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Extensive horse grazing improves grassland vegetation diversity, seed bank and forage quality of artificial embankments (Rhône River - southern France)

Influence of extensive horse grazing on artificial embankments

Cannelle Moinardeau^{a,*}, François Mesléard^{a,b}, Hervé Ramone^a, Thierry Dutoit^a

^a Institut Méditerranéen de Biodiversité et Ecologie, UMR CNRS-IRD, Avignon Université, Aix-Marseille Université, IUT d'Avignon, 337 chemin des Meinajariés, Site Agroparc BP 61207, 84911 Avignon, cedex 09, France

^b Institut de Recherche de la Tour du Valat, Le Sambuc, 13200 Arles, France

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ABSTRACT

Grazing by herds of herbivores modifies plant communities in different ways, depending on the herbivore species. Horse grazing is already known to be effective in increasing plant diversity and maintaining herbaceous vegetation, creating different types of patches and thus ensuring spatial heterogeneity. On an artificial embankment at the Donzère-Mondragon hydroelectric facility in the Rhône Valley, extensive grazing by a rustic horse (Konik-Polski) was introduced several years ago to control shrub encroachment and to enhance plant grassland diversity. Vegetation monitoring surveys over a five-year period (2014–2018) showed that horse grazing maintained patches of open and short grasslands and increased species-richness, in particular of annual species, some of which have heritage value. In contrast, overly-low grazing pressure led to the dominance of an unpalatable perennial grass (*Brachypodium phoenicoides*) at the expense of the annual species that significantly enhance the forage value of the most heavily grazed patches. Horse grazing also had a positive impact on the permanent seed bank of the soil, increasing its heterogeneity and the density of viable seeds. Extensive horse grazing thus appears to be a relevant management tool to preserve the diversity and the forage quality of the most open and short grasslands. Nevertheless, grazing pressure here remained too low to allow restoration of grasslands already colonised by woody species. Combining different livestock species might be a better alternative to pure horse grazing, to increase heterogeneity and diversity. Our results are discussed in relation to extensive horse grazing on artificial ecosystems, such as the embankments bordering rivers and canals.

1. Introduction

Mankind today plays a major role in the widespread changes to ecosystems worldwide (Ellis, Klein Goldewijk, Siebert, Lightman, & Ramankutty, 2010). Human activities are generating 'new ecosystems' unconnected with earlier ones (Harris, Hobbs, Higgs, & Aronson, 2006; Murcia et al., 2014; Root & Schneider, 2006). Despite having lost part of their biodiversity, functions and ecosystem services, these ecosystems are nonetheless able to reorganise themselves. However, the new combinations of species are difficult to predict, because of ongoing changes worldwide (climate, land-use, biological invasions), and because the current typologies lack analogues on which to base predictions of their trajectories.

These 'new ecosystems' challenge the concepts and practices in the

ecology of conservation and restoration that have proved relevant to existing or earlier assemblages, but which do not take into account the new sites' potential. In Europe, many of the 'new ecosystems' result from the construction of dams, embankments and channels (Jensen, Trepel, Merritt, & Rosenthal, 2006). There is a need for suitable management practices which promote successional trajectories and enhance biodiversity, ecosystem functions and services associated with these often young and highly artificial habitats. In addition, it is largely unclear whether methods commonly employed to manage pioneer herbaceous plant formations, such as extensive grazing or mowing, can be effective within these new ecosystems, as has been demonstrated for many other semi-natural ecosystems (Carboni, Dengler, Mantilla-Contreras, Venn, & Török, 2015).

It has been widely demonstrated that moderate grazing can induce a

* Corresponding author.

E-mail address: cannelle.moinardeau@gmail.com (C. Moinardeau).

spatial heterogeneity favourable to plant diversity (McNaughton, 1984). Overly-low grazing intensity can lead to a decline in plant species-richness through weak control of competition (Valkó et al., 2018). In contrast, overly-high grazing pressure can result in the dominance of species highly tolerant to grazing or of unpalatable species, and the elimination of species unable to regenerate via the soil seed bank (Cousens, Dytham, & Law, 2008). The seed bank has also been recognised as a key compartment for community persistence, in particular where communities are exposed to regular disturbances such as grazing (Bakker, Poschlod, Strykstra, Bekker, & Thompson, 1996). However, certain species do not establish permanent seed banks in the long term, and this includes the majority of species typical of grazing herbaceous ecosystems (Milberg, 1992; Thompson & Grime, 1979).

For several decades, horse grazing in particular has been widely used for the management of semi-natural grasslands (Gilhaus & Hölzel, 2016; Köhler, Hiller, & Tischew, 2016; Loucougaray, Bonis, & Bouzillé, 2004). It enables vegetation to become structured in a mosaic of patches of shorter herbaceous strata that are more conducive to new plant species. Horses preferentially select plots where biomass is high (Duncan, 1992); in winter, horses can shift to the sites offering the highest consumable biomass, including the dead parts of plants. This selection creates a heterogeneous mosaic of patches of vegetation, ranging from very open short grasslands dominated by annual and biannual grass species, to tall grasslands dominated by perennial grass species and often dotted with the first shrubs heralding the closing up of the herbaceous vegetation by shrub thickets. Horses have a preference for grass, although they also consume forb species in winter (Cosyns, Degezelle, Demeulenaere, & Hoffmann, 2001; Duncan, 1992; Lamoot, Meert, & Hoffmann, 2005; Ménard, Duncan, Fleurance, Georges, & Lila, 2002).

Numerous studies have investigated the impact of horse grazing on plant communities and its potential to meet conservation management objectives (Duncan, 1992; Henning, Lorenz, von Oheimb, Härdtle, & Tischew, 2017; Köhler et al., 2016). However, there has been little research on horse grazing in a highly artificial ecosystem (Lindenmayer et al., 2008), and such studies have rarely examined two compartments (above-ground vegetation, seed bank) in relation to forage quality (Gilhaus & Hölzel, 2016). The present study explored the impact of extensive grazing by Konik-Polski horses on community composition, seed bank and forage value of vegetation of an artificial embankment along a tailrace channel situated in the lower Rhone Valley. We aimed, through a five-year monitoring period (2014–2018) to determine the possible feedback between these compartments and whether this management type could be used for the conservation of 'new ecosystems' resulting from the construction of dykes and embankments.

Thus, our main goal was to test whether grazing by horses has significant impacts on the composition and species richness on the seed bank of the mosaic of patches, and in particular whether species richness and the density of seeds in the soil increases in heavily grazed patches (Saatkamp, Henry, & Dutoit, 2017; Thompson & Grime, 1979). Because horse grazing alters the competition between plant species of the above-ground vegetation and changes its structure, the quality of grass resources can vary widely over time and space in line with the pattern of consumption at the origin of feedback loops (Crawley, 1983). We also tested the hypothesis that extensive horse grazing favours annual plant species, which can provide good forage, thus ensuring the sustainability of the grazing system (Vulink, Drost, & Jans, 2000). Finally, we sought any positive link between the impact of horse grazing on species-richness and on seed density of annual species and the improved quality of grass resources due to this impact, in the most heavily grazed grasslands (open short grasslands).

