobrychido-Brometum* grasslands (Pipenbaher et al. 2013). This could be due to the great abundance of the seed of ruderal plants in surrounding anthropogenic habitats (e.g. vineyards, fields, gardens; Pipenbaher et al. 2014). The meadows of *Bromo-Danthonietum calycinae* and *Scabioso hladnikianae-Caricetum humilis* are generally not located in the immediate vicinity of fields and settlements. They are, therefore, not exposed to eutrophication or the local effects of disturbance to the same extent.

The trait composition of *Bromo-Danthonietum calycinae* and *Scabioso hladnikianae-Caricetum humilis* associations are very similar. However, some characteristics of *Scabioso hladnikianae-Caricetum humilis* indicate a lower capacity for clonal growth compared to *Bromo-Danthonietum,* e.g. low values for rhizomes and high values for a splitting main root, which is a non-clonal organ (Klimešová & Klimeš 2008). These results may be due to poor resource availability (Klimešová & Herben 2014, Chelli et al. 2024) and xeric conditions, which are characteristic of *Scabioso hladnikianae-Caricetum humilis* grasslands, especially those on shallow rendzinas.

There are marked differences in species richness and diversity of CGOs in the three grassland communities. The species richness was high in the *Bromo-Danthonietum calycinae* and *Scabioso hladnikianae-Caricetum humilis* associations, which is probably due to the spatial heterogeneity of these habitats, as they are usually located on stony soils of varying depths over fissured limestone or dolomite. Spatial and temporal heterogeneity of the environment is known to favour floristically and functionally diverse plant communities (Grime 2001). Rosette species of plants were also more common in these meadows. Since the grasslands in the data set are not used as pastures, but as meadows with occasional grazing (in early spring and/or late summer), it is likely that drought selects for the same plant traits as grazing (Milchunas et al. 1998). This is also supported by the finding of a significantly high stress tolerance at these sites. It is interesting, but not surprising, that of all the CGO types in the grasslands studied, the root tuber (represented by orchids) was the only CGO that did not differ significantly among the three associations. Various orchids were recorded in the grassland plots studied, which confirms that, like European grasslands of the *Festuco-Brometea* class in general (Olmeda et al. 2019), Slovenian semi-dry grasslands are also an important habitat for these rare and endangered species (Supplementary Fig. S9 and S10).

The dimension of the plant trait space that differs in the relevés could be interpreted as the "clonal multiplication" dimension as suggested by Chelli et. al. (2024). It reflects a spectrum ranging from low (*Bromo-Danthonietum calycinae* and *Scabioso hladnikianae-Caricetum humilis*) to high (*Onobrychido-Brometum*) capacity for spreading by clonal growth and is a trade-off between competitive ability (*Onobrychido-Brometum*) and tolerance of stress (*Bromo-Danthonietum calycinae* and *Scabioso hladnikianae-Caricetum humilis*). Although in the *Onobrychido-Brometum* community the conditions were more favourable for clonal spread than in the other two grassland communities, it had the lowest average diversity of CGOs, which reflects the lower species richness of these grasslands. This study revealed a strong positive association between CGO diversity and species richness as reported by Wellstein & Kuss (2011).

Differences in productivity and moisture associated with soils of different depths seem to be the main factors determining the structure of clonal traits in the semi-dry grasslands studied. As suggested by Klimešová & Herben (2014), these gradients are also associated with a major change in clonal growth parameters in temperate plant communities in central Europe. These authors analysed clonal and bud bank characteristics in 32 EUNIS habitats, which include important types of central-European vegetation (Klimešová & Herben 2014). The results of this study may indicate that even at a finer scale of the association level, there are different ecological gradients that influence the clonal growth traits and functional structure of communities.

Conclusions and implications for conservation

This study provided the first detailed insight into the spectrum of clonal growth organs (CGOs) in semi-dry calcareous grasslands (alliance *Bromion erecti*, order *Brometalia erecti,* class *Festuco-Brometea*) in the central-European region of Slovenia. The diversity of CGOs and the characteristics of other similar traits (e.g. bud bank, number of offspring shoots/parent shoot) indicate that clonal growth is an essential feature of these species-rich grasslands. Consequently, it is important to consider the various mechanisms by which clonality influences community organization in these habitats because of their high conservation value, especially when managing these habitats. As predicted, there were marked differences in clonal growth and other life history traits among vegetation that is assigned to the same EUNIS and Natura 2000 habitats, but belongs to different plant associations. Many species-rich semi-dry grasslands in the area studied are currently subject to changes in agricultural use, e.g. from mowing to grazing, especially in hilly areas, in order to prevent abandonment and encroachment of these grasslands. However, the potential effects of grazing on vegetation and its response to grazing have not been investigated. Meanwhile, negative effects of even low levels of grazing on grasslands, such as erosion, are reported, particularly in areas where grasslands are classified as belonging to the *Onobrychido-Brometum* association (Supplementary Fig. S11) (Škornik et al. 2023). It is likely that grazing increases erosion in these grasslands by negatively affecting the dominant rhizomatous species, e.g. grasses as their rhizomes prevent soil erosion (Yu et al. 2008, Vannoppen et al. 2017). The tussock graminoids are reported to respond negatively to grazing (Díaz et al. 2007). The results of the current study indicate that for maintaining the characteristic species and functional composition of all types of grassland, conservation and restoration measures should be carried out at a finer scale (e.g. at the level of associations) than at the level of EUNIS and Natura 2000 habitats, as is currently the case in Slovenia (Škornik et al. 2023).

