Effect of tall-grass invasion on the flowering-related functional pattern of submediterranean hay-meadows

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Abstract
Several studies demonstrated that abandonment changes the functional composition of grasslands; nevertheless, little is known about the effects of grassland abandonment on the flowering-related functional pattern. We hypothesized that invasion by tall grasses affects this pattern. We counted the number of flowering shoots per species at five times during the growing season, in 80 plots placed in mown and in abandoned grasslands (central Apennines), and assessed the differences in the trait composition of flowering species between the two treatments. The selected traits were linked to resource acquisition and stress tolerance strategies. Our results indicated that abiotic environmental control is prevalent in determining the phenological pattern in both conditions and in accordance with the phenological “mid-domain hypothesis”. We demonstrated that when the dominant species is a tall grass with competitive behaviour, the magnitude of this phenomenon is amplified due to the abiotic changes yielded by the tall grass invasion. Indeed, in the central and late phases of the growing season (when invasive tall grasses are growing and blooming), abandoned grasslands were marked by a set of traits devoted to stress tolerance or underlying a long reproductive cycle or linked to competition for light.

Keywords: Acquisition strategies, Brachypodium genuense, flowering phenology, grassland abandonment, plant trait, stress tolerance strategies

Abbreviations: ISA, indicator species analysis; MRPP, multi-response permutation procedures

Introduction
The timing of flowering is an important component of community assembly (Puppi 2011). Indeed, flowering phenology affects the composition of plant communities through its effect on species interactions, i.e. by facilitation for pollination (Rathcke & Lacey 1985) or competition for resources (Cleland et al. 2006). Moreover, flower production is resource-intensive (Ashman & Schoen 1994; Obeso 2002), which might tend to favour reproduction during times of low environmental stress, as postulated by the phenological “mid-domain hypothesis” (Morales et al. 2005). Nevertheless, if flowering time is critical to competition for resources or avoidance of stress, it could be considered a part of a larger plant strategy that incorporates other functional traits (Craine et al. 2012).

Grime (2001) stated that dominant species tend to bloom in the central phases of the growing season, when no stress acts in the system, day-length and light intensity allow a high rate of photosynthesis, and a long time is available for seed maturation. These species do not need functional strategies allowing fast pre-emption of the canopy or tolerance to stresses (Catorci et al. 2012b). Instead, subordinate and accidental species (sensu Grime 2001) have functional strategies that allow them to flower before or after the dominant ones or to share the same period through a different type of space occupation (Catorci et al. 2012a). Catorci et al. (2012b) stated that the functional set underlying the flowering pattern of subordinate and accidental species has a dual ecological meaning. It limits competition with dominant species and enables tolerance to environmental stresses, which change throughout the growing season (i.e. low soil temperature in spring and water shortage in summer).
It is well documented that the floristic composition and variability of pastures are strongly related both to the spatial variation of environmental features and constraints (Catorci & Gatti 2010; Blasi et al. 2012; Ribeiro et al. 2013) and to the management type (Catorci et al. 2012c; Ibanez et al. 2013). Moreover, abandonment of farming activities leads to the reduction of landscape complexity and promotes vegetation dynamics processes, a factor that could be detrimental for the conservation of biodiversity (Gargano et al. 2012).

Several studies demonstrated that, as a consequence of abandonment, invasion by dominant tall grasses (e.g. Brachypodium pinnatum, B. rupestre, Calamagrostis epigejos and Bothriochloa ischaemum) changes the species diversity and the functional composition of pastures (Wilson et al. 1995; Buckland et al. 2001; Bonanomi & Allegrezza 2004; Peco et al. 2005, 2006, 2012; Díaz et al. 2007; de Bello et al. 2006, 2007; Sebastià et al. 2008; Somodi et al. 2008; Házi et al. 2011; Szentes et al. 2012). Furthermore, it alters the site ecology besides the plant community structure (Hurst & John 1999; Markham et al. 2009; Catorci et al. 2011a). Grime (2001) also argued that micro-scale alterations may act jointly with macro-environmental factors in intensifying stress because of local or temporary depletion of resources, thus strongly influencing the competitive interaction among plants (Peltzer & Wilson 2001).

Because invasion by tall grasses represents a key driver in plant community assemblage (Díaz et al. 2004; de Bello et al. 2005), and changes the resource availability and the grassland canopy structure and persistence throughout the year, we hypothesized that it may affect the flowering-related functional pattern in abandoned meadows. To test this hypothesis, we addressed the following questions: (i) Are temporal patterns of traits between mown and abandoned grassland similar (abiotic environmental control is prevalent; cf. Primack 1985)? Or, (ii), according to Catorci et al. (2011a), are these patterns different due to biotic control of invasive tall grasses? (iii) If differences emerge, which ecological strategies underlie these changes after abandonment?

Materials and methods

Study area

The study area (central coordinates 43°01’16”N, 13°13’36”E) is located in the Sibillini Mountains National Park (central Italy) at 1350–1450 m a.s.l. on northern slightly steep slopes and is characterized by a limestone bedrock. Soils are 40–50 cm deep, with sub-acid pH (5.5–6.0) and clayey–sandy texture. Annual rainfall is 1400 mm and the mean annual temperature is 7.5°C, with winter mean minimum temperatures below 0°C; a water scarcity period occurs in August. Seasonal trends (referred to 2009) of soil temperature and moisture, and phytomass in mown and in abandoned meadows, as well as the trend of mean daily air temperature are shown in Figure 1.