The following questions were addressed:

- How does extensive horse grazing affect the species richness, the associated seed bank and the heterogeneity of different vegetation patches in 'new ecosystems'?

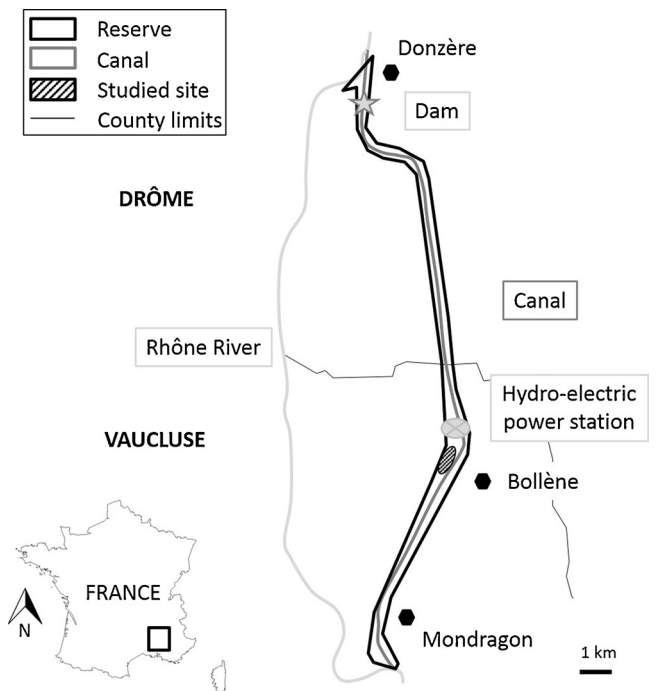


Fig. 1. Location of the Donzère-Mondragon study site in the lower Rhone valley in south-eastern France. Location of the study site (dashed lines), boundaries of the reserve (black lines), hydro-electric plant (light grey dots), channel (dark grey lines), the Rhone (light grey lines).

- How is the forage quality of the vegetation (mineral content, digestibility) affected by extensive horse grazing?
- Is extensive horse grazing a useful and sustainable method of conserving the herbaceous vegetation of 'new ecosystems'?

2. Materials and methods

2.1. Study site

The site (27 ha) is located along a channel of the Rhône river about 50 km north of Avignon, downstream of the hydroelectric power station of Donzère-Mondragon (N: 44°18'13.3" E: 4°44'32.9", Fig. 1). The dam was built in the early 1950s using millions of tons of alluvial sediment extracted during the digging of the canals; see (Moinardeau, Mesléard, & Dutoit, 2016; Moinardeau, Mesléard, Ramone, & Dutoit, 2019). The site is a part of a fauna and flora reserve named "Réserve Naturelle de Chasse et de Faune Sauvage de Donzère-Mondragon" and created in 1954 (Roux et al., 2012). The dominant vegetation is herbaceous vegetation covering 53 % of the site in 2017, including a tussock grass (*Brachypodium phoenicoides*) which covered 35 % in 2017 and some annual species (*Lysimachia arvensis*, *Filago germanica*, *Crepis sancta*, *Galium parisiense*, etc.). Different shrub species (*Crataegus monogyna*, *Cornus sanguinea*, *Rubus sp.*, etc.) had also colonised the site and covered 47 % in 2017.

For conservation purposes, four Konik-Polski mares were introduced in 2008 and in 2014 after two years without grazing. The horses grazed the whole site throughout the year, which represented a grazing pressure of 0.04 Livestock Unit (LU) per ha per year. In 2016, three new mares were added which represented a grazing pressure of 0.07 LU.ha. year⁻¹.

The local climate of the area is Mediterranean, with an average rainfall of 600 mm mostly in autumn and to a lesser extent in early spring. The year 2017 was characterised by particularly low rainfall precipitation (Table 1). During the five years of the study (2014–2018), the average temperature remained close to 15 °C, without major inter-

Table 1

Meteorological data for study site during period monitored. Location of weather station: Latitude 44.133, Longitude 4.833, Height 55 m above sea level. Data: www.freemeteo.fr.

Year	Mean temperature (°C)	Rainfall (mm)
2014	15.01	814.8
2015	14.79	770.7
2016	15.05	546.4
2017	15.15	299.2
2018 (First half-year)	12.75	525.6

annual variation.

2.2. Vegetation monitoring

Aerial photographs were used to characterise the different vegetation patches during the absence of horses in 2012 and 2013 and after their reintroduction we used. We distinguished six types of vegetation patches: open grasslands (OG) with bare zones corresponding to areas with more silt and clay deposits; short grasslands (SG) totally covered by herbaceous vegetation 10–20 cm in height; tall grasslands (TG) dominated by *B. phoenicoides* 20–30 cm in height; tall grasslands dotted with shrubs (TGS) of 62 % cover in 2017; shrub thickets (ST) and ungrazed tall grasslands, outside the grazed fenced areas, used as controls without management (C).

We monitored vegetation in permanent quadrats (five per type of patches, $5 \times 6 = 30$ quadrats) whose sizes (2×2 m) were determined for each type of patch by calculating the Minimum Area (Guinochet, 1973). We estimated the abundance of each plant species by assigning cover classes as above: 1 = less than 5% of the plot, 2 = between 5 and 25 %, 3 = between 26 and 50 %, 4 = between 51 and 75 %, 5 = more than 75 %, and + = a single individual present. Vegetation cover (%), height (cm) and bare soil cover (%) were recorded each year between 2014 and 2018 in May, when most plants are identifiable. The nomenclature of vascular plants follows (Tison, Jauzein, & Michaud, 2014).

We calculated alpha-diversity (species richness per plot, mean species number) and beta-diversity by the Bray–Curtis distance between the five quadrats for each type of patch to compare the different vegetation patches in terms of species-richness and composition similarity

(Borcard, Gillet, & Legendre, 2011).

2.3. Soil seed bank

We sampled the soil seed bank in three grassland patches (OG, SG, TG) and in the ungrazed tall grasslands considered as control (C) during winter 2016–2017. Ten replicates were randomly distributed for each vegetation patch. Each sample consisted of one dm^3 of soil (corresponding to the sample of a 25×25 cm quadrat) and at a depth of 15 cm. We extracted the seeds from the soil according to the sample concentration method (ter Heerdt, Verweij, Bekker, & Bakker, 1996). We dipped each sample in water during 30 min and then concentrated them by sifting under a water column through a mesh of 2–4 mm and 200 μm . To prevent possible tegumental dormancy, we lightly rubbed the seeds. We spread out concentrated soil in a thin layer (< 0.5 cm) on seeding trays filled with a 2 cm layer of vermiculite coupled with compost (30 %), and covered with a sterile 2 μ medical compress. The trays were placed in a greenhouse (20–25 °C) under constant conditions and regularly watered. We recorded and counted seedlings each week and removed them to avoid any competition. We stopped the monitoring after 6 months after observing a significant period without any germination. Seedlings were identified using the flora of Mamarot (2002), Muller (1978), Tison et al. (2014).

