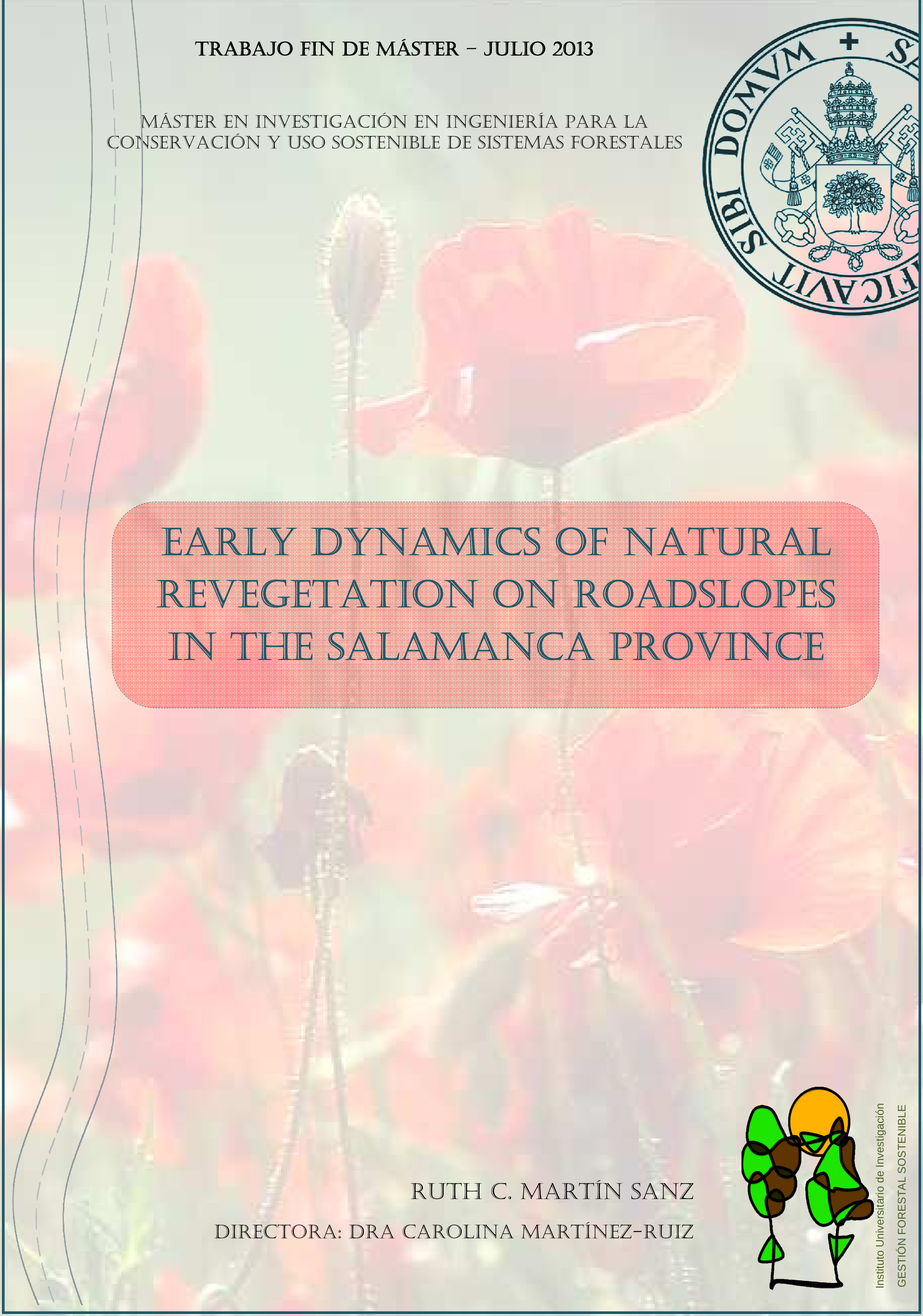

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MÁSTER EN INVESTIGACIÓN EN INGENIERÍA PARA LA
CONSERVACIÓN Y USO SOSTENIBLE DE SISTEMAS FORESTALES

EARLY DYNAMICS OF NATURAL REVEGETATION ON ROADSLOPES IN THE SALAMANCA PROVINCE

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Julio, 2013

Science is not only a discipline of reason but, also, one of romance and passion.