Although *Festuco-Brometea* grasslands also occur in the Slovenian Dinaric region (Kaligarič & Škornik 2002), the current study was restricted to a region in central Europe, as the data on clonal traits is only available for this region (Klimešová et al. 2017). Further research and systematic studies focusing on clonal plant traits are needed, as this would improve the understanding of the effect of land use and global change on the functioning of ecosystems.

Supplementary materials

Fig. S1. Number of clonal growth organs within a single relevé.
Fig. S2. Clonal growth organ diversity in relation to species richness.
Fig. S3. Detrended correspondence analysis with relevés and species.
Fig. S4. Detrended correspondence analysis with syntaxa.
Fig. S5. Principal component analysis of community weighted mean trait values.
Fig. S6. Principal component analysis of community weighted mean trait values and with families.
Fig. S7. Photo of the *Onobrychido-Brometum* association.
Fig. S8. Photo of the *Scabioso hladnikianae-Caricetum humilis* association.
Fig. S9. Photo of the *Onobrychido-Brometum* association with *Anacamptis pyramidalis*.
Fig. S10. Photo of the orchid species *Ophrys holosericea* and *Himantoglossum adriaticum*.
Fig. S11. Photo of semi-dry meadow and pasture in Haloze region.
Table S1. Synoptic table of three semi-dry grassland associations (*Festuco-Brometea*).
Table S2. Pearson correlations between community weighted mean trait values.

Supplementary materials are available at https://www.preslia.cz.

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Klonální vlastnosti rostlin subxerofilních luk na vápnitých substrátech Slovinska

Vzhledem k významu klonality u rostlin je zkoumání mechanismů, jimiž jsou vlastnosti klonálního růstu propojeny s organizací společenstev, zásadní pro porozumění druhovému složení vegetace. Analyzovali jsme výskyt klonálních a dalších funkčních vlastností rostlin v druhově bohatých subxerofilních trávnících (svaz *Bromion erecti*, řád *Brometalia erecti*, třída *Festuco-Brometea*) středoevropské oblasti Slovinska. Cílem výzkumu bylo vyhodnotit diverzitu orgánů klonálního růstu (CGO) a dalších funkčních vlastností v polopřirozených suchých trávnících a zjistit rozdíly v jejich zastoupení ve třech rostlinných společenstvech (asociacích). Byla použita data z 224 fytocenologických snímků, obsahujících 247 druhů, k nimž bylo přiřazeno devět funkčních vlastností; pro každý snímek byl vypočítán vážený průměr společenstva (CWM) pro všechny zkoumané funkční vlastnosti. Ukázalo se, že více než polovina rostlinných druhů byla klonálních. Nejčastějšími orgány klonálního růstu byly vytrvalý hlavní kořen (typický pro neklonální rostliny), epigeogenní oddenky a hypogeogenní oddenky. Klíčovými faktory spojenými s rozdíly v klonálním růstu ve zkoumaných asociacích jsou vlhkost půdy a produktivita společenstva. Klonální trsnaté rostliny s oddenky a druhy s bohatou bankou pupenů a vysokým počtem klonálního potomstva byly hojné v mezických trávnících na hlubokých půdách (asociace *Onobrychido-Brometum*). Pro suchomilnější trávníky na kamenitých půdách na vápencích či dolomitech byly charakteristické druhy s přízemní listovou růžicí a klonální rostliny s hypogeogenními oddenky (*Bromo-Danthonietum calycinae*) a neklonální rostliny s vytrvalým hlavním kořenem (*Scabioso hladnikianae-Caricetum humilis*). Diverzita znaků souvisejících s klonálním růstem ukazuje, že klonalita je zásadní vlastností těchto druhově bohatých trávníků. Výsledky studie navíc dokládají, že pro zachování charakteristických druhů a funkčního složení všech typů polopřirozených suchých trávníků by měly být realizovány plány péče na jemnější škále (např. na úrovni asociací), než jakou představují typy biotopů podle systémů EUNIS a Natura 2000.

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