Figure 1. Trends of soil temperature (°C), soil moisture (%) and aboveground phytomass (g m⁻²) in mown and abandoned meadows, and of mean daily air temperature (°C), in the study area. The trends refer to the growing season 2009, before hay cutting and the water scarcity period. Data are partly drawn from Catorci et al. (2011a, 2012b) (black and white symbols indicate mown and abandoned meadows, respectively; triangles, circles, squares and the grey line indicate soil temperature, soil moisture, aboveground phytomass and mean daily air temperature, respectively).
Traditionally, pastures were mown at the end of June, and then grazed by sheep. In the last decades, these practices underwent a collapse, and starting from 1980 to 1985, only mown (in mid- to late July) or abandoned grasslands are present. Catorci et al. (2011b) demonstrated that the change of the traditional management (mowing and grazing) mostly reflects on a decrease in the number of accidental species, like the annual ones. Thus, because of the long-term cessation of grazing, we can argue that at present the managed grasslands are likely evolutionary adapted to mowing.

Mown grasslands are referred to the \textit{Filipendulo vulgaris}–\textit{Trifolium montani}. Biondi et al. (2005) included this plant community (attributing it to a sub-association of \textit{Brachypodium genuesis} sub-alliance of the \textit{Phleum ambigui}–\textit{Bromion erecti} alliance, which were placed in the \textit{Scorzonero villosae}–\textit{Chrysopogonetaea grylli} order (Biondi & Galdenzi 2012). Abandoned meadows are referred to the \textit{Nardo strictae}–\textit{Brachypodietum genuesis} (Di Pietro et al. 2005).

Catorci et al. (2011b) demonstrated that, after management cessation, dominant species \textit{(sensu Grime 2001)} spread quickly. Indeed, the cover value of \textit{Brachypodium genuesis} is greater than 80% in the abandoned condition and ranges from 15% to 30% in mown meadows.

\textit{B. genuesis} is a perennial grass (30–50 cm tall) with lateral clonal spread (Lucchese 1988). Because of its silica-rich hairy leaves, it is a poorly palatable plant (Roggero et al. 2002). Catorci et al. (2011a) indicated that its growing period starts in May and leaves reach their maximum size at the end of June. Most individuals (90%) reach full flowering in mid-July.

**Data collection**

To reduce the number of environmental variables, we selected an area of about 300 ha that was homogeneous in terms of altitude (1350–1450 m a.s.l.), slope angle (5–10°) and aspect (north-facing slopes). Within this area, we chose 10 mown and 10 abandoned (for 20 years) sites. Then, we fenced 80 plots (2 m × 2 m), 40 of which in mown sites and 40 in abandoned ones. Data were collected five times during the 2010 growing season (\textit{t}_1–\textit{t}_5), on 5 May, 25 May, 13 June, 2 July and 21 July. In each plot, we counted the number of flowering shoots per species at each time (we considered shoots with more than 70% of flowers in full blooming). On the basis of previous studies (Catorci et al. 2012a, 2012b), we assumed that the time interval between two consecutive observations was wide enough to record the flowering time for all the species and to avoid to count flowering shoots twice during the subsequent times of sampling.

Traits used for the functional assessment of the flowering pattern were chosen according to indications of Weiher et al. (1999), Grime (2001), Diaz et al. (2004) and Lavorel et al. (2007), following the hypothesis that analysis of traits related to resource acquisition and stress tolerance may help to understand the species coexistence mechanisms. First, plant height, occurrence and type of vegetative propagation, type of space occupation (horizontally and vertically) and leaf persistence were selected as indicators of resource acquisition strategies. Second, leaf anatomy, leaf persistence, occurrence and type of storage organs, and seed weight were selected as indicators of stress tolerance.

Data on traits (Appendix I) were gathered from bibliographic resources (Grime et al. 1988; Klotz et al. 2002; Klimešová & Klimeš 2006) and supplemented by field observations and laboratory measurements.

To assess the coenological role of each species, 40 vegetational relevés (10 m × 10 m), 20 in mown and 20 in abandoned conditions, were performed in 30 June 2010. Species cover percentages were visually evaluated and averaged (Appendix II). Following the Grime’s indication (2001) adapted to submediterranean condition (Catorci et al. 2012b), species were aggregated into three groups on the basis of the mean cover value (dominant species, >25.0%; subordinate species, 1.1–25.0%; accidental species: ≤1.0%).

**Statistical analysis**

To quantify the similarity in composition of functional traits of flowering species between the two different treatments at each time, we calculated the Bray–Curtis index of similarity (Bray & Curtis 1957; Bloom 1981), according to the following formula:

$$BC_{i,k} = \frac{2 \sum_{j=1}^{n} \min(x_{i,j}, x_{k,j})}{\sum_{j=1}^{n}(x_{i,j} + x_{k,j}),}$$

where \(x_{i,j}\) is the number of occurrences (absolute frequency) of the \(j\)th item (i.e. trait state of the flowering species set) in the relevés of the \(i\)th group, \(x_{k,j}\) the number of occurrences (absolute frequency) of the same item in the relevés of the \(k\)th group and \(n\) the number of items over all relevés.