(Stephen Hawking)

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ÍNDICE

0.- ABSTRACT

The increasing global rate of road construction is leading to a parallel increase of environmental degradation, which is causing the increase of our environmental awareness, and thus the need to restore affected areas is increasingly important. Revegetation of road slopes has an undeniable interest both from a landscape point of view as from soil protection and erosion control, but this interest collides with the lack of information on spontaneous colonization and subsequent dynamics of vegetation in them. Natural revegetation studies over time allow us to classify species according to the successional stage in which gain importance and to select the most suitable species for revegetation of a particular area. In this context, this study, based on the hypothesis that successful spontaneous colonizers are the most suitable species for revegetation of these degraded areas, try to analyze and improve our understanding of the factors that control the natural processes of colonization, establishment and early dynamics of vegetation on semiarid Mediterranean road slopes in the province of Salamanca (Spain). We selected 52 road slopes varying in time since construction (≤ 1 year to 10 years) on the three dominant lithologies (tertiary sediments, slates and granites) and on two aspects (north/south). Environmental factors were monitored and related to species cover using a combination of multivariate analysis and Huisman-Olff-Fresco modeling. We found that most represented taxa were Poaceae, Asteraceae and Fabaceae both in species richness and cover, and also prevailed therophytes. Lithologie, surrounding vegetation and proximity between slopes had a great effect on the floristic composition of plant communities during succession. The age influence was not equally evident on all lithologies, as the steepness, and height and type of slope, only significant when lithologie is considered separately, and no influential on granites, where succession was slower. There was a tendency for taxonomical group, life-form and dispersal-mode replacement during early succession, although anemochorous therophytes continue to be the most common species. Our results indicate that in a relatively short time, vegetation communities spontaneously installed on road slopes are rich in species.

KEYWORDS: ecological restoration, road slopes, Mediterranean environment, species composition, natural plant colonization, vegetation dynamics.

0.- RESUMEN

La tendencia creciente de construcción de carreteras a nivel global está dando lugar a un aumento paralelo de la degradación del medio ambiente, que está potenciando además la conciencia medioambiental de la sociedad y, por lo tanto, la necesidad de recuperar las zonas afectadas es cada vez más importante. La revegetación de taludes de carreteras tiene un indudable interés tanto desde un punto de vista paisajístico como de protección del suelo y el control de la erosión, pero este interés choca con la falta de información sobre la colonización natural y la posterior dinámica de la vegetación en ellos. Los estudios de sucesión vegetal en taludes de carreteras permiten clasificar las especies de acuerdo a la etapa de sucesión en la que ganan importancia y seleccionar las más adecuadas para revegetar un área en particular. En este contexto, el presente estudio, basado en la hipótesis de que las especies autóctonas colonizadoras son las más adecuadas para la revegetación de estas áreas degradadas, trata de analizar y mejorar nuestra comprensión de los factores que controlan los procesos naturales de colonización, establecimiento y dinámica de la vegetación en taludes de carreteras de clima mediterráneo semiárido en la provincia de Salamanca (España). Para ello, se seleccionaron 52 taludes con diferente edad desde su construcción (≤ 1 año a 10 años) en las tres litologías dominantes (sedimentos terciarios, pizarras y granitos) y en dos orientaciones (norte/sur). Los factores ambientales fueron analizados y referidos a la cobertura de las especies usando una combinación de análisis multivariantes y modelización de Huisman-Olff-Fresco. Encontramos que los taxones más representados fueron *Poaceae*, *Asteraceae* y *Fabaceae* tanto en riqueza como en cobertura, y también prevalecieron los terófitos. La litología, la vegetación circundante y la proximidad entre los taludes tuvieron un gran efecto en la composición florística de las comunidades vegetales durante la sucesión. La influencia de la edad no fue igualmente evidente en todas las litologías, como la inclinación y la altura y el tipo de talud, sólo significativos cuando las litologías se consideraron por separado; no se encontró influencia en granitos, donde la sucesión es más lenta. Obtuvimos una tendencia de sustitución para el grupo taxonómico, la forma de vida y el modo de dispersión durante la sucesión temprana, aunque las terófitas anemócoras siguieron siendo las especies más comunes. Nuestros resultados indican que, en un tiempo relativamente corto, las comunidades de vegetación espontánea instaladas en taludes de carreteras son ricas en especies.

PALABRAS CLAVE: restauración ecológica, taludes de carreteras, ambiente mediterráneo, composición de especies, colonización natural, dinámica de la vegetación.

1. INTRODUCTION

In view of the remarkable increase of linear transport infrastructure construction (Nicodème *et al.*, 2012; European Union, 2012) and the resulting environmental degradation (Garañeda *et al.*, 2002; Balaguer *et al.*, 2012), our society has increased its environmental awareness and the need to restore affected areas has become more important (Cortina *et al.*, 2004; Balaguer *et al.*, 2012). In this sense, we should look for solutions that response the specific needs of the site, not only in terms of the type of construction and slope, but also the climate, topography, environmental sensitivity and social requirements that will achieve the restoration of degraded ecosystems and the sustainable development of the area (PNUMA, 2001).