2.4. Forage values

Above-ground plant biomass sampling was carried out on a seasonal basis, from autumn 2016 to summer 2017 (4 seasons in October, January, May and July). We collected five replicates (handful size) of fresh biomass in each patch distinguished (OG, SG, TG, TGS, ST, C). Plants were cut at a height of 3 cm to avoid mineral contamination from the soil. We only collected leaves for shrub species, considering that horses mainly feed on leaves when grazing is extensive. No debarking was observed (Moinardeau, pers. obs.). On the day of collection, the samples were taken to the laboratory (Laboratoire Teyssier) for analysis to the standards used by AFNOR Paris (1985) and Jarrige (1988).

The dry matter content of the samples was measured after 4 h of oven-drying at 103 °C. The mineral matter content was measured after 6 h of calcination in the oven at 550 °C. The gross cellulose content was estimated by the WEENDE method (Henneberg & Stohmann, 1864). The digestibility of the organic matter was calculated using regression

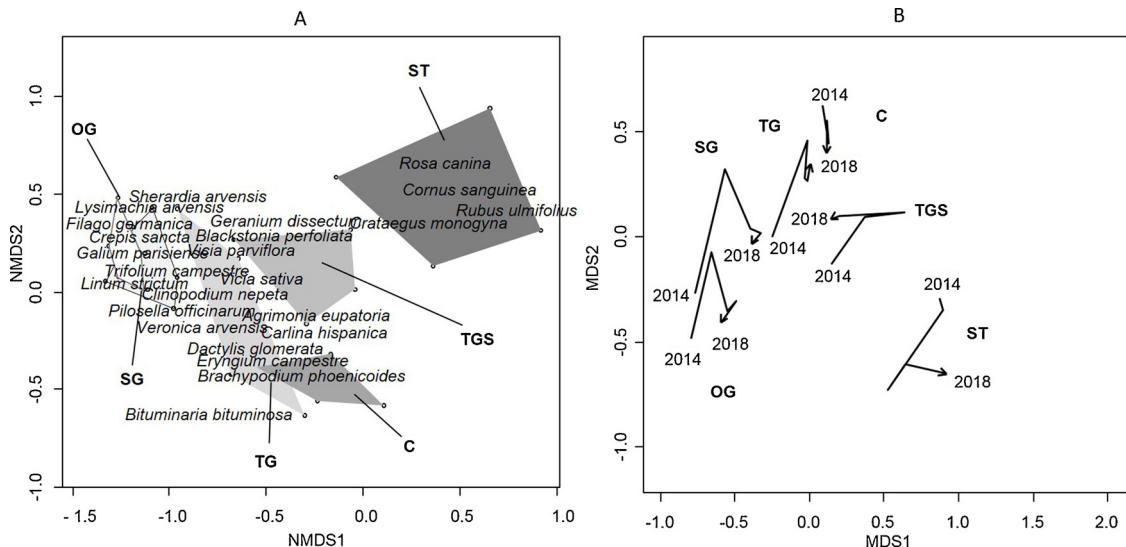


Fig. 2. NMDS ordination (NMDS stress = 0.17) based on vegetation surveys (30 quadrats \times 141 species) carried out in different patches of vegetation at the study site grazed by horses. Fig. 2A showed the 2018 samples grouped by vegetation type (polygons): open grasslands with bare soil (OG), short grasslands (SG), tall grasslands (TG), tall grasslands dotted with shrubs (TGS), shrub thickets (ST) and ungrazed control (C). Only the species most closely correlated with the first two axes are listed. Fig. 2B showed vegetation dynamics per vegetation type, according to the position of their centroids, for the five years of vegetation monitoring (2014–2018).

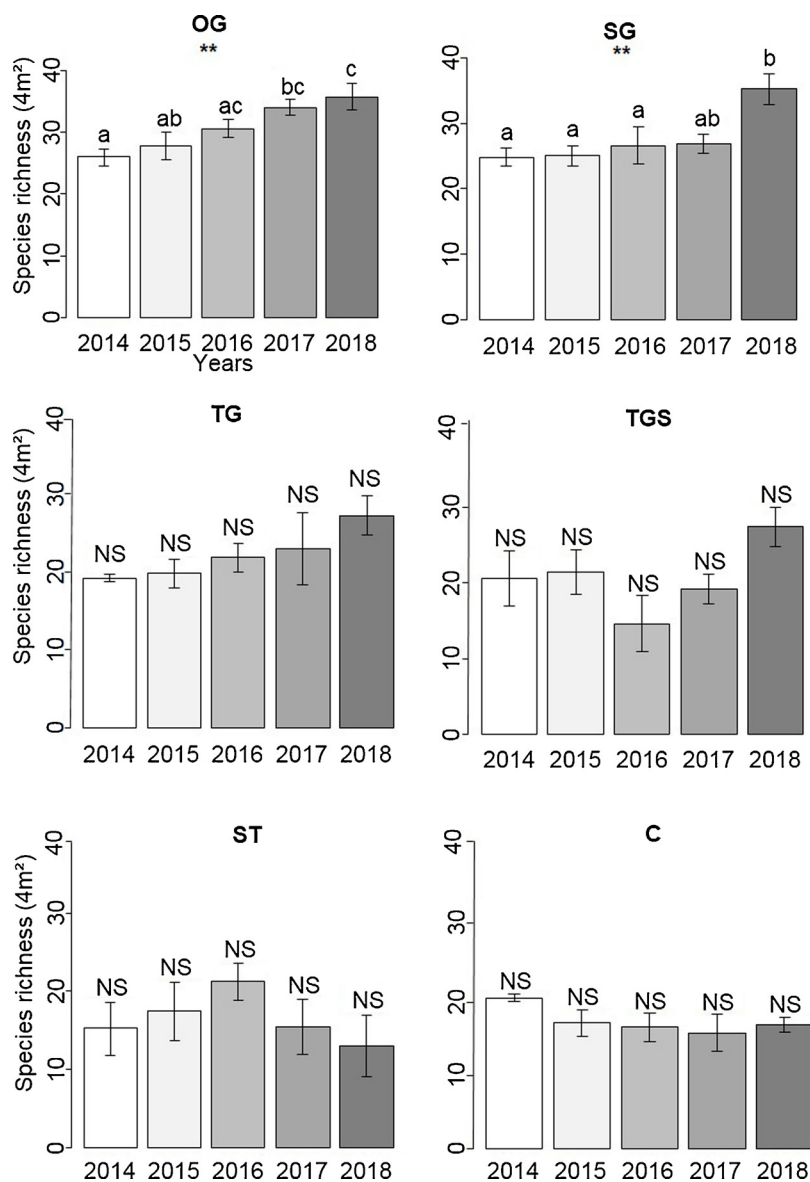


Fig. 3. Mean and standard error for species richness per patch of vegetation and per year (2014-2018) on the study site grazed by the horses: open grasslands (OG), short grasslands (SG), tall grasslands (TG), tall grasslands dotted with shrubs (TGS), shrub thickets (ST) and ungrazed control (C), (N = 5 for each patch, each year). Histograms with common letters do not show a significant difference between vegetation types for the same year, according to ANOVA test following with Tukey's post-hoc test. P value: * < 0.05, ** < 0.01, *** < 0.001.

