CLONAL GROWTH MODES IN PLANT COMMUNITIES ALONG A STRESS GRADIENT IN THE CENTRAL APENNINES, ITALY

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Abstract: A simplification from species to functional groups using the concept of clonality is particularly attractive for predictive modelling of vegetation processes and preparing guidelines for nature conservation. This important functional trait based on a modular structure including resource-acquiring units (ramets, *feeding sites*) and spacers, has been studied in three plant communities (xeric grassland, mesic grassland, and beech forest) under different levels of environmental stress (related to soil moisture and fertility) in the Montagna di Torricchio Nature Reserve near Camerino, Central Apennines, Italy. The study sought to reveal patterns of clonal growth modes (CGMs) in the three plant community types, and to test a series of hypotheses on the importance of selected CGMs along the stress gradient. Clonality was shown to have different importance in the grassland communities, due to differences in the importance of various CGMs (representing syndromes of clonal traits). Below-ground positioning of CGOs, shorter spacers, higher multiplication potential, permanent physical connection between ramets, large bud bank, and increased importance of bud protection were frequently found in water-stressed xeric grasslands, suggesting the adaptive value of these clonal traits. The major differences between grassland communities were due to the dominant CGMs: turf graminoids (with an effective way of protecting growth meristems in dense tussocks) dominated xeric grasslands, whereas rhizomatous graminoids (typical of competitive resource-rich habitats) dominated mesic grasslands. The beech forest had fewer clonal species (67%) and lower CGM diversity. Based on the assumption that different environments promote different selection pressures, the tests revealed the following results: (1) Plants with clonal organs below ground have significantly higher cover values in stressed habitats. (2) Species with short spacers are more frequent in less favourable environments, and their importance is almost ten times higher in the xeric grassland than in the forest (71% to 7.6%). (3) The number of species able to produce numerous ramets is highest in the most stressed habitat. (4) The number of species with a potential for long-lasting connection between ramets increases towards stressed environments. In contrast to our expectations, the mesic grasslands (occupying the central position along the studied stress gradient) have the highest number of species with storage organs. (6) In stressed habitats, species with forms of bud protection were the most frequent.

Introduction

Plant species respond individually to their environment, and in order to better understand this behaviour in the context of complex natural systems, researchers have suggested examining this in terms of functional species groups with similar adaptations, and hence similar responses to environmental gradients [10, 28]. Increasing demands for a predictive ecology and its application in guidelines for nature conservation have further stimulated the interest in functional plant ecology. Life-history traits, believed to carry functional messages, offer an effective tool for this purpose [26]. The crucial step in classifying plants into functional types involves selecting a list of key traits held to be informative for predictive theories [46]. Following Harper's concept, clonality itself is a trait [46] based on a modular structure [48] including resource-acquiring units (ramets, *feeding sites*) and spacers [1, 29].

Klimeš *et al*. [20] developed a classification system of Clonal Growth Modes (CGM) that can help reveal the relationship between the types of clonal growth and the functions that are attributed to clonality at higher levels of organization. Most vascular plants of Central Europe were classified into 21 (later extended) hierarchically related categories based on a combination of criteria, including origin and placement of Clonal Growth Organs (CGOs), storage functions, and spacer length and longevity. The differences in the pattern of distribution of clonal plant traits in different habitats can raise important questions about the adaptation of certain traits to special environments, and hence about the underlying mechanisms of functional processes.

Recognition of the importance of spatio-temporal scales [4, 18, 33] and of the interconnection of pattern and process in community ecology [45], calls for a re-evaluation of the role that clonality plays in community organization, functioning and maintenance of diversity level [15, 19]. In fact, clonal plant growth leads to the formation of intricate hierarchical spatial structures [7, 14, 30], of vital importance in creating vegetation patchiness at smaller scales.

In this paper, using the CGM classification system developed by Klimeš *et al*. [20], we compare the occurrence of various CGMs in selected plant communities in the Central Apennines. The selected communities form a ecocline ranging from high-stress (dry grasslands) to low-stress (mesic grasslands and forests) communities. We suppose that different environments impose different selection pressures by favouring certain mechanisms of clonal growth, with consequent differences in shaping CGM spectra. This information may prove useful in better understanding mechanisms of species coexistence, diversity level and dynamics processes in these secondary plant communities.

The following clonal traits, assumed to be of adaptive importance in stressed environments (low nutrient content and low water retention capacity) were targeted: (*a*) position of the connection between the mother and daughter ramets with respect to the soil surface (above- or below-ground); (*b*) spacer length (shorter or longer than 10 cm; excluding categories without a rhizome or stolon); (*c*) the possibility for multiplication (frequent – numerous ramets produced every

year; infrequent – ramets produced in some years only); (*d*) longevity of connection between ramets (shorter or longer than 2 years); (*e*) the presence of storage (specialized organs, e.g. tubers, bulbs, or storage in organs other than those operating for clonal growth); (*f*) bud protection by specialized leaves.

We postulate that under more stressed (xeric) conditions:

(H1) connections between the mother and daughter ramets are more likely to be found below-ground than above-ground

The soil environment affords some degree of protection to susceptible (often short-lived) connections, in contrast to the stress-intensive above-ground environment, where the chance of desiccation is higher.

(H2) spacers will be shorter than they are in mesic conditions

Stressed environments bottleneck production of biomass and increase energy expenditure costs. Short spacers also imply low transport costs [16].