Following Catorci et al. (2012b), for each flowering species listed in each plot, we calculated the proportion of flowering shoots occurring at each time out of the total number of flowering shoots in the whole considered period. For each trait and coenological role, we grouped the species sharing the
same state and averaged their percentage of flowering according to the formula:

\[ F_{x,t} = \frac{\sum_{i=1}^{S} (n_{x,i,t}/n_{tot})}{S_x}, \]

where \( F_{x,t} \) is the mean proportion of flowering shoots occurring in plot \( x \) at time \( t \), \( n_{x,i,t} \) is the number of flowering shoots of a species counted in plot \( x \) at time \( t \), \( n_{tot} \) is the total number of flowering shoots of a species counted in all the blooming period in plot \( x \), and \( S_x \) is the number of flowering species sharing the same coenological role/trait state in plot \( x \) at time \( t \). \( F_{x,t} \) values were the elements of a “relevés \( \times \) coenological role/trait state” matrix used for the subsequent statistical processing (Catorci et al. 2012b). Average values of \( F_{x,t} \) per plot at each time \( (F_{av,t}) \) were also calculated according to the formula:

\[ F_{av,t} = \frac{\sum_{i=1}^{N} F_{x,i,t}}{N}, \]

where \( N \) is the number of plots.

In our research, we were interested in comparing the overall pattern of traits of flowering species at the community level, during the growing season and between two different management conditions at different times of the growing season. To achieve this aim, we used a statistical approach based on multi-response permutation procedures (MRPPs). MRPP is a nonparametric procedure for testing the hypothesis of no difference between two or more groups of entities (McCune & Grace 2002). More specifically, MRPPs compare the observed delta (within-group average distance, weighted by the relative group size), with the average distance resulting from every permutation of all the observations among the groups under the null hypothesis (i.e. all partitions have the same chance of occurrence). The test statistic \( T \) (which describes the separation between the groups) was calculated from Pearson type III distribution to derive the probability value of a delta smaller than the observed. The statistic \( A \) (chance corrected within group agreement, which describes within-group homogeneity compared to the random expectation), calculated from the observed and expected deltas, was used to measure the homogeneity within the groups. An \( A = 1 \) indicates that all samples within each group are identical; an \( A \) equal to zero or lower than zero indicates that within-group heterogeneity is equal or greater, respectively, to that expected by chance (McCune & Grace 2002).

The hypothesis of no difference among times \( (t_1\ldots t_5) \) in each treatment in relation to traits composition of flowering species was tested through the MRPP applied, using the Bray–Curtis distance measure, to the matrices “relevés \( \times \) coenological role/trait state” \( (F_{x,t} \) values) and “relevés \( \times \) time \( (t_1\ldots t_5) \)”, where time was the grouping variable. The weight applied to the distances within groups was the number of items in each group out of the number of items in all the groups. To test the significance of differences between consecutive times, pairwise comparisons between times were run as well. A Bonferroni correction for multiple comparisons was used to avoid Type I error.

Similarly, we also used MRPP to test the hypothesis of no difference between mown and abandoned condition at each time, by making five elaborations (one for each time) of the “relevés \( \times \) coenological role/trait state” \( (F_{x,t} \) values) and “relevés \( \times \) management type (mowing/abandonment)” matrices, where management type was the grouping variable.

To determine the indicator traits of each time in mown and in abandoned conditions, we performed indicator species analysis (ISA). The ISA is a nonparametric method for identifying those species that show significantly preferential distribution (frequency and abundance) with respect to an a-priori treatment group. An indicator value is calculated by multiplying the relative abundance of each species in a particular group and the relative frequency of the species occurrence in the sample of that group (Dufrène & Legendre 1997). We performed ISA on the “relevés \( \times \) coenological role/trait state” matrix \( (F_{x,t} \) values) and “relevés \( \times \) time \( (t_1\ldots t_5) \)”, where time was the grouping variable. We also performed an ISA at each time on the “relevés \( \times \) coenological role/trait state” \( (F_{x,t} \) values) and “relevés \( \times \) management type (mowing/abandonment)” matrices, where management type was the grouping variable, to determine the indicator traits of mown and abandoned conditions. We evaluated the statistical significance \( (P < 0.001) \) of the observed maximum indicator values using the Monte Carlo test, based on 4999 permutations, where samples are reassigned and recalculated. The number of randomized indicator values higher than the observed ones was used to calculate the probability value (McCune & Grace 2002). We considered of interest only indicator values greater than 30.

ISA and MRPP were run using the PCORD 5.0 software (McCune & Mefford 2006).