Table 2

Differences in species richness of each vegetation patch between each year studied. Results of the tests and their significance, as well as the mean value and standard deviation are shown in the table, significance: $p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***. [Fig. 3].

Vegetation patches	F value (Df = 4)	p value	2014	2015	2016	2017	2018
Species richness (/ 4m ²)							
OG	5.34	**	26 ± 1.38	27.8 ± 2.26	30.6 ± 1.43	34 ± 1.30	35.8 ± 2.22
SG	4.58	**	24.8 ± 1.32	25 ± 1.61	26.8 ± 2.84	26.8 ± 1.49	35.2 ± 2.35
TG	1.49	NS	19.2 ± 0.49	19.8 ± 1.77	21.8 ± 1.82	23 ± 4.58	27.2 ± 2.51
TGS	2.28	NS	20.6 ± 3.65	21.4 ± 2.94	14.6 ± 3.72	19.2 ± 1.95	27.4 ± 2.6
ST	0.81	NS	15.2 ± 3.41	17.4 ± 3.77	21.2 ± 2.33	15.4 ± 3.47	13 ± 3.89
C	1.17	NS	20.6 ± 0.50	17.2 ± 1.77	16.6 ± 1.91	15.8 ± 2.51	17 ± 1.04

equations. The gross protein content was gauged using the method of Kjeldhal (Kjeldahl, 1883). The main minerals (magnesium, calcium, potassium, phosphorus) were measured using an atomic adsorption spectrophotometer (Thermo Scientific Company). The Horse Forage Unit was calculated using the standard equations (Jarrige, 1988).

2.5. Statistical analyses

2.5.1. Vegetation monitoring

Composition and abundance of plant species were ordinated using non-metric multidimensional scaling (NMDS) based on Bray-Curtis similarity (Borcard et al., 2011). Trajectories of the centroids of the

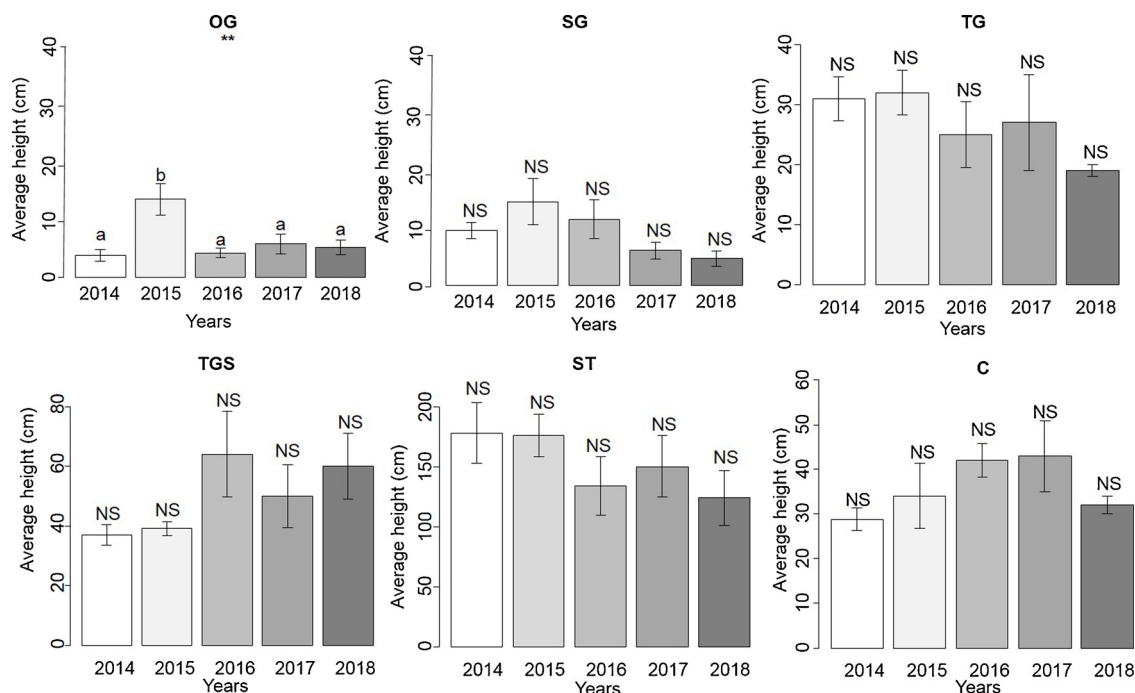


Fig. 4. Mean and standard error for mean height of herbaceous vegetation of the six vegetation patches on the study site grazed by horses (OG, SG, TG, TGS, ST and C) per year of monitoring (2014-2018), (N = 5 for each patch, each year). Histograms with common letters do not show a significant difference between vegetation types for the same year, ANOVA test following with according to Tukey's post-hoc test. P value: * < 0.05, ** < 0.01, *** < 0.001.

Table 3

Seed bank species identified for each vegetation patch sampled (open grasslands, short grasslands, tall grasslands, non-grazed control). Number of seeds and species in the seed bank are indicated, as well as number of species in the vegetation surveys in 2017.

Type of grassland patches	Soil seed bank		Vegetation
	Seedlings	Species	Species
Open grasslands (OG)	1184	33	64
Short grasslands (SG)	921	47	58
Tall grasslands (TG)	698	49	57
Non-grazed Control (C)	581	50	43

polygons of the vegetation patches were analyzed to illustrate how plant community composition evolved. Comparisons of height of vegetation, species richness and Bray-Curtis distance between vegetation patches were performed using ANOVA tests for multiple comparisons when the data were normally distributed (Shapiro-Wilk or Lilliefors tests). When a significant difference was detected, we realized a Tukey post-hoc test from the model. When the data did not follow a normal distribution pattern, a Kruskal-Wallis non-parametric test or a Mann-Whitney-Wilcoxon non-parametric test was used, with the p value adjusted (Benjamini & Hochberg, 1995) for two-by-two comparison.

2.5.2. Soil seed bank

NMDS was performed on the mean number of seeds per sample and the mean number of seeds per species. We performed univariate analyses on species richness, density of germinated seeds, Evenness and Bray-Curtis distance, using the same method as for plant samples. We calculated the similarity between species composition of the seed bank and vegetation using Sørensen index (Mueller-Dombois & Ellenberg, 1974).