Due to this growing environment aware, to counteract land degradation and stabilize road slopes, restoration projects are frequently under-taken by construction companies and governments to minimize its environmental impact (Rivera, 2012). The main objectives of these projects are the establishment of vegetation to reduce erosion problems and landscape impacts (Andrés and Jorba, 2000; Montoro *et al*., 2000) and to assist in the conservation of biodiversity (Bote *et al.,* 2005), as well as a practical purpose since the effective stabilization of the slopes can avoid negative effects on traffic (Martinez-Ruiz *et al*., 2003; Balaguer *et al.*, 2012). In addition to the environmental challenge of the restoration of disturbed areas, their success may be accompanied by economic benefits for the companies operating those infrastructures (García-Fayos *et al*., 2000; Matesanz *et al*., 2006), which has raised the interest of both the scientific as the business world to study the factors influencing the restoration of these areas (Andrés and Jorba, 2000; Montalvo *et al*., 2002; Bochet and García-Fayos, 2004; Matesanz *et al*., 2006; Tormo *et al*., 2007; Bochet *et al*., 2010).

Although road slopes can be stabilized in part by physical means, these techniques are expensive and often short-lived. Thus, in restoration projects, the alternative is to cover roadside slopes with vegetation (Bochet *et al*., 2010), which is a long-term target. However, no clear criteria appear in relation to the characteristics of the plant communities to be favoured in the slopes (Matesanz *et al*., 2006) and our knowledge of its ecology and dynamics is quite scarce (Schaffers and Sykora, 2002).

The measures commonly referred to regenerate degraded ecosystems have been the application of hydroseeding (Bote *et al.,* 2005; Matesanz *et al*., 2006; Mola *et al*., 2011), plantations (Holl, 2002), arrangement of geotextiles meshes (Mitchell et al., 2003; Rickson, 2006) and spreading topsoil (Bote *et al*., 2005; Tormo *et al*., 2007; Bochet *et al*., 2010; Rivera, 2012). However, the effectiveness of these alternatives has been seriously debated by the scientific community, especially in Mediterranean environments with high water stress.

Regarding hydroseeding for example, it has been the most widespread method used for road slope revegetation in the past few decades (Enríquez de Salamanca *et al*., 2004).

However, in the most part of Spain (except the Atlantic area with a wetter climate), standard hydroseeding frequently renders poor results and the performance of standard commercial hydroseeded species (mixture of species used in northern countries and Eastern Europe) is usually poor from the very beginning (Andrés and Jorba, 2000; Martínez-Ruiz*,* 2000), besides the use of such commercial species is inadequate in many occasions causing suppression of autochthonous species. Furthermore, it has been recently demonstrate that there are situations in which the use of hydroseeding for revegetation is not needed (Matesanz *et al.,* 2006; Martínez-Ruiz *et al.*, 2007) and that any action which favours spontaneous processes of colonization, regeneration and succession will lead to more sustainable long term ecosystems (Martínez-Ruiz and Marrs 2007; Bochet *et al*., 2011). In these cases the arrival of propagules from the resources of the surrounding matrix and the ability of different species to establish in disturbed environments would be the critical factors for successful restoration (Alborch *et al*., 2003), although in this sense few progress have been made yet. Thus, the interest of road slopes revegetation often collides with the lack of information on spontaneous colonization and subsequent dynamics of vegetation in them (Martínez-Ruiz *et al*., 1996; Garañeda, 2001; Garañeda *et al.,* 2002). In other areas, such as mining, the study of these processes is providing valuable information on ecological principles involved and most important native species in these processes (Martínez-Ruiz *et al*., 2001; Martínez-Ruiz *et al*., 2005; Martínez-Ruiz and Marrs, 2007). Successional studies on disturbed sites are an excellent tool for identifying appropriate plant species to each situation-age. That is, the natural revegetation studies over time allow us to classify species according to successional stage in which gain importance and ultimately, allow us to select the most suitable species for revegetation of a particular area (Martínez-Ruiz, 2000; Martínez-Ruiz *et al.*, 2001).

Therefore, within this framework and taking into account that few studies have been made on natural plant succession of road slopes in Mediterranean ecosystems, arises this study, based on the hypothesis that successful spontaneous colonizers are the most suitable species for revegetation of these degraded areas. Our general objective is to analyze and improve our understanding of the factors that control the natural processes of colonization, establishment and early successional dynamics of vegetation on semiarid Mediterranean road slopes. The specific aims of this study are: (1) to describe and compare plant communities of different road slopes according to their age and lithological material on which they are placed (tertiary sediments, slates and granites); (2) to analyze the influence of the environmental variables considered on plant species composition and successional dynamics; (3) to model the response of individual species through time searching for general patterns by considering species traits; and (4) to establish recommendations on more suitable autochthonous species according to their colonization ability in these degraded sites, which might be used in future restoration projects.

2.- MATERIAL AND METHODS

2.1.- Site selection, description and sampling

The study was conducted into the Salamanca province, ‘Castilla y León’, central-western Spain (800 m a.s.l.; lat 40º10’−41º25’N, long 1º24’−3º6’W; Figure 1). The climate is mostly semi-arid Mediterranean with a mean annual rainfall of 400-650 mm, and acute summer drought during two-three months, between June and September, when there is no risk of frost (Martínez-Ruiz *et al.*, 2003); the mean annual temperature is ca. 12 ºC. The soils are mainly slightly acidic sandy-loam (pH 5.5−6.7) overlying granite or slate bedrock, or Tertiary sediments (MAPA, 1984). The most widespread soils, classified by the WRB-FAO, are dystric or eutric Cambisols and Regosols on slates and granites (initial stages of development and low potential for agriculture, but good for pasture), and haplic Luvisols and eutric Cambisols on sediments, which are generally of good quality and work well for certain crops (Dorronsoro, 1992).