(H3) the frequency of multiplication (formation of CGOs) is lower than it is in mesic conditions

Less frequent formation of ramets (and CGOs, for that matter) is an energy and matter saving strategy. Lack of excessive spreading (by formation of new ramets) results in a safe-site effect, which is basically an expression of lowering the risk of extinction or damage. These features might be controlled by allometric relations [22].

(H4) connections between ramets will be more persistent than they are in mesic conditions

Because of the adversity of the stressed environments, biomass and stored energy are worth conserving, hence preservation of the present status is the preferable strategy. Long-living (active) connections assure quick regeneration, thus serving as a buffer from damage that may happen [17, 30, 34].

(H5) the presence of storage organs is more frequent than it is in mesic conditions

We limit ourselves here only to grasslands since the stressful period in forests is qualitatively different from that in the grasslands. The growth rhythm of forest geophytes (bulbous or rhizomatous plants) is controlled to a large extent by the regime of light penetration to the under-storey [36]. In grasslands, the stress relates to decreased water availability (hence also nutrient lack). The storage organs are a mean of dispersal over time (designed to assist the plant in overcoming adverse time periods). Since the dry grasslands suffer higher water discharge, the plants may experience extreme drought conditions [41].

(H6) bud protection by specialised leaves will be more important than it is in mesic conditions

Protection of meristems in environments experiencing temporary stress is of vital importance for maintaining the regeneration pool [30].

Materials and Methods
Study area

The study area is the Montagna di Torricchio Nature Reserve near Camerino, in the Central Apennines (Italy) – an area of 317 ha strictly protected since 1970. The Torricchio Reserve spans altitudes between 820 and 1491 m, and is situated on two slopes of the Val di Tazza, divided by a deep valley running SW-NE. The mean annual precipitation here is c. 1250 mm, and the mean annual temperature about 11° C. The area is dominated by Jurassic-Cretaceous calcareous rocks [5]. Soils on these calcimorphic substrates show very little taxonomic differentiation. Poorly developed, shallow and skeletal soils on steep slopes are a result of erosion associated with the presence of rocky outcrops [42].

Previous syntaxonomical studies [8, 24, 32, 42] distinguished two major grassland groups in Torricchio: **dry grasslands** (*Centaureo bracteatae–Brometum erecti* Biondi *et al.* 1986 on soft marly substrate, *Seslerio nitidae–Brometum erecti* Bruno & Covarelli 1968 and *Asperulo purpureae–Brometum erecti* Biondi & Ballelli 1981 on hard rocks called "scaglia rosata") and **mesic grasslands** (*Campanulo glomeratae–Cynosuretum cristati* Ubaldi 1979 on the valley-bottom, and *Brizo mediae–Brometum erecti* Biondi & Ballelli 1982 in the semi-mesophilous high-altitude areas). These grasslands have been surveyed in 34 and 31 relevés respectively. We have also included five relevés from the **beech forest** (*Polysticho–Fagetum* Feoli & Lagonegro 1982) in our analyses. Basic information on the character of the communities studied and the data sources are given in Tab. 1.

Table 1: Geomorphological and pedological characterisation of plant communities present in the "Torricchio Mountain" Nature Reserve and their categorisation as vegetation complexes based on the most important stress factors.

Vegetation complexes	Slope	Moisture status	$A_{0 (cm)}$	Soil depth	Erosion	No. of relevés	Sources
Xeric grassland							
Centaureo bractatae-Brometum erecti	24°	xeric	0-10	shallow	strong	18	[32]
Seslerio nitidae-Brometum erecti	35°	extremely xeric	0-10	very shallow	strong	7	[32]
Asperulo purpurae-Brometum erecti	17°	xeric	0-4	shallow	medium	9	[32]
Mesic grassland							
Brizo medie-Brometum erecti	5°	semi-mesic	0-6	medium	weak	10	[32]
Campanulo glomaretae-Cynosuretum cristati	7°	mesic	0-7	deep	very weak	21 (8 + 13)	[9] + [32]
Beech forest							
Polysticho-Fagetum	26°	mesic	0-15	deep	weak	5	[4]

These three plant communities form a natural coenocline differentiated by levels of ecological stress, here defined as temporary deficiency of water in soils linked to low nutrient content (*e.g.* organic matter). The dry grasslands and forests range over the driest and most mesic extremes of the coenocline, respectively.

Data collection

In the classification system used, the CGMs are defined on the basis of a combination of the criteria of CGO origin (stem, root, other), CGO initial and final

position (above-ground *vs*. below-ground), presence of special storage organs (tuber and bulbs), and the length and longevity of spacers between ramets [20] (Tab. 2). Most species in the study region were classified in clonal categories using the CLO-PLA2 database of Klimeš & Klimešová [21]. Of the 271 species here, about 75% were found in the database. We revised the classification by Klimeš & Klimešová (l.c.) with direct field observations for the dominant species of each of the 12 CGM categories. The remaining taxa (not featured by the Klimeš & Klimešová database) were classified into the CGMs on the basis of specimens collected (Appendix) using the same criteria as Klimeš *et al*. [20]. Nomenclature follows Pignatti [31].