2.5.3. Forage value

To compare the mineral elements and nutritive values among the different patches of vegetation and between season, a multivariate Principal Component Analysis (PCA) was performed on the major mineral elements (magnesium, calcium, potassium, phosphorus), cellulose, proteins by patches and for each season studied. Univariate analyses were carried out for each of the elements per season and then for each vegetation patch per seasons. Finally, Spearman correlation tests were applied to the data from the botanical sampling carried out the same year, in spring 2017.

All statistical analyses were performed with R software version R 3.2.2 (The R Foundation for Statistical Computing). The native packages were used for univariate analyses and the additional packages ade4 and nortest (Chessel, Dufour, & Thioulouse, 2004; Dray & Dufour, 2007) for multivariate analyses (PCA and NMDS).

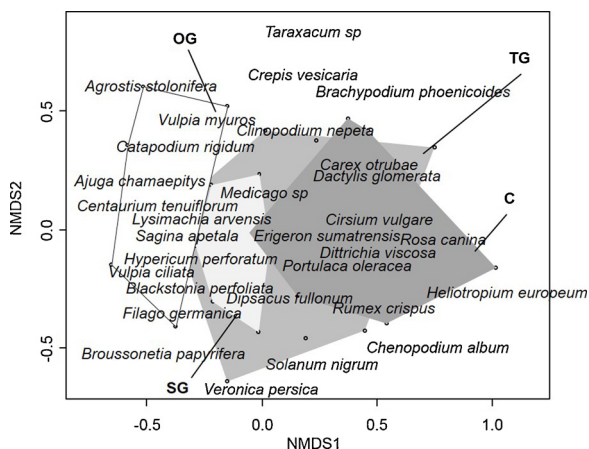


Fig. 5. NMDS ordination on seed bank data (N = 36, 90 species, NMDS stress = 0.24) collected from the study site grazed by horses. Vegetation patches studied are represented by polygons: open grasslands (OG), short grasslands (SG), tall grasslands (TG), and ungrazed control (C). For simplicity, only the plants most closely correlated with the first two axes are listed.

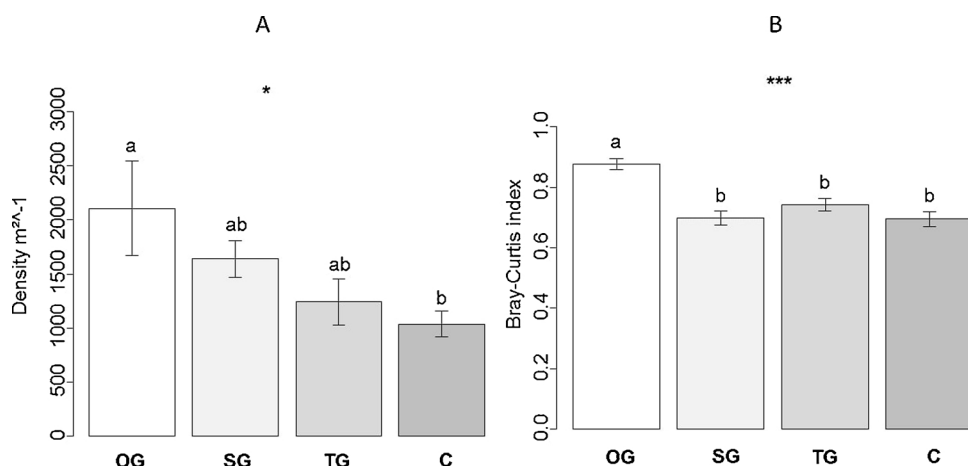


Fig. 6. A. Mean seed density and standard error per patch of vegetation (N = 9 for each patch) on the study site grazed by horses: open grasslands (OG), short grasslands (SG), tall grasslands (TG) and ungrazed control (C). Histograms with common letters do not show a significant difference among vegetation type, according to Tukey's post-hoc test. P value: * < 0.05, ** < 0.01, *** < 0.001. B. Mean and standard error of the Bray-Curtis index calculated per patch of vegetation studied (N = 9 for each patch) at the site grazed by horses: OG, SG, TG and C. Histograms with common letters do not show a significant difference among vegetation type, according to Wilcoxon's post-hoc test. P value: * < 0.05, ** < 0.01, *** < 0.001.

3. Results

3.1. Vegetation monitoring

Plant community composition

The NMDS analysis (stress NMDS = 0.17, Fig. 2A) performed on the vegetation monitored in 2018 (30 quadrats x 141 species, Appendix A) showed a clear gradient between the different patches identified on axis 1. The most heavily grazed grasslands (OG and SG) were not differentiated by species composition, both being dominated by the same annual species (*Lysimachia arvensis*, *Filago germanica*, *Crepis sancta*, *Galium parisiense*, etc.). A certain number of these species were reported as rare, including *Limonium echinoides* and *Ranunculus parviflorus*, whose only known station in the Vaucluse area is our study site (Roux, Noble, Barcelli, & Roux, 2012)

These patches differed in composition from the tall grasslands (TG) still present in the grazed areas and from the control (C) without grazing. They possessed a common pool of species, with a predominance of perennial gramineous species (*B. phoenicoides*, *Dactylis glomerata*) and of species rejected by grazing animals (*Eryngium campestre*). While the grasslands dotted with woody species (TGS) did not possess strictly correlated species, as might be expected they have species in common with the tall grasslands (*Geranium dissectum*, *Blackstonia perfoliata*, *Vicia sativa*, etc.). The shrub thickets (ST) were mainly characterised by the dominance of deciduous or semi-evergreen woody shrub species (*Rosa canina*, *Cornus sanguinea*, *Rubus ulmifolius*, etc.).

The 2014–2018 trajectories of the centroids of the polygons of the vegetation patches illustrate how plant community composition evolved under the effect of horse grazing (Fig. 2B). The grasslands exposed to the highest grazing pressure (OG and SG) showed similar trajectories. In contrast, TG, TGS, less grazed, showed trajectories close to C. ST followed a trajectory opposite to that of all the other patches.

Plant community species-richness

Five years of monitoring revealed that the species richness of OG and SG was significantly higher in 2018 than in 2014 (Fig. 3, Table 2).

Plant community height

The mean height of OG was significantly greater than those of the other patches in 2015 (F = 5.85, df = 4, p < 0.01, Fig. 4). Non-significant trends were also measured for TG regarding increased species-richness (Fig. 3), reduced mean height (Fig. 4) and differing composition compared to the tall grasslands (Fig. 2A).

3.2. Soil seed bank

A total of 3384 seeds germinated, corresponding to 90 species of which 52 were annuals (Appendix B and C). The total number of

germinated seeds and the species-richness of the above-ground vegetation showed a gradient. OG had the highest abundance of seeds (1184) and the highest above-ground vegetation species-richness (64), whereas C had the lowest seed abundance (581) and above-ground vegetation species-richness (43). This gradient was, however, not observable for seed bank species-richness, where the lowest value is recorded for the open grasslands (33) (Table 3).