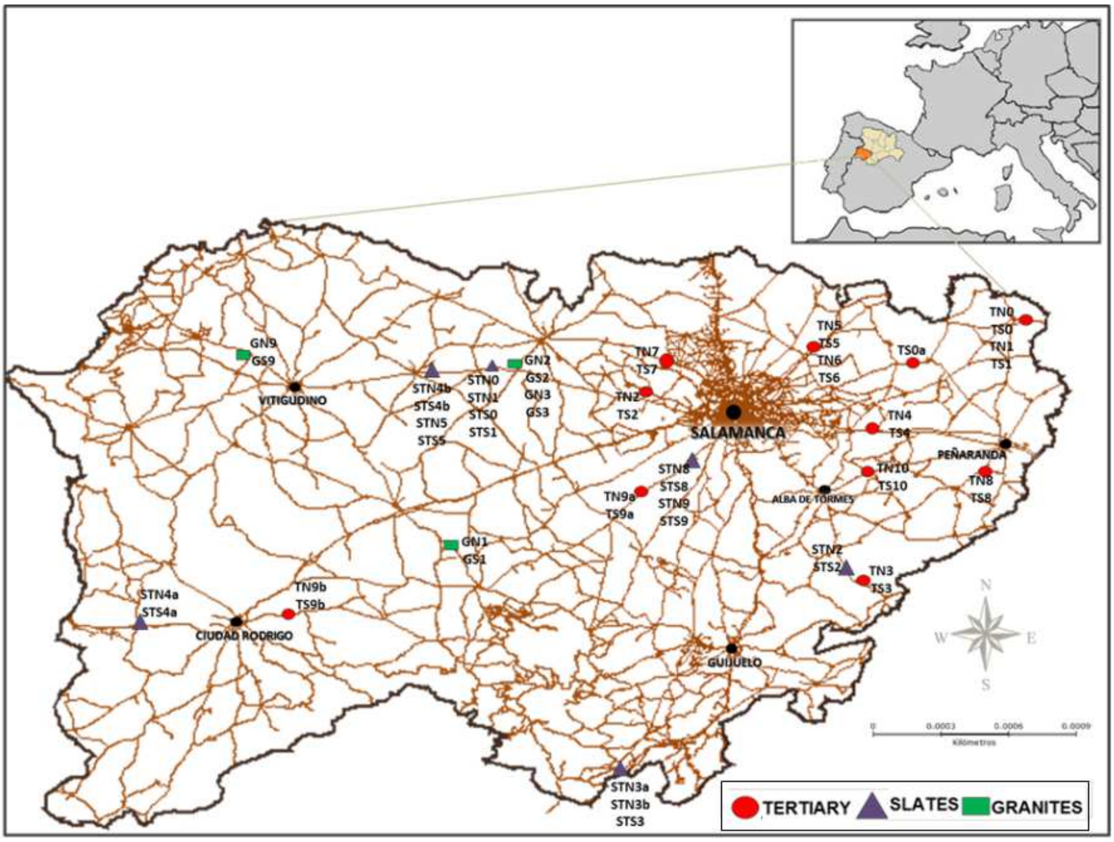

Figure 1. Location of the 52 road slopes selected for study in the province of Salamanca. Red circles (25), purple triangles (19) and green squares (8) refer to slopes on tertiary, slates and granites, respectively. Slopes identified by lithologie (T, tertiary sediments; ST, slates; G, granites), aspect (N, north; S, south) and age (years after construction).

In 1995, 52 road slopes, mostly cutslopes (92%), varying in time since construction, from the most recent (in 1995 ≤ 1 year) to the oldest (10 years), on the three dominant lithologies (sedimentary rocks, slates and granites) and on two aspects (north/south) were selected to provided six chronosequences (Figure 1). Any restoration method was used at the road slopes selected for study. Most slopes were located in areas suitable for tree growth, according to the Aridity Index of De Martonne, and within the Lower Dry Supra-Mediterranean holm-oak domain according to the Thermicity Index of Rivas-Martínez (Martínez-Ruiz *et al.*, 2003).

Within each of the 52 road slopes, eight 0.25-m^2 quadrats were located randomly across the whole of each site (100-200 m^2); a total of 416 quadrats were sampled. The sample size (n=8) was tested in pilot studies using the 'pooled quadrat' method (Pielou, 1969) to encompass at least 90% of all species (Martínez-Ruiz *et al.*, 2007). The cover (%) of all species present in each quadrat was estimated visually in early June, and because of overlapping vegetation strata, cover values frequently exceeded 100%. A total of 237 species (67% annuals/biennials, 27% perennial herbs, 6% woody) from 38 families were found and species nomenclature follows Tutin *et al.* (1964–1980).