Data analyses

The habitat groups were compared on the basis of both presence-absence and cover data. Species cover was estimated on the basis of Braun-Blanquet's scale [2] in all studies that served as data sources. Prior to statistical analysis, the cover codes were converted into a mean percentage scale [43]. In the classification system of Klimeš *et al*. [20], a number of plants can have more than one single type of clonal growth; only the dominant (most important) one was considered in the analyses. Counting species by combining several modes of clonal growth separately for each type (as they were different species) did not influence the results for frequency data. Statistical comparisons between the habitats targeted the participation of CGMs and clonal traits by using the non-parametric Kruskal-Wallis test (after percentage standardization and arcsine transformation for cover data [38]). Diversity was calculated for each sampling unit based on the frequencies of species belonging to each clonal growth category, using the Shannon-Wiener diversity index. A *t*-test allowed the diversities of the three habitat groups to be compared [25].

Results
Patterns of clonality in plant communities

Xeric and mesic grasslands contain 88% and 84% of clonal plant species, respectively. Species with some forms of clonal growth were more frequent here than in the forest – 67% (Fig. 1). The differences were more pronounced when cover was considered as the basis for the comparisons. The mean total cover of clonal plants was as high as 128% and 126% in the xeric and mesic grasslands, respectively, while in the beech forest only 58% of the total cover was accounted for by clonal plants. The mean total cover of all species (incl. non-clonal ones) was the highest in the forest (180%), due to the effect of summarizing all the vegetation layers. The total cover of xeric and mesic grasslands was 140% and 136%, respectively (Table 3).

The forest is differentiated from both grassland types significantly (*t* test; *p*<0.001; Shannon-Wiener index) by diversity of CGMs. The forest supports a lower number of species belonging to a restricted number of CGMs, while in the grasslands a higher number of clonal plants form a wider spectrum of CGMs.

Table 2: Characteristics of Clonal Growth Modes (CGO) that formed the basis of clonal traits with possible adaptive functions to stressed environment [20].

Clonal Growth Mode	CGO origin	CGO position	Spacer length	Multiplication	Integration longevity	Storage	Bud bank	Bud protection	Spread
1. Trifolium pratense	root	below	-	infrequent	long	-	-	-	rare
2. Alliaria petiolata	root	below	short	infrequent	long	-	large	-	rare
3. Rumex acetosella	root	below	short	frequent	long	-	large	-	fast
4. Ranunculus ficaria	root	below	-	infrequent	short	special	small	-	rare
5. Lycopodium annotinum	stem	above	long	frequent	long	-	large	-	fast
6. Festuca ovina	stem	below	short	frequent	long	-	large	special	slow
7. Rumex obstusifolius	stem	below	short	frequent	long	-	large	-	slow
8. Rumex alpinus	stem	below	long	frequent	long	-	large	-	slow
9. Dactylis glomerata	stem	below	short	frequent	long	-	large	-	fast
10. Aegopodium podagraria	stem	below	long	frequent	long	-	large	-	fast
11. Fragaria vesca	stem	above	long	frequent	long	-	large	-	fast
12. Caltha palustris	stem	below	short	frequent	short	-	small	-	slow
13. Asperula odorata	stem	below	long	frequent	short	-	small	-	fast
14. Calystegia sepium	stem	below	long	frequent	short	special	large	-	fast
15. Lycopus europaeus	stem	below	short	frequent	short	special	large	-	rare
16. Corydalis solida	stem	below	-	-	short	special	small	-	rare
17. Corydalis cava	stem	below	-	infrequent	long	special	small	-	rare
18. Galanthus nivalis	stem	below	-	-	short	non CGO-	small	special	rare
19. Ornithogalum gussonei	stem	below	-	frequent	short	non CGO	small	special	rare
20. Tulipa sylvestris	stem	below	short	-	short	non CGO	small	special	rare
21. Polygonum viviparum	special	above	-	frequent	short	non CGO	small	special	rare
22. Cardamine pratensis	special	above	-	frequent	short	non CGO	small	-	rare
23. Dentaria bulbifera	special	above	-	frequent	short	non CGO	small	-	rare
24. Aldrovanda vesiculosa	special	below	-	frequent	short	non CGO	small	-	rare
25. Lemna gibba	special	below	-	frequent	short	non CGO	small	-	rare
26. Elodea canadensis	special	below	-	frequent	short	non CGO	small	-	rare
27. Botomus umbellatus	special	below	-	frequent	short	non CGO	small	-	rare

Table 3: Relative importance of clonal traits in the three habitat types. Presence-absence and cover data standardised by the total number of species and the total cover for each relevés (mean ±SE) are given in italics. The results of nonparametric Kruskal-Wallis tests performed on arcsine transformed data, are indicated for the respective median values (n=5 for the beech forest, 31 for mesic and 34 for xeric pastures).The mean cover of clonal plant and the mean total cover are based on the original data (in bold).