Results

The Bray–Curtis index showed high similarities in frequencies of flowering-related traits between mown and abandoned meadows, with a maximum in \( t_3 \) \((0.93)\), and lower values in \( t_1, t_2 \) \((0.86)\), \( t_4 \) and \( t_5 \) \((0.91)\).
Flowering patterns in abandoned meadows

MRPP elaboration rejected the hypothesis of no difference among times (t₁–₅) for both mown (T = −104.36; A = 0.496; P < 0.001) and abandoned (T = −102.65; A = 0.405; P < 0.001) treatments. The pairwise comparisons between consecutive times indicated that, in mown meadows, differences became less pronounced as the growing season proceeded, while in abandoned meadows the differences fluctuated (Table I). MRPP also rejected the hypothesis of no difference in trait composition between mown and abandoned treatments for each considered time (t₁–₅) (Table II). Differences were more marked in t₃ (T = −21.75; A = 0.073; P < 0.001), decreasing at its extremes.

Appendix III shows the average proportion of flowering shoots occurring at time t for species sharing a coenological role/trait state (Fₘₖₜ). Only a few of them underwent dramatic changes (e.g., overwintering green leaves, succulent leaf anatomy and heavy seed weight having higher value in mown condition, succulent leaf anatomy and heavy seed weight having higher value in abandoned condition), while several of them showed a shift from t₂ to t₃ of the flowering peak in abandoned condition.

As regards the functional assessment of differences among times within each considered treatment (i.e. abandoned and mown grasslands), ISA pointed out (Table III) that in the earlier phase of the growing season (t₁), in both conditions the blooming plants had root tuber, spring green leaves or were species with narrow basal leaves and leafless stems. Species blooming in t₂ and t₃ had mainly the accidental or subordinate coenological role besides storage organs, vegetative propagation modes and low-intermediate classes of plant height. As regards leaf anatomy and persistence, ISA highlighted mesomorphic, mesomorphic/hygromorphic, scleromorphic/mesomorphic leaves, as well as overwintering, summer and persistent green leaves. Moreover, the system fostered the blooming of species capable of active space occupation (reptant), with caespitose or pleiocormic architecture, and the intermediate seed weight classes. The dominant coenological role was an indicator of t₄, while the main characteristics of species flowering in t₅ were low seed weight and scleromorphic leaves.

Several traits showed a delay of the Fₘₖₜ peak in the abandoned meadows. From t₂ to t₃, the indicator traits involved in these shifts were small size (species less than 20 cm tall), epigeogenous stems, presence of vegetative propagation, reptant and hemirosulate upright forb growth forms, as well as seed weight ranging from 1.0 to 2.0 mg. Instead, from t₃ to t₄, the shifting traits were hypogeogenous stem, caespitose/reptant growth form and seed weight ranging from 2.01 to 4.00 mg.

As for the functional assessment of differences between treatments in each time (e.g. t₁ of abandoned grassland vs t₁ of mown grassland), Table IV shows the indicators of abandoned and mown meadows for each considered time. No indicator trait states emerged in t₁; in t₂, several trait states were indicator of mown treatment, while none characterized the abandoned condition. In t₃ and t₄, the following indicators emerged in the abandoned condition: presence of vegetative propagation (rhizome and runner-like rhizome) and storage organs (rhizome); accidental and subordinate coenological role; mesomorphic, scleromorphic/

### Table I. Pairwise comparison between consecutive observation times (t₁–₅), with regard to plant trait flowering percentages in mown and abandoned meadows, as performed by MRPP (T – test statistics; A – chance-corrected within-group agreement).

| Observation times comparison | T    | A    |
|------------------------------|------|------|
| Mown meadows                 |      |      |
| t₁ vs t₂                     | −52.06 | 0.491 |
| t₂ vs t₃                     | −48.84 | 0.288 |
| t₃ vs t₄                     | −40.84 | 0.172 |
| t₄ vs t₅                     | −38.12 | 0.165 |
| Abandoned meadows            |      |      |
| t₁ vs t₂                     | −41.85 | 0.321 |
| t₂ vs t₃                     | −45.17 | 0.233 |
| t₃ vs t₄                     | −38.73 | 0.166 |
| t₄ vs t₅                     | −44.86 | 0.229 |

Note: All P values (probability of a smaller or equal weighted mean within-group distance) were lower than 0.001 after the Bonferroni correction.

### Table II. Pairwise comparison between mown and abandoned meadows for each observation time (t₁–₅), with regard to plant trait flowering percentages, as performed by MRPP (T – test statistics; A – chance-corrected within-group agreement).

| Observation time | Mown vs abandoned meadows | T    | A    |
|------------------|---------------------------|------|------|
| t₁               | −12.51                    | 0.072 |
| t₂               | −15.70                    | 0.069 |
| t₃               | −21.75                    | 0.073 |
| t₄               | −17.58                    | 0.058 |
| t₅               | −11.42                    | 0.045 |

Note: All P values (probability of a smaller or equal weighted mean within-group distance) were lower than 0.001.
Table III. Indicator coenological roles and trait states (with regard to the mean flowering proportions of species sharing each coenological role/trait state) of different times during the growing season \( (t_{1} – 5 \text{ May}; t_{2} – 25 \text{ May}; t_{3} – 13 \text{ June}; t_{4} – 2 \text{ July}, t_{5} – 21 \text{ July}) \) within each treatment (mown and abandoned meadows), as determined by ISA.