In addition, a range of landscape variables were characterized for each road slope: type of slope (embankment or cutslope), steepness (º), slope height (with three levels: high, medium, low), proximity (differentiating two areas from the Salamanca city: eastern and western) and surrounding vegetation (woody, crops and pastures, no vegetation).

2.2.- Data analysis

DCA (Detrended Correspondence Analysis) was used to obtain estimates of gradient lengths in standard deviation (SD) units of species turnover, thereby assisting in the decision of whether to use a linear or unimodal approach to the data (Becker *et al.,* 1988; ter Braak and Šmilauer, 2002).

The influence of constrained explanatory variables in this study on vegetation was then assessed, within the whole data set and for each lithologie according with results of preliminary DCA, using a forward selection procedure in CCA (Canonical Correspondence Analysis). Forward selection was used to select significant variables, the Monte Carlo test being used to assess significance, with 499 permutations for exploratory analyses and 9999 for final results (Legendre and Legendre, 1998). In all permutation tests, an unrestricted permutation structure was used. This process was combined with an examination of inflation values, to remove those variables that were highly multicollinear. In the case of granites, due to the low number of road slopes available (n=8), the number of explanatory variables to be included in the CCA forward selection procedure had to be reduced to n-1 (ter Braak and Šmilauer, 2002). For this, sample ordination scores in DCA were previously tested for a significant correlation with the explanatory variables by means of Spearman correlation coefficient, and only those significant were considered for further analyses.

The response of individual species through time was then examined, for each lithology in which age was significant (tertiary sediment and slates), using Huisman-Olff-Fresco (HOF) models (Huisman *et al.*, 1993). These are a hierarchical set of five response models, ranked by their increasing complexity (Model I, no species trend; Model II, increasing or decreasing trend; Model III, increasing or decreasing trend below maximum attainable response; Model IV, symmetrical response curve; Model V, skewed response curve: Huisman *et al*., 1993). HOF models are a means of describing species responses, which may result from both environmental conditions and intra- and inter-specific interactions (Lawesson and Oksanen, 2002). The AIC statistics (Akaike, 1973) was used to select the most appropriate response model for each species (Burnham and Anderson, 2002; Johnson and Omland, 2004). HOF response curves were computed for 39 and 24 species, respectively, on the slopes on tertiary sediments and slates to illustrate the broad trends of compositional change. Finally, the location of optima (μ) and niche widths (2*t*) for those species with unimodal responses were derived from the HOF models. The 2*t* values were found by solving for the gradient points of the fitted HOF model relative to a strict Gaussian model at 2*t* (Lawesson and Oksanen, 2002). In the case of a symmetric unimodal response, the lower and upper *t* values are identical, while with a skewed model, the 2*t* intervals are not necessarily equal.

Ordination analyses were carried out using the CANOCO 4.5 (ter Braak and Šmilauer, 2002), with standard options and no down weighting of rare species. HOF models were carried out using the GRAVY package (Oksanen and Minchin, 2002; Oksanen, 2004) implemented in the R software environment (version 2.4.1; R Development Core Team, 2006). Correlation analyses were carried out using STATISTICA software v. 6.

3.- RESULTS

3.1.- Initial data exploration

DCA performed on the complete data set produced an ordination with a first axis gradient length of 4.219 SD units, which together with the high number of zeros in the species data suggested that the unimodal CCA model was appropriate to describe the relationship between species and environmental variables (ter Braak & Šmilauer, 2002). The eigenvalues (λ) for the first four DCA axes were 0.507, 0.306, 0.243 and 0.177, respectively. Slopes on tertiary sediments and slates, located in the eastern of the Salamanca province, cluster together in the left lower area of the diagram, whereas slopes on granites (all located in the western of the Salamanca province), together with some slopes on slates and tertiary sediments also in that part of the province, cluster on the upper right area (Figure 2a).

This suggests a gradient strongly associated with lithologie (tertiary sediments, slates and granites) influencing species composition of plant communities, although modified by the proximity between slopes (from eastern or western of the Salamanca province) and, also, by the effect of other explanatory variables such as CCA shows below. Indeed, 20, 14 and 3% of the whole species are exclusive of slopes on tertiary sediments, slates and granites, respectively, and only 31% of the whole species are common to the three lithologies, sharing the higher percentage of common species the slopes on slates and tertiary sediments (58%), in contrast to the 33 and 35% of common species between granites and tertiary sediments, and between granites and slates, respectively.