In the seed bank, the most abundant species for all patches combined were: *Erigeron sumatrensis* (475 seedlings, present in 99 % of seed trays); *Dipsacus fullonum* (504 seedlings, present in 93 % of seed trays); and *Blackstonia perfoliata* (1071 seedlings, present in 92 % of seed trays).

The NMDS analysis (stress NMDS = 0.24) performed on the identified seedlings from the seed banks (Fig. 5) distinguished clearly between three patches: OG, dominated by small annual species such as *Centaurium tenuiflorum*, *Catapodium rigidum*, *Lysimachia arvensis*; SG, mainly dominated by *Dipsacus fullonum* or *Medicago sp.*, and the ungrazed control, C, dominated by perennial species such as *Dactylis glomerata*, *Rumex crispus*, *Cirsium vulgare*. TG patch was not clearly distinguished with regard to species composition, overlapping with two other patches (SG and C) according to the NMDS (Fig. 5).

Species-richness of seed banks did not differ significantly between the different patches of vegetation studied (F = 2.315, df = 3, p > 0.05). A trend can nonetheless be observed, with the OG patch having fewer species than the other patches (Table 2). The seed bank of this patch showed the highest density of seedlings (2104.88 ± 439.32 seeds/m²), significantly different from that of the control (1032.88 ± 119.97 seeds/m²; F = 3.19, df = 3, p < 0.05; Fig. 6A). The Bray-Curtis index differed between the patches (Kruskal-Wallis chi-squared = 19.41, df = 3, p < 0.001, Fig. 6B). Evenness did not differ significantly between patches, although OG had the highest heterogeneity (0.87 ± 0.01). The proportion of seedlings of *B. phoenicoides* was significantly higher in TG and also in C, not statistically different from each other types (Kruskal-Wallis chi-squared = 9.7114, df = 3, p < 0.05, Fig. 5).

The similarity between the soil seed bank and the herbaceous vegetation taken as a whole showed a clear gradient: 37 % for OG, 30 % for SG, 26 % for TG and only 17 % for C (Table 4). Thus the closing of the vegetation and its dominance by *B. phoenicoides* were correlated with a decline in the Sørensen similarity index. This pattern was observed more for annual species than for perennials.

3.3. Forage values

3.3.1. Seasonal variations in forage values between vegetation patches

Axis 1 of the different PCAs performed for each season in the different patches of grassland and for the leaves of shrub thickets

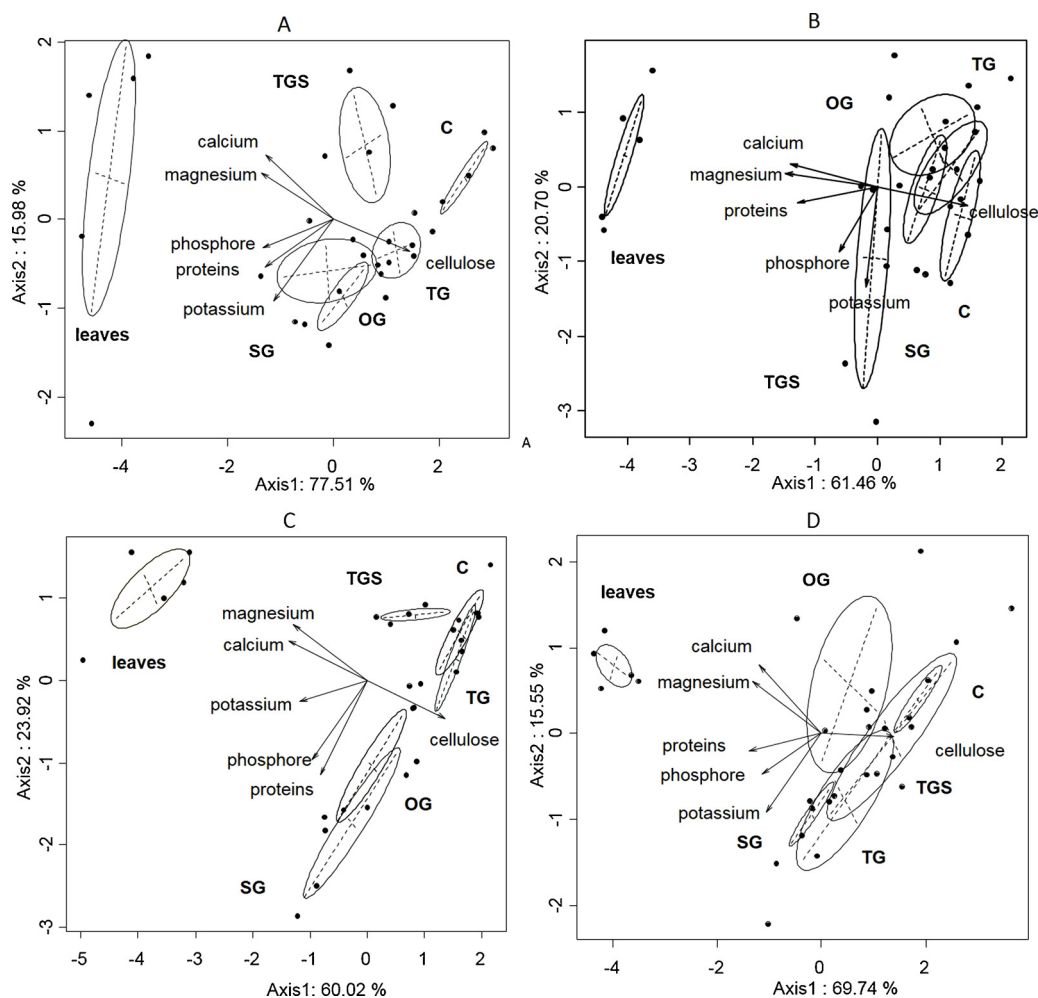


Fig. 7. Principal Component Analysis (PCA) based on 30 samples and 6 mineral value variables for the study site grazed by horses, per season studied in 2016-2017. A: Spring, B: Summer, C: Autumn, D: Winter. Open grasslands (OG), short grasslands (SG), tall grasslands (TG), tall grasslands dotted with shrubs (TGS), leaves (ST) and ungrazed control (C).

preventing the further spread of competitive grasses (Henning et al., 2017). Various examples of creation and maintenance of a heterogeneous mix of open, short and tall grasslands by horse grazing have already been reported in semi-natural areas (Cosyns et al., 2001; Duncan, 1992; Köhler et al., 2016).

Furthermore, our study showed no significant difference in species richness between the permanent seed banks of the different patches of grazed or ungrazed vegetation, confirming the findings of a previous study (Meissner & Facelli, 1999). At our site, the 10 years of grazing that led to the different patches identified in the above-ground vegetation was not long enough to significantly change their permanent seed bank. The most open patches showed the highest number of seeds and the highest heterogeneity, echoing the results obtained for the above-ground vegetation. This dissimilarity stems from the dominance of perennials with clonal multiplication in the less grazed or ungrazed vegetation, where it is unlikely that numerous seeds will persist in the soil due to low production at the surface (Marage, Rameau, & Garraud, 2006).