| Coenological role of species | Mown meadows | Abandoned meadows |
|-----------------------------|--------------|------------------|
|                             | Max. flow. time | \( t_1 \) | Max. flow. time | \( t_1 \) |
| Accidental                  | \( t_2 \) | 39.3 | \( t_3 \) | 37.8 |
| Dominant                    | \( t_4 \) | 47.0 | \( t_4 \) | 62.5 |
| Subordinate                 | \( t_3 \) | 33.7 | \( t_5 \) | 39.5 |

| Trait                        | Trait state | Max. flow. time | Iv | Max. flow. time | Iv |
|------------------------------|-------------|-----------------|----|-----------------|----|
| Storage organs               | Presence    | \( t_3 \) | 34.1 | \( t_5 \) | 36.5 |
| Absence                      | \( t_4 \) | 39.1 | \( t_5 \) | 47.2 |
| Type of storage organs       | Bulb (sometimes with bulbils) | \( t_2 \) | 67.5 | \( t_2 \) | 41.0 |
| Epigeogenous stem (rhizome)  | \( t_2 \) | 46.8 | \( t_5 \) | 38.9 |
| Hypogeogenous stem (rhizome) | \( t_3 \) | 33.2 | \( t_4 \) | 50.3 |
| Persistent tap root          | \( t_3 \) | 38.1 | \( t_3 \) | 36.3 |
| Root tuber                   | \( t_1 \) | 51.9 | \( t_1 \) | 49.9 |
| Vegetative propagation       | Presence    | \( t_2 \) | 34.3 | \( t_5 \) | 38.2 |
| Absence                      | \( t_3 \) | 38.4 | \( t_5 \) | 35.7 |
| Type of vegetative propagation | Bulb (sometimes with bulbils) | \( t_2 \) | 67.5 | \( t_2 \) | 37.2 |
| Epigeogenous stem (rhizome)  | \( t_2 \) | 46.6 | \( t_5 \) | 38.7 |
| Epigeogenous stem (runner-like rhizome) | \( t_3 \) | 33.8 | \( t_3 \) | 40.7 |
| Hypogeogenous stem (rhizome) | \( t_3 \) | 33.2 | \( t_4 \) | 47.9 |
| Root shoot                   | – | – | \( t_5 \) | 45.7 |
| Root splitter                | \( t_3 \) | 74.5 | \( t_3 \) | 74.6 |
| Root tuber                   | \( t_2 \) | 46.6 | \( t_2 \) | 34.0 |
| Plant height (cm)            | \( < 20 \) | \( t_2 \) | 34.5 | \( t_5 \) | 36.2 |
|                             | \( 21 – 40 \) | \( t_3 \) | 36.6 | \( t_3 \) | 44.4 |
|                             | \( 41 – 60 \) | \( t_3 \) | 30.6 | \( t_3 \) | 32.0 |
|                             | \( 81 – 100 \) | \( t_5 \) | 37.6 | – | – |
| Leaf anatomy                 | Mesomorphic | \( t_3 \) | 33.4 | \( t_5 \) | 38.5 |
| Mesomorphic/hygromorphic     | \( t_2 \) | 73.8 | \( t_3 \) | 63.0 |
| Scleromorphic                | \( t_5 \) | 59.9 | \( t_5 \) | 64.0 |
| Scleromorphic/helomorphic    | \( t_4 \) | 36.4 | – | – |
| Scleromorphic/mesomorphic    | \( t_3 \) | 32.9 | \( t_3 \) | 46.2 |
| Succulent                    | – | – | \( t_5 \) | 40.4 |
| Leaf persistence             | Overwintering green | \( t_2 \) | 54.9 | \( t_2 \) | 37.5 |
| Persistent green             | \( t_3 \) | 33.4 | \( t_3 \) | 32.1 |
| Spring green                 | \( t_1 \) | 53.6 | \( t_1 \) | 48.5 |
| Summer green                 | \( t_3 \) | 39.2 | \( t_3 \) | 48.3 |
| Type of horizontal space occupation | Absent | \( t_1 \) | 47.7 | \( t_2 \) | 37.4 |
| Caespitose                   | \( t_3 \) | 34.9 | \( t_3 \) | 51.7 |
| Caespitose and reptant       | \( t_3 \) | 37.2 | \( t_4 \) | 48.3 |
| Pleiocorm                    | \( t_3 \) | 43.8 | \( t_3 \) | 47.0 |
| Pleiocorm and reptant        | – | – | \( t_3 \) | 30.3 |
| Reptant                      | \( t_2 \) | 36.2 | \( t_3 \) | 39.4 |
| Rosulate                     | \( t_5 \) | 50.3 | – | – |
| Type of vertical space occupation | Broad leaves either scattered or tightly packed along the stem (hemirosulate upright forb) | \( t_2 \) | 36.7 | \( t_3 \) | 32.9 |
| Broad leaves equally spaced along the stem (erosulate upright forb) | \( t_3 \) | 41.1 | \( t_3 \) | 49.6 |
| Leafy stem, narrow leaves (grass) | \( t_3 \) | 39.7 | \( t_3 \) | 40.4 |
| No leafy stem, broad basal leaves (rosette forb) | \( t_2 \) | 55.4 | \( t_2 \) | 50.1 |
| No leafy stem, narrow basal leaves (sedge) | \( t_1 \) | 47.3 | \( t_1 \) | 63.3 |
| Seed weight (mg)             | \( 0.01 – 0.20 \) | \( t_3 \) | 39.5 | \( t_4 \) | 42.9 |
|                             | \( 0.21 – 0.50 \) | \( t_3 \) | 36.1 | \( t_3 \) | 38.3 |
|                             | \( 0.51 – 1.00 \) | \( t_2 \) | 40.9 | \( t_3 \) | 30.1 |
|                             | \( 1.01 – 2.00 \) | \( t_2 \) | 47.0 | \( t_3 \) | 44.6 |
|                             | \( 2.01 – 4.00 \) | \( t_3 \) | 62.1 | \( t_4 \) | 62.4 |
|                             | \( 4.01 – 10.00 \) | – | – | \( t_5 \) | 35.6 |