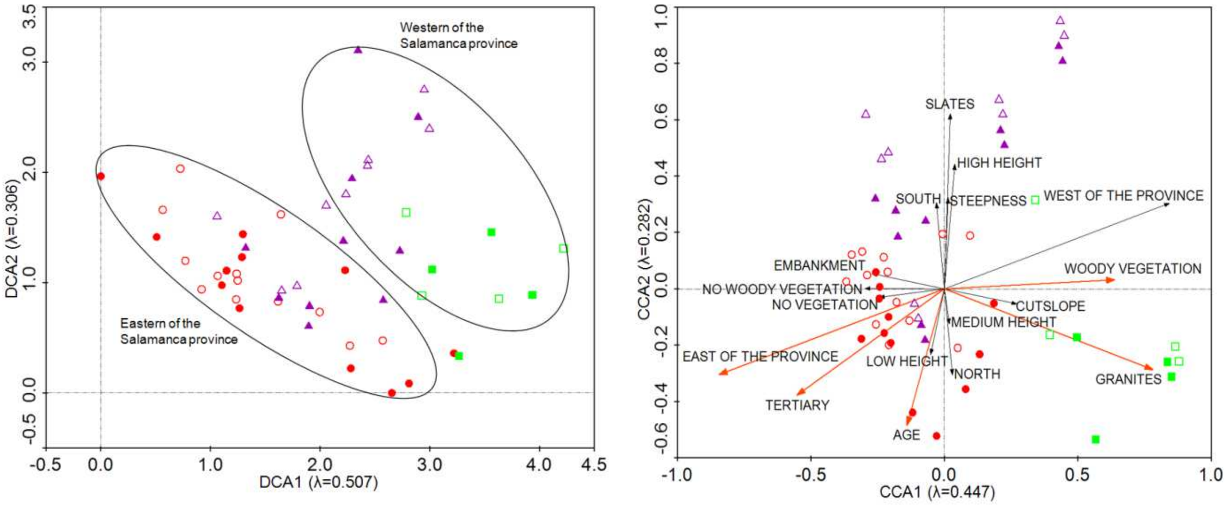

Figure 2. (a) DCA ordination of 52 road slopes selected for study. **(b)** CCA biplot with explanatory variables and slopes; vectors in orange colour correspond to significant environmental variables (*p*<0.05). Red circles (25), purple triangles (19) and green squares (8) refer to slopes on tertiary, slates and granites, respectively; full and empty symbols refer to north and south aspect, respectively.

The CCA forward selection procedure identified the proximity between slopes, lithologie, age and surrounding vegetation as the more influential factors on vegetation dynamics in road slopes of the Salamanca province (Table 1; Figure 2b). The first three axes of the CCA explained 47.4 % of the variation. The eigenvalues for the first three CCA axes were 0.447, 0.282 and 0.244, respectively, and the model was significant according to the Monte Carlo test, with 9999 permutations, for both the first axis (F=2.731, *p*=0.0001) and all canonical axes (F=1.511, *p*=0.0001). Axis 1 reflected a clear gradient of proximity between slopes (those located in the eastern of the Salamanca province on the left half of the diagram and those located in the western part on the right half), closely linked with lithologie (slopes on granites and tertiary sediments on the positive and negative end of CCA1, respectively, and those on slates in the middle) and type of surrounding vegetation (slopes with woody vegetation in their vicinity on the positive end of CCA1). The age is correlated with CCA3, not showed in Figure 2b, and, therefore, the age gradient will probably be distinguishable only within some lithologie. Axis 2 seems to be correlated with aspect and height of slopes, if we consider $p<0.1$ (Table 1), which probably will be explanatory variables within some particular lithologie, as the high height of slopes on slates (Figure 3b).

Table 1. Order and significance of the 12 explanatory variables included in the model, once collinear variables were excluded, responsible for the differences in floristic composition between slopes, after the CCA forward selection procedure. ** $p<0.01$; * $p<0.05$; • $p<0.1$; n.s. Not significant.

Variable	F-	*p*	Variance explained (%)
ESTERN PART	2.84	0.002 **	38
GRANITES	1.94	0.002 **	25
AGE	1.86	0.002 **	24
WOODY VEGETATION	1.40	0.030 *	17
WESTERN PART	1.39	0.066 •	18
TERTIARY SEDIMENTS	1.29	0.038 *	16
CUTSLOPE	1.27	0.146 n.s.	16
LOW HEIGHT	1.27	0.052 •	15
NORTH ASPECT	1.22	0.068 •	15
HIGH HEIGHT	1.18	0.146 n.s.	15
NO WOODY VEGETATION	1.03	0.382 n.s.	12
STEEPNESS	0.86	0.738 n.s.	11

These results suggest, as expected, that site conditions (proximity between road slopes, lithologie and surrounding vegetation) influence the floristic composition of plant communities during succession and may have a stronger effect than age itself. In particular the separation of the slopes in three groups along DCA1 and CCA1 (Figure 2) justified analysing these three data subsets separately to asses the effect of site conditions on vegetation composition. Gradient lengths of the first axis from DCA for the tertiary sediments, slates and granites were 3.77, 3.65 and 2.39, respectively. This fact, together with the high β-diversity demonstrated elsewhere by the high spatial heterogeneity registered in the road slopes (Martínez-Ruiz *et al.*, 2003) suggest that the unimodal model was acceptable for analyses on the data subsets.