4.2. Application of extensive horse grazing and forage quality

Recurrent grazing maintains the quality of the forage at a high and relatively stable level by stimulating plant regrowth (Ringmark, Skarin, & Jansson, 2019; Wallis De Vries, Bakker, Bakker, & Wieren, 1998). Thus, when the forage supply is sufficient, herbivores tend to concentrate on herbaceous areas that have already been extensively grazed

(McNaughton, 1984). Our analyses showing that grazing was mainly concentrated in the most open grasslands are consistent with these findings.

The thickets consist of dicotyledons, whose leaves have been found to be richer in minerals than those of monocotyledons. This is reflected in results from our site: the thicket leaves contain high concentrations of calcium and magnesium and less cellulose than the grasslands, and show higher digestibility of organic matter (dMO), (Selmi, Ben Gara, Rekik, & Rouissi, 2011). This may be explained by the greater number of cell wall constituents in the herbaceous plants.

The tall grassland patches and the non-grazed control at our site, both dominated by perennial species, have a lower digestibility rate (Gilhaus & Hölzel, 2016) than the other patches. Consequently, the energy value (Horse Forage Unit) is higher in thicket leaves and lower in tall grasslands and control. Above all, the tall grasslands are dominated by a perennial grass (*B. phoenicoides*) and are very poor in legume species (Moinardeau et al., 2016), which also explains the lower rate of proteins recorded in the non-grazed control, since legumes are richer in proteins than grasses (Wolter, 2014). The shrub dotted grasslands are a mixture of both *B. phoenicoides* and shrubs, and their protein content thus falls between those of the control and the thicket leaves. In the other grassland patches, the higher rates measured may be explained by the presence of rosettes of biannual plants (*Centaureum erythraea*, *Picris hieracioides*, *Crepis vesicaria*) where the horses had already grazed the previous year. The quantity of potassium was lower in the tall grasslands, where *B. phoenicoides* was also negatively correlated with the

Table 5

Results of tests carried out for each forage value by vegetation patches sampled: open grasslands (OG), short grasslands (SG), tall grasslands (TG), tall grasslands dotted with shrubs (TGS), leaves and ungrazed control (C). Test results and their significance, mean value and standard deviation are given for each vegetation patch. Patches with the same letters do not show a significant difference, df = 3, P value: * < 0.05, ** < 0.01, *** < 0.001.

Vegetation	Statistics	P	Spring	Summer	Autumn	Winter
Magnesium g kg⁻¹						
OG	F = 1.44	NS	1.34 ± 0.23–	1.06 ± 0.11–	1.02 ± 0.06–	1.40 ± 0.18–
SG	F = 15.55	***	1.17 ± 0.04a	0.78 ± 0.05b	1.05 ± 0.06ab	1.31 ± 0.05c
TG	F = 1.92	NS	0.93 ± 0.10–	0.70 ± 0.05–	0.95 ± 0.07–	0.98 ± 0.12–
C	χ ² = 9.57	*	0.73 ± 0.02a	0.61 ± 0.02ab	0.96 ± 0.06a	0.84 ± 0.12b
TGS	F = 7.47	**	1.45 ± 0.11a	0.85 ± 0.10a	1.60 ± 0.20a	1.66 ± 0.07b
Leaves	χ ² = 9.57	*	3.65 ± 0.35a	3.85 ± 0.26ab	5.63 ± 0.44a	4.49 ± 0.11b
Calcium g kg⁻¹						
OG	F = 0.47	NS	8.82 ± 1.12–	9.62 ± 1.92–	10.77 ± 1.48–	7.93 ± 2.22–
SG	F = 14.94	***	7.23 ± 0.27a	6.27 ± 0.28a	10.10 ± 0.68b	6.13 ± 0.53a
TG	χ ² = 5.74	NS	6.37 ± 0.67–	5.85 ± 0.72–	7.27 ± 1.05–	4.78 ± 0.52–
C	F = 8.68	**	5.53 ± 0.24a	5.08 ± 0.43a	7.75 ± 0.83b	4.36 ± 0.19a
TGS	F = 9.36	***	11.12 ± 1.10a	5.70 ± 0.75ab	13.08 ± 1.15a	9.18 ± 1.15b
Leaves	F = 20.14	***	18.15 ± 1.46a	15.82 ± 0.69a	27.72 ± 1.52b	19.80 ± 0.59a
Potassium g kg⁻¹						
OG	χ ² = 16.65	***	14.16 ± 1.34a	4.95 ± 0.56b	5.77 ± 0.29c	10.19 ± 0.37c
SG	F = 45.52	***	14.82 ± 0.69a	6.42 ± 0.52b	6.4 ± 0.64c	10.53 ± 0.49c
TG	F = 31.37	***	12.28 ± 0.78a	5.83 ± 0.77b	4.18 ± 0.41c	9.64 ± 0.56c
C	F = 32.73	***	7.27 ± 0.76a	4.09 ± 0.28b	3.63 ± 0.42c	10.88 ± 0.72c
TGS	F = 15.08	***	9.9 ± 0.83a	5.23 ± 0.85a	4.73 ± 0.23b	11.95 ± 1.35b
Leaves	χ ² = 15.77	**	18.21 ± 2.77a	6.89 ± 0.25b	9.57 ± 2.32c	10.35 ± 0.49c
Cellulose g kg⁻¹						
OG	χ ² = 7.70	*	311.80 ± 14.13a	379.96 ± 23.34b	362.32 ± 6.78b	357.69 ± 6.89b
SG	F = 6.99	**	330.99 ± 5.67a	345.28 ± 6.85b	372.33 ± 13.48b	379.12 ± 5.69ab
TG	F = 3.22	NS	344.43 ± 8.55–	377.28 ± 19.55–	406.72 ± 17.01–	379.12 ± 5.69–
C	F = 2.45	NS	376.82 ± 4–	367.08 ± 3.49–	392.84 ± 12.05–	378.93 ± 3.23–
TGS	F = 5.09	*	312.35 ± 16.44a	393.08 ± 17.79ab	382.36 ± 19.83b	338.44 ± 19.83b
Leaves	F = 23.86	***	155.19 ± 10.22a	226.62 ± 5.41a	164.63 ± 1.58a	172.49 ± 5.97b
Phosphorus g kg⁻¹						
OG	F = 10.46	***	1.44 ± 0.13a	0.73 ± 0.05b	1.07 ± 0.11ab	0.84 ± 0.06b
SG	F = 5.79	**	1.57 ± 0.13a	0.99 ± 0.03b	1.30 ± 0.15ab	1.04 ± 0.07b
TG	F = 2.37	NS	1.26 ± 0.09–	1.06 ± 0.16–	0.79 ± .012–	1.09 ± 0.11–
C	F = 1.95	NS	0.98 ± 0.16–	0.7 ± 0.08–	0.76 ± 0.12–	1.13 ± 0.17–
TGS	χ ² = 14.46	**	1.36 ± 0.04a	0.74 ± 0.10a	0.79 ± 0.07b	1.28 ± 0.09b
Leaves	F = 35.19	***	2.28 ± 0.12a	1.25 ± 0.02b	1.19 ± 0.05b	1.31 ± 0.10b
Proteins g kg⁻¹						
OG	χ ² = 16.06	***	112.04 ± 4.72a	72.18 ± 3.90b	81.11 ± 3.93c	56.54 ± 2.61c
SG	F = 12.78	***	104.41 ± 5.43a	79.62 ± 3.81b	85.89 ± 5.22c	65.55 ± 3.16bc
TG	F = 6.11	**	85.33 ± 6.23a	67.64 ± 4.18b	58.80 ± 2.86b	61.1 ± 5.45b
C	F = 3.56	*	64.13 ± 4.02a	49.54 ± 2.06ab	55.08 ± 2.73ab	55.92 ± 3.56b
TGS	F = 4.51	*	76.21 ± 4.82a	57.66 ± 5.24ab	55.75 ± 1.66b	63.09 ± 4.68b
Leaves	F = 23.01	***	141.07 ± 11.02a	98.44 ± 3.18bc	73.8 ± 0.87b	89.65 ± 3.37c
Digestibility						
OG	F = 16.46	***	61.02 ± 1.81a	52.6 ± 0.81b	53.28 ± 0.69b	51 ± 0.62b
SG	χ ² = 15.07	***	58.48 ± 0.72a	54.20 ± 0.80b	53.74 ± 0.79c	50.76 ± 0.31c
TG	χ ² = 7.41	*	54.88 ± 1.39a	52 ± 1.14ab	50.46 ± 0.06b	50.78 ± 0.45ab
C	χ ² = 13.02	**	51.22 ± 0.41a	50a	50.40 ± 0.03a	50.46 ± 0.11b
TGS	χ ² = 12.53	**	57.90 ± 2.09a	50.40 ± 0.40ab	51.72 ± 0.81bc	53.16 ± 1.13c
Leaves	χ ² = 18.48	***	72.20 ± 1.01a	69b	78.30c	68.54 ± 0.02d
HFU						
OG	F = 14.61	***	0.64 ± 0.02a	0.53 ± 0.01b	0.53 ± 0.01b	0.51 ± 0.008b
SG	F = 19.61	***	0.61 ± 0.008a	0.55 ± 0.009b	0.54 ± 0.01b	0.51 ± 0.004b
TG	F = 5.62	**	0.52 ± 0.006a	0.53 ± 0.01b	0.50 ± 0.007b	0.51 ± 0.006b
C	χ ² = 14.64	**	0.52 ± 0.006a	0.51a	0.48 ± 0.004b	0.51 ± 0.002a
TGS	F = 5.98	**	0.6 ± 0.02a	0.51 ± 0.003b	0.53 ± 0.01b	0.54 ± 0.01b
Leaves	χ ² = 17.91	***	0.77 ± 0.01a	0.73b	0.82 ± 0.005c	0.73d