| | Number of species | | | | | Cover (%) | | | | |
	Xeric grasslands	Mesic grasslands	Forest	Chi-square	Prob. value	Xeric grasslands	Mesic grasslands	Forest	Chi-square	Prob. value
CGO position										
above-ground CGO	6.48 (6.56±0.64)	4.44 (4.53±0.44)	0 (1.24±0.77)	14.55	0.00	7.03 (4.94±1.52)	9.03 (4.13±1.72)	0 (1.63±1.58)	5.58	0.06
below-ground CGO	81.60 (82.11±1.20)	80.64 (79.73±1.34)	70.83 (65.80±4.44)	11.28	0.00	75.53 (89.96±1.80)	68.44 (85.27±1.75)	34.15 (29.64±3.65)	18.93	0.00
Spacers length										
long spacers	21.70 (23.73±1.26)	22.85 (23.07±1.03)	27.58 (29.12±3.03)	3.29	0.19	16.97 (17.19±2.93)	22.20 (19.45±2.66)	22.85 (17.17±2.09)	2.55	0.28
short spacers	48.47 (47.62±1.09)	42.85 (41.96±1.49)	25 (30.67±4.00)	15.46	0.00	60.34 (71.04±3.17)	52.64 (62.30±3.14)	11.83 (7.62±2.92)	17.90	0.00
Multiplication ability										
frequent multiplication	63.48 (64.84±1.93)	60.52 (61.70±1.45)	58.62 (57.72±2.98)	2.65	0.27	66.95 (84.38±1.59)	63.97 (78.14±2.37)	29.73 (23.07±2.99)	17.69	0.00
infrequent multiplication	18.51 (17.94±1.17)	14.63 (15.07±0.84)	3.57 (3.29±0.88)	14.86	0.00	13.94 (7.36±0.91)	10.61 (5.19±0.89)	3.71 (3.95±3.66)	8.22	0.02
Connection permanency										
Long-lasting connection	70.71 (71.38±1.21)	66.66 (67.32±1.40)	41.66 (41.13±3.96)	17.34	0.00	72.11 (86.22±1.91)	59.87 (75.42±2.26)	26.26 (17.44±3.31)	27.58	0.00

	Number of species			Chi-square	Prob. value	Cover (%)			Chi-square	Prob. value
	Xeric grasslands	Mesic grasslands	Forest			Xeric grasslands	Mesic grasslands	Forest		
short-lasting connection time	17.31 (17.29±0.63)	17.64 (16.94±1.04)	25 (25.92±2.87)	7.31	0.03	13.79 (8.68±1.17)	19.16 (13.97±2.28)	20.38 (13.84±2.52)	7.43	0.02
Storage organs specialised organs	2.98 (3.72±0.64)	5 (6.05±0.64)	4.16 (3.98±1.14)	7.74	0.02	5.83 (2.42±0.85)	4.71 (4.13±2.02)	7.56 (2.62±1.49)	0.08	0.96
nonCGO storage	3.64 (4.23±0.46)	4 (4.59±0.68)	5.26 (4.81±1.44)	0.35	0.84	3.65 (1.03±0.35)	6.21 (2.41±0.62)	3.71 (5.53±3.66)	10.25	0.01
Size of bud bank large bud bank	59.00 (59.94±1.43)	59.10 (58.13±1.33)	37.50 (38.55±3.42)	12.81	0.00	66.78 (80.94±2.00)	60.47 (73.68±2.46)	18.51 (13.54±2.53)	18.71	0.00
small bud bank	18.39 (17.58±0.79)	15.55 (16.95±1.36)	26.31 (27.96±3.57)	8.16	0.02	13.99 (8.72±1.17)	14.73 (11.53±2.30)	24.38 (17.69±4.08)	5.06	0.08
Bud protection with specialised leaves	14.28 (14.62±0.76)	10 (10.68±1.02)	7.14 (6.05±1.54)	15.06	0.00	48.79 (52.51±3.74)	27.23 (21.42±3.46)	7.56 (2.98±1.78)	30.25	0.00
Vegetative spreading fast spread	27.54 (28.99±1.52)	28.88 (29.56±1.35)	31.03 (26.52±3.38)	0.61	0.74	27.70 (26.93±3.37)	43.49 (47.50±4.30)	22.42 (17.69±3.41)	16.52	0.00
insignificant spread	59.59 (57.90±1.38)	55.55 (54.02±1.80)	33.33 (38.44±5.32)	10.24	0.01	59.30 (65.95±3.85)	39.94 (38.80±3.71)	15.96 (11.60±4.39)	28.56	0.00
rare spread	2.27 (1.78±0.26)	0 (0.68±0.25)	2.63 (2.07±0.88)	10.36	0.01	3.43 (2.02±0.86)	0 (3.10±2.03)	2.73 (1.72±1.56)	6.26	0.04
Clonal plants	31.09±1.15	28.16±1.31	20.00±2.45			128.28±5.08	126.18±7.46	58.40±10.58		
Total	35.09±1.27	33.52±1.54	29.60±2.29			136.00±6.02	140.69±7.82	180.90±17.19		
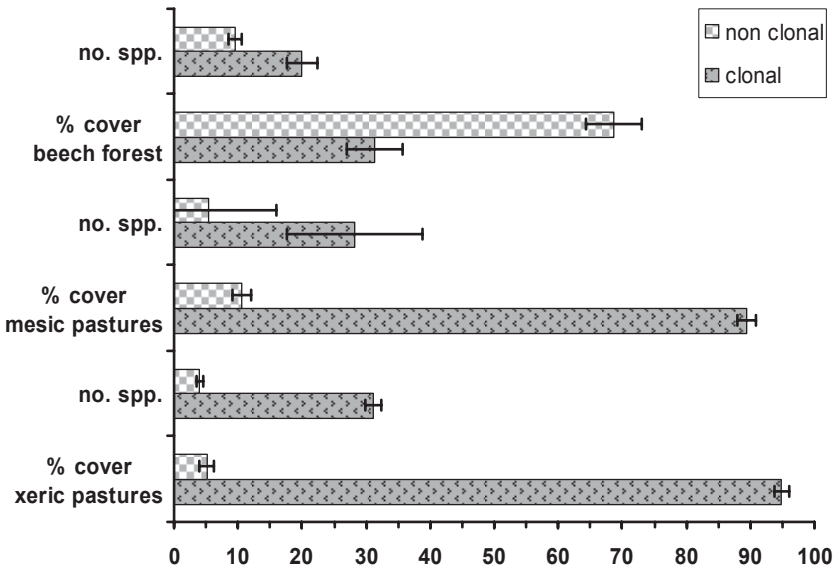
Fig. 1: The participation of clonal and non-clonal plants in the three vegetation complexes. Bars and whiskers represent mean±SE of the number of species and percentage cover (standardised data) for each category.