Notes: Indicator values (Iv) in the five times are shown. Only significant indicator values \((P < 0.001)\) greater than 30 are reported (max flow. time – time with maximum observed indicator value). Coenological roles and trait states with maximum indicator value at different times in mown and in abandoned meadows are marked in bold.
Table IV. Indicator coenological roles and trait states (with regard to the mean flowering proportions of species sharing each coenological role/trait state) of different treatments, namely mown (m) versus abandoned (a) meadows in each considered time of the growing season (t1 – 5 May; t2 – 25 May; t3 – 13 June; t4 – 2 July, t5 – 21 July), as determined by ISA.

| Coenological role of species | Type of management with maximum indicator value |
|-----------------------------|-----------------------------------------------|
|                             | t1  | t2  | t3  | t4  | t5  |
| Accidental                  |     |     |     |     |     |
| Dominant                    |     |     |     |     |     |
| Subordinate                 |     |     |     |     |     |

| Trait                           | Trait state | t1  | t2  | t3  | t4  | t5  |
|---------------------------------|-------------|-----|-----|-----|-----|-----|
| Storage organs                  | Presence    |     | m***| –   | a** | –   |
|                                 | Absence     |     | –   | m***| m*  | –   |
| Type of storage organs          | Bulb (sometimes with bulbils) | m* | –   | –   | –   | –   |
|                                 | Epigeogenous stem (rhizome)   | m***| a*  | –   | a***| –   |
|                                 | Hypogeogenous stem (rhizome)  | m***| –   | a***| m** | –   |
|                                 | Persistent tap root            | m***| –   | –   | –   | –   |
| Vegetative propagation          | Presence    |     | m***| a** | –   | –   |
|                                 | Absence     |     | –   | m*  | a** | –   |
| Type of vegetative propagation  | Bulb (sometimes with bulbils) | m* | –   | –   | –   | –   |
|                                 | Epigeogenous stem (rhizome)   | m***| a*  | –   | a***| –   |
|                                 | Epigeogenous stem (runner-like rhizome) | m***| a*  | a***| m** | –   |
|                                 | Hypogeogenous stem (rhizome)  | m***| –   | a***| m** | –   |
|                                 | Root tuber |     | m***| –   | –   | –   |
|                                 | Runner      |     | m***| –   | –   | –   |
| Plant height (cm)               |             | 20  | m** | –   | m** | –   |
|                                 |             | 21–40| m***| a** | –   | –   |
|                                 |             | 41–60| m***| –   | a*  | a***|
|                                 |             | 61–80| m***| –   | m***| m** |
|                                 |             | 81–100| m***| –   | m** | –   |
| Leaf anatomy                    | Mesomorphic | m***| a*  | a*  | –   | –   |
|                                 | Scleromorphic/helomorphic      | m***| m***| m** | –   | –   |
|                                 | Scleromorphic/mesomorphic      | m***| a***| a*  | m***|
|                                 | Succulent |     | m*  | a** | –   | –   |
| Leaf persistence                | Overwintering green | m* | –   | –   | –   | –   |
|                                 | Persistent green               | m***| –   | a***| –   | –   |
|                                 | Spring green                   | m*  | –   | –   | –   | –   |
|                                 | Summer green                   | m***| a***| a*  | m** |
| Type of horizontal space occupation | Absent | m*  | a** | –   | –   | –   |
|                                 | Caespitose | m***| a*  | –   | –   | –   |
|                                 | Caespitose and reptant         | m***| a** | –   | –   | –   |
|                                 | Pleioicorm                     | m***| –   | –   | –   | –   |
|                                 | Pleioicorm and reptant         | a***| m***| m** | –   | –   |
|                                 | Reptant                        | m***| a***| –   | –   | –   |
|                                 | Rosulate                       | m***| m*  | –   | –   | –   |
| Type of vertical space occupation | Broad leaves either scattered or tightly packed along the stem (hemirostate upright forb) | m*  | a*  | m*  | –   | –   |
|                                 | Broad leaves equally spaced along the stem (erosulate upright forb) | m** | a** | –   | –   | –   |
|                                 | Leafy stem, narrow leaves (grass) | m***| a** | –   | –   | –   |
|                                 | No leafy stem, broad basal leaves (rosette forb) | m** | –   | –   | –   | –   |
|                                 | No leafy stem, narrow basal leaves (sedge) | m***| –   | –   | –   | –   |
| Seed weight (mg)                | 0.01–0.20 | m*  | –   | –   | –   | –   |
|                                 | 0.51–1.00 | m*  | –   | –   | –   | –   |
|                                 | 1.01–2.00 | a** | m** | m*  | –   | –   |
|                                 | 2.01–4.00 | m** | a***| –   | –   | –   |
|                                 | 4.01–10.00| m*  | a** | –   | –   | –   |