3.2.- Assessing effects of site conditions within each lithologie.

The CCA forward selection procedure applied to the slopes on tertiary sediments identified the age (F=1.81, $p=0.002$, 36% of variance explained) as the main influential factor on vegetation dynamics followed by steepness (F=1.43, $p=0.016$, 28% of variance explained). The two first axes of the CCA explained 41.3% of the variation (Figure 3a). The eigenvalues for these axes were 0.414 and 0.324, respectively, and the model was significant according to the Monte Carlo test, with 9999 permutations for both the first axis (F=1.46, $p=0.0320$) and the all canonical axes (F=1.13 $p=0.0483$). Axis 1 reflected an age gradient (Figure 3a); from the younger slopes in the upper left hand area of the diagram (with species characteristics as *Chenopodium album*, *Hordeum murinum*, *Lupinus hispanicus*, *Polygonum aviculare*, *Spergularia rubra* or *Senecio gallicus*), to the oldest slopes characterized by later colonisers such as *Aphanes cornucopioides*, *Centaurea melitensis*, *Herniaria glabra*, *Lotus subbiflorus*, *Plantago holosteum*, *Thymus zygis* or *Trifolium cherleri* in the lower right hand area. There is also an orthogonal gradient associated with steepness, which is more evident for the medium-age slopes (5-7 years old); steepness increasing to the lower left area of the diagram with the presence of species such as *Lophocloa cristata, Scirpus holoschoenus, Silena vulgaris* and *Stellaria media*.

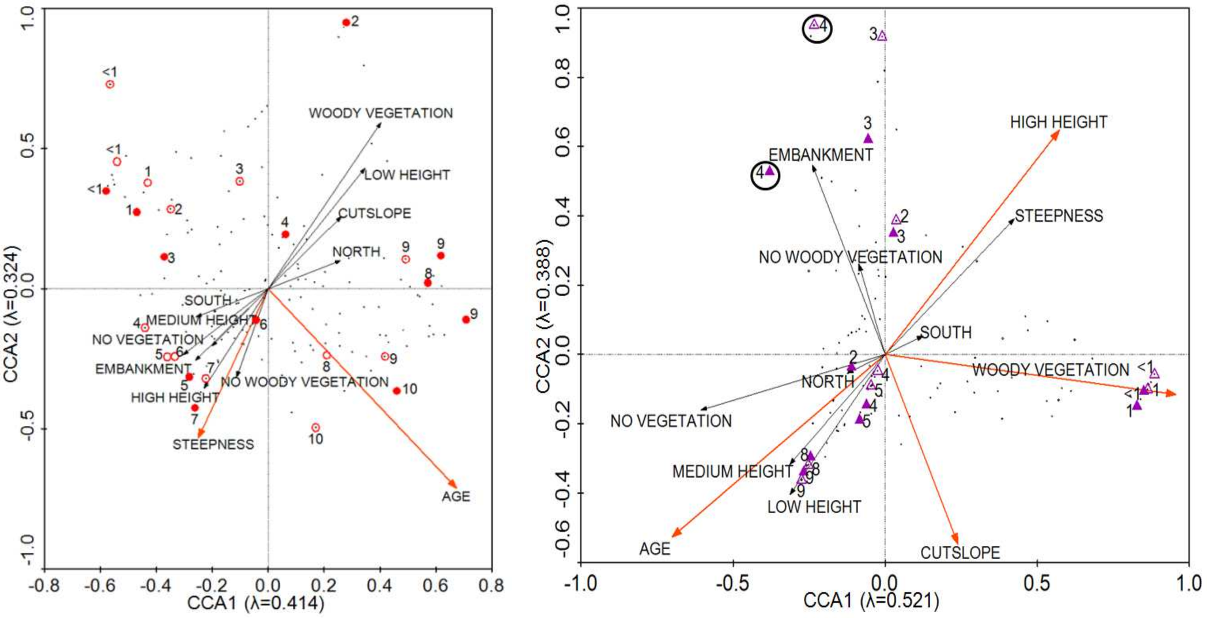

Figure 3. CCA biplots for slopes on tertiary sediments **(a)** and slates **(b)**, with explanatory variables (vectors in orange colour correspond to significant ones, *p*<0.05), slopes indicating their age and species pool (small dots). Symbols of the road slopes as in Figure 2.