Species capable of fast vegetative spread did not show any preference for a community, but their abundance was significantly higher in mesic grasslands than in the other two communities. Plants with poor vegetative spread (<0.05 m per year) dominated the vegetation of xeric grasslands (when both frequency and cover data are considered) and were found to be less important in mesic habitats (Fig. 2).

The spectrum of CGMs varied between the communities, in particular between the group of grasslands and the beech forest (Fig. 3). In both grasslands, the top five CGMs (contributing more than 80 % in cover) were identical, though they differed in the order of importance.

The *Festuca ovina* CGM contributed to 66% of vegetation cover in xeric grassland, whereas the other CGMs played only a minor role in this community. Mesic grasslands were dominated by the *Dactylis glomerata* CGM (40%), followed by *Festuca ovina* CGM (26%). Lower cover values characterised the forest, with the *Asperula odorata*, *Aegopodium podagraria* and *Corydalis cava* CGMs as the more important ones (with 16.5%, 10% and 8%, respectively).

Our forest differs from the grasslands studied primarily in the layer of (non-clonal) trees. By considering the cover of the trees we have contributed to diminishing the importance of clonal species in quantitative (cover) terms in the forest. At the same time, the tree foliage creates a level of stress for the understorey species through the effect of shade. Traits found to be characteristic for the

beech forest (showing higher frequency and/or abundance than in the grasslands) were the short permanence of connection between ramets, and the presence of specialized storage organs. The former trait occurred especially in the *Asperula odorata* CGM (represented by *Galium odoratum* and *Cardamine bulbifera* – plants with short-lived below-ground plagiotropic stems) and in some geophytes. Species having specialized storage organs were geophytes, with the spring ephemeroid *Corydalis cava* dominating the herb-layer. However, we acknowledge that their importance might have been underestimated because of the timing of vegetation sampling (when most of the above-ground foliage of *Corydalis cava* had already withered).

The grasslands showed high mutual similarity. Although differences regarding the relative importance of certain CGMs were found between them, these mainly resulted from the higher cover of clonal plants present in the xeric grasslands (Fig. 2). Almost all traits could be explained by one or two highest ranked CGMs, for example, the *Festuca ovina* CGM in the xeric grasslands, and *Dactylis glomerata* CGM joined by the *Festuca ovina* type in the mesic grasslands. Species attaining undisputed dominant status in the xeric grasslands were *Bromus erectus*, a matrix grass of the *Centaureo bracteatae–Brometum erecti*, and *Sesleria nitida* in the *Seslerio nitidae–Brometum erecti*. In the mesic grassland, *Festuca circummediterranea, Arrhenatherum elatius, Dactylis glomerata* and *Lolium perenne* contributed to the dominance of *Dactylis glomerata* CGM, while *Bromus erectus, Cynosurus cristatus* and *Koeleria splendens* were the most important representatives of the *Festuca ovina* CGM.

The most striking difference between the two grassland types was found in the "bud protection by specialized leaves" trait (a characteristic trait of many species in xeric grasslands), and in the "capability for vegetative spread" (prevalent in mesic habitats). In fact, the dominant CGMs for the two grassland types had almost identical growth characteristics, except for a few traits, including bud protection and vegetative spread. Plant species belonging to the *Festuca ovina* CGM possess specialised leaves that protect buds, whereas vegetative spread in the *Dactylis glomerata* CGM can be fast, covering several metres per year. The presence of the *Aegopodium podagraria* CGM in the mesic grasslands, marked by species capable of fast vegetative spread (*Galium verum* and *Lathyrus pratensis*) was also conspicuous (Fig.2).