Note: Only significant indicator values (***P < 0.001; **P < 0.01; *P < 0.05) greater than 30 are reported.
mesomorphic and succulent leaves; plant height 21–40 and 41–60 cm; summer green leaves; caespitose and reptant as types of horizontal architecture; grass and erosulate upright forb as types of vertical architecture; heavy seeds. In $t_5$, abandoned meadows were characterized by subordinate coenological role, epigeogenous stem (rhizome), absence of vegetative propagation and of horizontal space occupation, succulent and persistent green leaves, and plant height 41–60 cm.

Discussion

Our results highlighted a flowering-related functional pattern in both mown and abandoned conditions. They mostly differed in the flowering proportion in each considered time (as suggested by MRPP and ISA), for species sharing a trait state, rather than in trait composition, as indicated by the high values of the Bray–Curtis similarity index. These results are consistent with Primack’s hypothesis (1985) that the selection pressures due to environmental constraints are the first determinants of timing and patterns of phenological events in a plant community.

Previous research (Catorci et al. 2011a, 2012d; Figure 1) demonstrated that Brachypodium genuense spreading after abandonment alters the ecological status of the site (with regard to soil moisture and temperature), especially in the central phases of the growing season. These factors may explain the shifting (several traits showed a delay of the peak of average proportion of flowering shoots in the abandoned condition, as shown in Appendix III) and differences recorded between the two treatments that, as demonstrated by MRPP (Table II), were more marked in mid-June.

The comparison of the two management conditions as regards the indicator trait states of times, mown and abandoned treatments had the same indicator trait states of $t_1$ (Table III). At this time, no trait state emerged as an indicator of a certain type of treatment (Table IV). The indicator traits of $t_1$ are devoted to an early and fast growth strategy (root tuber, small-sized plants with narrow leaves next to the ground and spring green leaves). In fact, the mobilization of reserves stored in underground organs during the previous growing season ensures early and fast growth of the spring green leaves (Bolmgren & Cowan 2008). Grime (2001) argued that, thanks to their fast reproductive cycle, the early flowering geophytes are adapted to exploit a temporal niche when other species cannot grow, mostly because of low soil temperature (Bonan 2008). As stated by Sun and Frelitch (2011), this strategy, allowed also by the small plant size (Grime 2001), is of key importance in dense grasslands because competition for light may be intense, especially in the central phases of the growing season.

The environmental conditions of $t_2$ (high soil moisture and still quite low soil temperature, see Figure 1), as well as the need to avoid competition with dominant species (indicators of $t_4$) by fast growth and seed maturation, may be considered as the main driving forces in determining the trait composition of the flowering species set. In fact, the presence of storage organs (bulbs, root tubers and rhizomes), and leaf persistence type (overwintering green) allow rapid foliage expansion and leaf canopy pre-emption, affording a competitive advantage (Grime 2001). Moreover, species do not need leaf-anatomic strategies for protection against water loss (mesomorphic/hygromorphic leaf anatomy was an indicator trait). The comparison between mown and abandoned grasslands highlighted that the indicator traits identified in $t_2$ emerged in mown meadows because of their higher average flowering percentages ($F_{\text{vsi}}$) (Table IV). This result is probably related to the changes in spatial niche availability due to the spread of $B.$ genuense (Figure 1; Catorci et al. 2011a). Indeed, the spread of dominant species leads to the decrease in flowering individuals of other species (Bergmeier & Matthäus 1996; Catorci et al. 2011a) and thus to the decrease in abundance of the related trait states.

In $t_3$ and $t_4$ (mid-June/early July), the favoured space occupation modes were those of grasses, caespitose or caespitose/reptant, and pleiicorm species. Species with subordinate and accidental coenological roles had their flowering peak before that of dominant species in both conditions, confirming the existence of a temporal reproductive niche partitioning that allows non-dominant species to avoid competition with dominant ones (Grime 2001; Catorci et al. 2012b). In the abandoned condition, during this period, the $B.$ genuense individuals reach their final dimension and leaf canopy pre-emption, starting the flowering phenological phases. The wide horizontal space occupation of $B.$ genuense reduces the abundance of non-dominant phases. The wide horizontal space occupation of $B.$ genuense reduces the abundance of non-dominant plants. This may explain why accidental coenological role (i.e. species with average cover value lower than 1%) emerged as an indicator of abandoned meadows in $t_4$ (Table IV).