presence of calcium and magnesium, confirming the low concentrations of these ions in the patches rich in perennial grasses (control and tall grasslands). The phosphorus content of grasses decreases rapidly during their cycle, while that of the legume species decreases more slowly. On this embankment, a strong pattern of seasonal variation was observed, in particular for digestibility, which was distinctly higher in spring.

With the approach of winter, and the stress associated with the cold and the reduced solar irradiance, the grass growth rate declines and the senescence of the above-ground biomass increases (Wallis De Vries et al., 1998). The herbivores are then confronted with a depletion of good quality forage and must rely on forage of poorer quality or turn to other resources, such as the leaves of thickets, all semi-deciduous

	HFU	Mg	Ca	P	protein	K	richness	annuals	<i>B. phoenicoides</i>	cellulose
dmo	1	0.91	0.85	0.71	0.86	0.68	0.78	0.78	0.78	-0.95
HFU		1	0.85	0.7	0.87	0.69	0.78	0.78	0.78	-0.95
			1	0.64	0.7	0.52	0.63	0.76	-0.36	-0.92
				1	0.53	0.61	0.41	0.41	-0.41	-0.9
					1	0.66	0.66	0.66	-0.63	-0.69
						1	0.87	0.87	-0.74	-0.74
							1	0.4	0.4	-0.57
								1	0.86	-0.68
									1	0.64
										1

Fig. 8. Matrix of correlations between measured values (Mg, Ca, P, proteins, K, cellulose, digestibility), species richness, the presence of *Brachypodium phoenicoides* and annual species in the vegetation surveys conducted in the spring of 2017 on the study site. Correlation coefficients are shown as percentages. Non-significant correlations are crossed out.

shrubs. Our results highlight the importance of shrubs in providing winter food for the herd (Dutoit and Alard, 1997) and in diversifying its bolus during this season. Thus, the persistence of the full mosaic of patches identified would appear to guarantee the animals a balanced diet throughout the year.

4.3. Implications for management of the vegetation of the embankment

Between 2014 and 2018, the extensive horse grazing applied at our study site had a mainly positive impact on the most open grassland patches. This positive impact included an increase in the species-richness and the heterogeneity of the surface vegetation and a greater number of viable seeds in the seed bank. The reduction in the mean height of the vegetation via the reduction in *B. phoenicoides* cover also boosted forage value due to the appearance of annual species considered as good forage (*Trifolium* spp., *Vicia* spp.). However, our results indicate the need to maintain the diversity of these patches of vegetation so as to ensure a balanced diet for the horses year-round.

In contrast, little or no impact from grazing was found on the tall grasslands and the shrub thickets, where only the leaves are consumed (no debarking). This rate of consumption was thus insufficient to have a significant impact on shrub encroachment on our site (Rotherham, 2013). It has already been demonstrated that alternating park grazing systems might increase the animals' impact on the vegetation and the sustainability of grasslands, subject to good management with optimum control of the herd according to the objectives targeted (Manning et al., 2017). While the traditional approaches used have produced results at local level, it is difficult to extend this to large-scale geographical areas (Duro, Coops, Wulder, & Han, 2007). At our study site, grazing pressure seems to be slightly increased. Combining several herbivorous species could also be attempted, given the potential of different breeds to exploit heterogeneous environments (Edwards & Hollis, 1982; Henning et al., 2017). Goats for example, which consume woody plant species, could be mixed with a herd of horses to reduce the surface area of shrub dotted patches and thickets, poor in species, thus ensuring greater availability of light within the plant communities (Kotowski & van Diggelen, 2004; Moinardeau et al., 2019). Mixed grazing using

ruminant and non-ruminant species such as cattle, horses, sheep or donkeys is known to be an appropriate management tool (Süss & Schwabe, 2007; Henning et al., 2017).

Declaration of Competing Interest

The authors declare they have no conflict of interest.

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