Position of clonal organs

The majority of CGMs in our data have below-ground CGOs, and thus not much information can be gained from species frequency data alone. The cover data for above-ground CGOs is also restricted, and shows no difference between habitats. Species with below-ground CGOs have significantly higher cover values ($p<0.001$) in the grasslands than in the forest. The relative importance of this habit (in terms of total cover of species) also differed significantly between the xeric (90%) and mesic grasslands (85%; $p<0.05$). The difference was partly due to species having root-derived CGOs (CGMs 1–4 in the system of Klimes *et al.* 1997) and those with an extensive perennial root system.
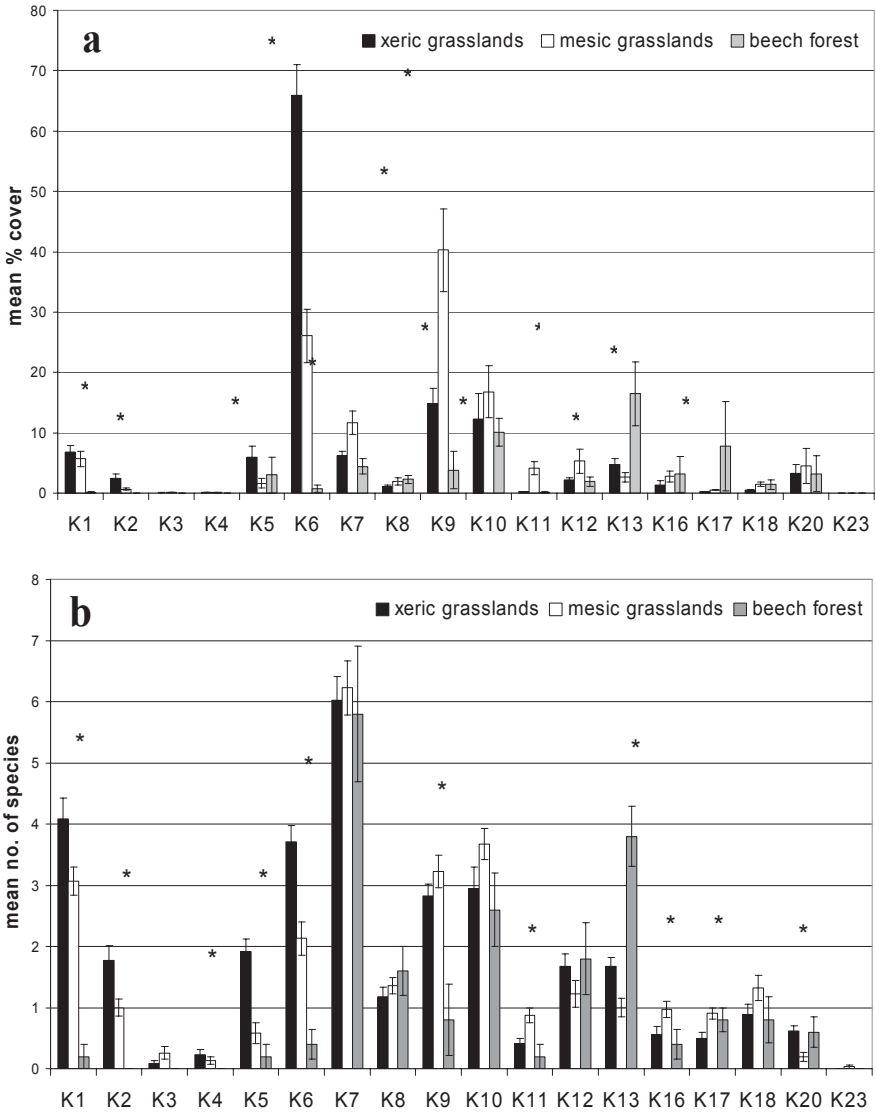
Fig. 2: The importance of clonal growth modes in xeric grasslands, mesic grasslands, and beech forest based on mean cover (a) and mean species number (b). Codes on the x axis indicate clonal categories according to Table 2. Standard errors and significant differences at p<0.05 based on the nonparametric Kruskal-Wallis test are indicated. (n=5 for the beech forest, 31 for mesic and 34 for xeric pastures).
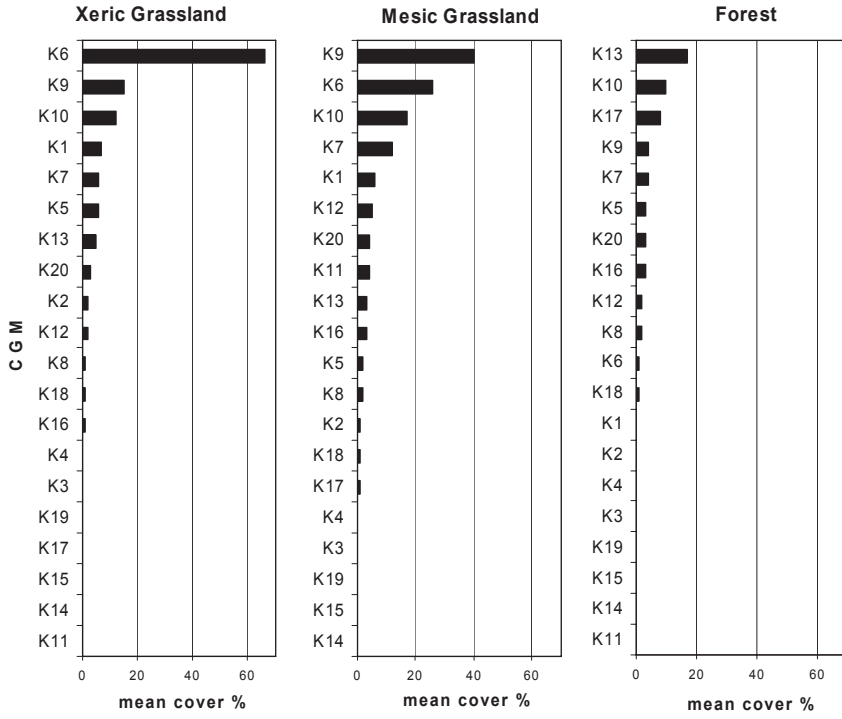
	Xeric Grassland	Mesic Grassland	Forest
H (Shannon)	2.25	2.22	1.86
Clonal cover (%)	94.90	89.39	31.28
Non clonal cover (%)	5.10	10.61	68.72

Fig. 3: The abundance-dominance of clonal growth mode (CGO) in the three vegetation complexes based on the standardised mean cover values. Numbers indicate clonal categories according to Table 2.