One could argue that the environmental modifications due to the growth and spread of $B.$ genuense (decrease in photosynthetically active radiation at the ground level and of the soil water content; see Catorci et al. 2011a, 2012d) produce high stress intensity in abandoned systems, filtering the functional response of the flowering species. Plants may tolerate stress by retaining resources in rhizomes that increase the likelihood of plants to establish in stressful habitats (Grime et al. 1997) by improving their uptake of water and nutrients (Newell & Tramer 1978; Tissue & Nobel 1988; Friedman &
Alpert 1991). Rhizomes also function as clonal growth organs and are a tool for overcoming sexual recruitment problems under unfavourable conditions (van Groenendael et al. 1996). Actually, the presence of vegetative propagation, storage organs and rhizomes (epi- and hypogeogenous stems) were the indicator traits of the abandoned condition in comparison with the mown treatment in $t_3$ and/or $t_4$. Instead, the competition for light owing to the dense canopy of B. genuense tussocks filtered the upright growth form, with leaves arranged around the stem and not close to the ground. As regards the leaf persistence trait states, summer green leaves emerged as indicators of abandoned condition, probably due to the lack of hay cut and thus to the availability of the entire summer to uptake and store resources (avoided in mown condition because of leaf removal). The long time available to complete the reproductive cycle and the availability of the whole summer period (characterized by water scarcity) to complete seed maturation may also explain the flowering of species with heavy seeds (4.01–10.00 mg) in the abandoned condition. In fact, Bolmgren and Cowan (2008) argued that heavy seeds are typical of species that can have a long time for the reproductive cycle. Furthermore, Baker (1972) associated a larger seed mass with dry habitats, owing to the correlation between seed size and stress resistance (Chapin et al. 1993).

Scleromorphic leaves and light seeds were indicator traits of $t_5$ in both mown and abandoned meadows. These traits are drought tolerance mechanisms. Scleromorphic leaves allow plants to avoid water losses by limiting evapotranspiration (Burghardt & Riederer 2003), light seeds grant the ability to predate the water scarcity period and/or a disturbance event (mowing in the study case) because of their fast maturation (Bolmgren & Cowan 2008; Du & Qi 2010), and to overcome the winter cold period by dormancy (Moles et al. 2000).

The establishment of succulent leaf anatomy as indicator trait of abandoned condition in comparison with mown treatment in both $t_4$ and $t_5$ highlights the greater effect of drought stress in abandoned meadows. Indeed, succulent leaves are suitable to preserve plants from water scarcity by storing water reserves (Hanscom & Ting 1978). The establishment of persistent green leaves as indicator trait state of abandoned condition in $t_5$ highlights a stress tolerance strategy as well because this kind of leaves can photosynthesize throughout the year without seasonal photosynthetic tissue regrowth (Al-Mufti et al. 1977; Grime 1977).

Finally, the absence of storage organs in the flowering species set of $t_5$ might be filtered by the low stress intensity in mown condition, while the occurrence of an epigeogenous stem (runner-like rhizome) as indicator trait may underline the establishment of a strategy aimed at enabling fast reoccupancy of the canopy after mowing thanks to a large number of reserve buds (Klimeš & Klimešová 2000, 2002).

Conclusions

Our results confirm that the selection pressures due to environmental constraints are the first determinants of phenological events. As indicated by Ansquer et al. (2009) and Catorci et al. (2012b), and in accordance with the phenological “mid-domain hypothesis” (Morales et al. 2005), species with life forms different from those of the dominant species tend to avoid the flowering co-occurrence with dominant plants, which reach their maximum phenological forwardness in the middle of the vegetative season. Catorci et al. (2012a) indicated that higher the presence (cover value) of dominant species, higher the “edge” effect in the flowering patterns of the subordinate and accidental ones. In the present study, we demonstrate that when the dominant species is a tall grass with competitive behaviour (sensu Grime 2001), the magnitude of this phenomenon is amplified, enhancing a set of traits devoted to stress tolerance or underlying a long reproductive cycle. Moreover, the alteration of site ecology due to invasion by competitive tall grasses drives some changes in the flowering-related functional pattern of abandoned communities. In the first phenological phases, when a relatively long time is still available to complete the reproductive cycle, the community response to abandonment is a delay of the flowering events of some species and a general decrease in the average traits abundance. Instead, starting from mid-June (when individuals of B. genuense are growing and blooming), the effect of the dominant species invasion plays a stronger role in that it filters a set of traits devoted to stress tolerance (i.e. rhizomes, heavy seeds, persistent green leaves, succulent leaves and vegetative reproduction). Moreover, the absence of disturbance allows the spread of species with traits devoted to a long reproductive cycle lasting all summer (i.e. heavy seeds, summer and persistent green leaves).

Our findings also broaden Grime’s definition of the behaviour of subordinate species in a plant community. Grime (2001) argued that such species have a precise and local placement in the foraging structure. Our results highlighted that their precise foraging strategy involves not only the spatial but also the temporal niche partitioning.

Finally, we can state that the observed changes in the flowering-related functional pattern may help to explain the ecosystem’s functional response to the cessation of anthropogenic disturbance.
Supplemental data

Supplemental data for this article can be accessed at doi:10.1080/11263504.2014.980353.

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