Spacer length

The number of species with the capacity to develop long spacers did not differ among the three communities studied. Species with short spacers became more frequent (and important in terms of cover) in less favourable habitats. The importance of species with short spacers was almost ten times higher in xeric grasslands than in the forest (71% to 7.6%).

Multiplication ability (and bud bank)

Species producing numerous ramets every year were frequent in all three communities, but their importance was the highest in the xeric grasslands (expressed in terms of cover: 84%, as compared to 78% for mesic grasslands and 23% for the forest).

A large bud bank is a pre-requisite for an advantageous strategy under unfavourable conditions, for it allows flexibility in growth response, and thus in

multiplication ability. We have not submitted this bud bank as a clonal trait to direct testing, because of its high level of correlation with the trait of multiplication ability [11].

Connection permanency

CGMs characterised by long-lasting connections between ramets are encountered more frequently in the grassland communities than in the forest. The xeric grasslands had significantly higher number of species characterised by long-lasting connections than the mesic ones (71% and 67%, respectively). Clonal plants with long-lasting connections contributed 86% of the total cover in xeric and 75% in mesic grasslands. In the beech forest, on the contrary, the number of species with short-lasting connections is higher than in grasslands.

Storage organs

The presence of storage organs and the abundance of species with this feature were supposed to differ between the studied communities, as storage could be a useful strategy for surviving periods unfavourable to plants. In contrast to our expectations, the only significant difference found was that the mesic grasslands hosted more species with CGOs with this storage function, compared to the total number of species, than the other two habitats. The beech forest was expected to differ from the grasslands, because of the widespread occurrence of spring-flowering geophytes in this community. However, only a few geophytes were found in the herb layer of the forest, and all had low cover values. This can be ascribed to the late date of vegetation sampling, carried out in summer when most of the geophytes had already withdrawn into the subterranean stage. At the same time, species with such specialised storage organs were present in the grasslands as well (*e.g.* orchids, *Ranunculus bulbosus*, *Eranthis hyemalis*).

Bud protection

The relative number of species with bud protection tended to increase as the habitat changed from xeric grasslands to mesic grasslands, and to forest. The cover data was one order of magnitude higher in the grasslands than in the forest. Species with bud protection provided twice the cover in xeric grasslands than they did in the mesic (53% and 21%, respectively).

Discussion

The major approaches applied to study plant clonality consider (*i*) detailed demographic studies of a limited number of species under a restricted variety of environmental conditions (experiments not conducted in the field, or observations of a small number of habitats; see [44]) that allow for studying correspondence between clonal behaviour and habitat characteristics; (*ii*) comparative morphological studies of a large number of species from large geographic areas at higher taxonomic levels in the search for evolutionary trends [27]; and (*iii*) spatially explicit simulation techniques [40] that help to determine the potential adaptive value of certain growth patterns in different environments. Our study largely follows the first approach while assuming some elements of the second. The large number of species (271) included in the analysis did not allow a detailed

demographic study, and the evaluation of Clonal Growth Modes in the field could not be carried out for all species at this stage. However, including such a high number of species and analysing clonal traits in habitats that are part of an important successional context in the Central Apennines, has afforded interesting results on the adaptive value of certain growth forms and on their role in spatial patterns and processes of secondary vegetation.

The beech forest is a community on its own, obviously very different from the grasslands, in terms of both clonal plant occurrence and CGM diversity. Clonal plants were found to play only a minor role in the forest, and the morphological diversity of clonal species was lower here than in the grasslands. At the same time, the clonal growth mode-abundance curve was rather even, showing the equalised importance of various modes. Traits important in this community are linked to geophyte life form, considered to be very important in deciduous temperate forests [36].

Structure and processes of grassland ecosystems are usually determined by a few keystone species; in our case, these were found to be long-lived, clone-forming graminoids in mesic and high alpine grasslands [7, 12]. We found the mono-dominance of *Festuca ovina* CGM in xeric grasslands and the dominance of *Dactylis glomerata* CGM along with *Festuca ovina* CGM in mesic grasslands. The two CGMs differ only in a few characteristics. *Festuca ovina* CGM includes turf graminoids with long-lived, below-ground stems formed above-ground. Buds are protected by specialized leaves in this type, and young ramets start to photosynthesize immediately after their initiation. The *Dactylis glomerata* CGM has long-lived, below-ground plagiotropic stems formed below-ground. Species belonging to this type tend to have additional types of CGOs and can show secondary thickening. Vegetative spread can be fast and cover several metres per year [20]. The differences between the two CGMs and the role that they play in the two communities bring to mind the responses of modular plants to mesic and tundra environments [3, 47]. Callaghan [3] found that abiotic control in tundra vegetation was associated with deterministic growth (cushion and tussock formation) and weak competitive ability. Cushion form is efficient in buffering extreme conditions (low temperatures and drought), and the outer ring of dead modules in the tussock growth form provide protection and nutrients for young modules. The *Festuca ovina* CGM represents this "protective strategy" adaptive to harsh environments of exposure, extreme temperatures, and mineral soils. Mesic grasslands, on the contrary, are relatively resource-rich, but the closed vegetation results in a strongly competitive environment. Clonal perennial plants are characterized by higher plasticity of modular constructions that allows foraging for resources and the avoidance of interspecific competition in mesic habitats [3]. The *Dactylis glomerata* CGM capacity for intensive lateral spread and the presence of additional growth modes indicate a "competitive strategy" adaptive to environments under phytocoenotic control (i.e. competition).

Below-ground position, short spacers, the capacity for frequent multiplication, the maintenance of physical connection between ramets, large bud

bank, and bud protection prevailed in xeric grasslands compared to mesic grasslands, accord with our expectations. Plants showing potential for fast lateral spread were more important in mesic grasslands, whereas species characterized by insignificant spread abilities dominated xeric grasslands. Storage organs played a more important role in mesic grasslands, in contrast to our expectations. This can be explained by the fact that many different organs can serve as storage sinks in clonal plants [41], but very few species were characterised by special storage organs (such as bulbs and corms) in the CGM system used [20].

The correspondence between clonal traits and ecological characteristics is a sign of adaptive behaviour [13, 20, 39]. Tightly packed modules were reported to be advantageous in open habitats [3]. Most traits associated with xeric grasslands (short spacers, potential of frequent multiplication, prolonged period of physical connection between ramets) can be interpreted as mechanisms that determine tight packing of modules.

The mechanism of fast lateral spread was more important in the mesic grasslands, whereas species characterized by insignificant spread abilities dominated the xeric grasslands. The clonal "spread ability" can be adopted as a measure of "plant mobility". Sammul *et al*. [35] introduced "ramet turnover speed" (a plant demographic measure) and found an increase of importance of this clonal feature in fertilized grassland communities – an interesting finding, which they related to species-richness depletion. In our study we found higher species richness in xeric grasslands – where low-mobility is more common – than in the other two communities. Klimeš [19] looked into plant turnover of seasonally dry, species-rich grasslands. He found that the mobility of a group of species characterized by potential extensive clonal growth was not much higher than clonal plants with poor clonal growth. More importantly, he concluded that low plant mobility does not mean high species richness – a fact indirectly supported by our data as well. However, even if plant mobility is not directly linked with diversity, a high level of different growth forms may promote coexistence in species-rich grasslands.

Clonal plants show high morphological plasticity in terms of spacer length and branching intensity as well as in changing resource acquisition strategies [6]. Moreover, it is difficult to judge whether the occurrence of various traits is a result of adaptations to a particular habitat or whether it reflects evolutionary processes of the past [23], or possibly both. The system of Clonal Growth Modes [20] does not provide for testing how individual life-history traits respond to ecological factors. However, since it assumes the adaptive value of a group of traits, such as the type and location of the organs of clonal growth, it offers an effective exploratory tool for searching out evolutionary and macro-ecological patterns in multi-species systems.

These aspects draw our attention to the importance of and need for specific field studies targeting how clonal traits interact with community structure and functions, in order to formulate more appropriate guidelines for systems conservation and restoration [37].

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Appendix

Species	Clonality I.	II.	III.
Acer obtusatum	N		
Adenostyles australis	7		
Alyssum minus	N		
Anchusa barrelieri	N		
Arabis collina	7		
Armeria canescens	7		
Asperula purpurea	13	7	
Asphodelus albus	10		
Astragalus depressus	2		
Astragalus sempervirens	10		
Avenula praetutiana	6		
Bupleurum baldense	N		
Calepina irregularis	N		
Campanula apennina	7		
Cardamine greca	N		
Cardamine heptaphylla	13		
Carex macrolepis	7		
Carlina corymbosa	7		
Centaurea ambigua	7		

Species	Clonality I.	II.	III.
Festuca curvula	6		
Festuca inops	6		
Galium lucidum	13		
Genista januensis	N		
Helianthemum oelandicum	5		
Helichrysum italicum	7		
Helleborus bocconei	8		
Inula montana	10		
Knautia purpurea	7		
Leontodon cichoraceus	12	17a	
Leontodon crispus	12		
Linum bienne	N		
Medicago lupulina	2	N	
Narcissus poeticus	18		
Ostrya carpinifolia	N		
Phleum ambiguum	6		
Polygala major	N		
Polygala nicaeensis	N		
Primula veris	8		

Species	Clonality		
	I.	II.	III.
Cerastium ligusticum	N		
Chamaecytisus hirsutus	N		
Cirsium arvense	N		
Colchicum lusitanum	16	16a	
Coronilla minima	N		
Crepis lacera	N		
Crepis vesicaria	N		
Crupina vulgaris	N		
Cyclamen repandum	17		
Cynoglossum magellense	N		
Cytisus sessilifolius	5	N	
Daphne laureola	N		
Dianthus sylvestris	7		
Digitalis micrantha	8		
Eryngium amethystinum	1	2	
Erysium pseudorhaeticum	N		
Euphorbia gasparrini	10		
Festuca circunmediterranea	9		

Species	Clonality		
	I.	II.	III.
Ranunculus millefoliatus	16	4	
Rubia peregrina	13		
Rubus ulmifolius	N	14	
Sanguisorba minor	2		
Saxifraga bulbifera	18	19	23
Senecio apenninus	12		
Sesleria nitida	6	9	
Silene italica	9	2	
Solenanthus apenninus	N		
Stachys tymphaea	N		
Thlaspi alliaceum	N		
Thymus longicaulis	5		
Tragopogon samaritani	N		
Valeriana tuberosa	17a		
Veronica orsiniana	7		
Vicia onobrychioides	10		
Viola eugeniae	13		