The CCA forward selection procedure applied to the slopes on slates identified, in this order, surrounding vegetation (F=2.38, *p*=0.002, 50% of variance explained), slope height (F=1.76, *p*=0.002, 35% of variance explained), type of slope (F=1.52, *p*=0.008, 30% of variance explained) and age (F=1.51, *p*=0.004, 28% of variance explained) as the main influential factors on vegetation dynamics. The first two axes of the CCA explained 40.1% of the variation (Figure 3b). The eigenvalues for these axes were 0.521 and 0.388, respectively, and the model was significant according to the Monte Carlo test, with 9999 permutations for both the first axis (F=1.46, *p*=0.0002) and the all canonical axes (F=1.57, *p*=0.0001). The first axis of the CCA showed a strong positive correlation with the type of vegetation surrounding the road slopes, being the most influential the woody vegetation of ‘Dehesa’ formations and pine woodlands surrounding youngest slopes (≤1 year), with some characteristic woody species such as *Cytisus multiflorus*, *C. scoparius*, *Dorycnium pentaphyllum* and *Rosmarinus officinalis*, and herbaceus species such as *Erodium cicutarium*, *Holcus setiglumis*, *Leontodon taraxacoides*, *Lepidium heterophyllum*, *Silene scrabiflora*, *Senecio lividus* or *Xolantha guttata*. CCA1 was also negatively correlated with age, being oldest road slopes located in the lower left area of the diagram and characterized by species such as *Elymus repens*, *Cirsium arvense*, *Lotus corniculatus*, *Moenchia erecta*, *Muscari comosum*, *Plantago holosteum*, *Reseda luteola*, *Scabiosa atropurpurea* or *Thymus zygis*. The second axis of the CCA was positively correlated with high altitude of the slopes, being also the highest slopes the steepest and youngest ones (characteristic species: *Aira caryophyllea*, *Holcus lanatus*, *Jasione montana*), and with the type of road slope, all of them cutslopes except for those marked with a circle in Figure 3b, which were embankments with particular species such as *Marrubium vulgare*, *Papaver rhoeas* and *Silene vulgaris*.

The CCA forward selection procedure applied to the slopes on granites identified the surrounding vegetation (F=1.77, *p*=0.012, 37% of variance explained) as the only influential factor on vegetation dynamics. The first two axes of the CCA explained 61% of the variation (Figure 4). The eigenvalues for these axes were 0.376 and 0.253, respectively, and the model was significant according to the Monte Carlo test, with 9999 permutations (F=1.35, *p*=0.0108; for all canonical axes). Axis 1 showed a strong positive correlation with the type of vegetation surrounding the road slopes, from those surrounded by woody vegetation on the right with *Aira caryophyllea*, *Anthemis arvensis*, *Campanula lusitanica*, *Eryngium tenue*, *Erodium cicutarium*, *Leucanthemopsis pulverulenta*, *Quercus ilex* subsp. *ballota* or *Thymus zygis* as more abundant species.

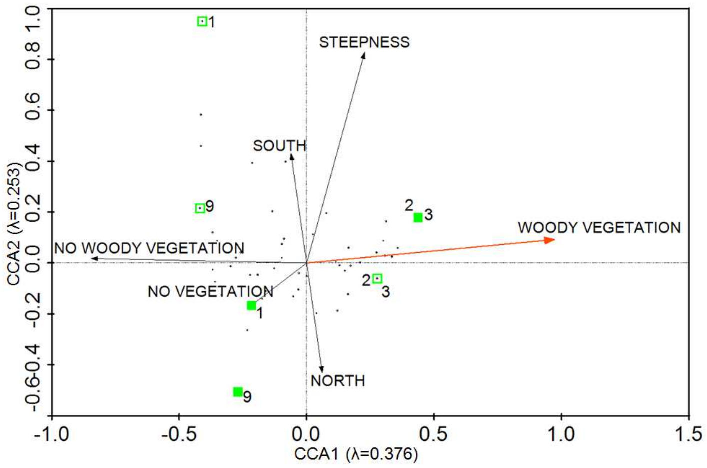

Figure 4. CCA biplot for slopes on granites, with explanatory variables (vector in orange colour correspond to significant one, $p<0.05$), slopes indicating their age and species pool (small dots). Symbols of the road slopes as in Figure 2.

3.3.- Assessing compositional change through time.

Responses of individual species are detailed in Appendix 1. The temporal responses of species on the road slopes on tertiary sediments (Figure 5) separated the species into three groups. Group 1 (HOF model I) included eight species, most of them with a short life-span (annuals) and anemochorous dispersion, being *Poaceae* the best represented family. Their cover ranged from 1 to 2.5%, except for *Bromus hordeaceus* and *Petrorhagia nanteuilli* with cover <1% and for *Vulpia myuros* with ca. 5% cover. These species showed no response to age and are not shown on Figure 5. Group 2 (HOF model II, decreasing trend, and HOF model IV with optima below the age of 5 years; Table 2) contained mainly species of the family *Asteraceae*, annuals and anemochorous; these species had greatest cover in the youngest materials with a subsequent reduction with age. In group 3 (HOF model II, increasing trend, and HOF model IV with optima above the age of 5 years) gained importance grasses and legumes. Perennial herbs, mostly hemicryptophytes, dominated in this group, which also included one woody species (Onr). Although anemochory was still significant, dispersion through animals increased with transition from ectozoochory towards endozoochory along the temporal gradient. These species reached its maximum cover towards the second half of the available temporal gradient. The niche optima and niche widths in years of species with HOF model IV are shown in Table 2, and suggest a gradual turnover in these species between 1 and 8 years.

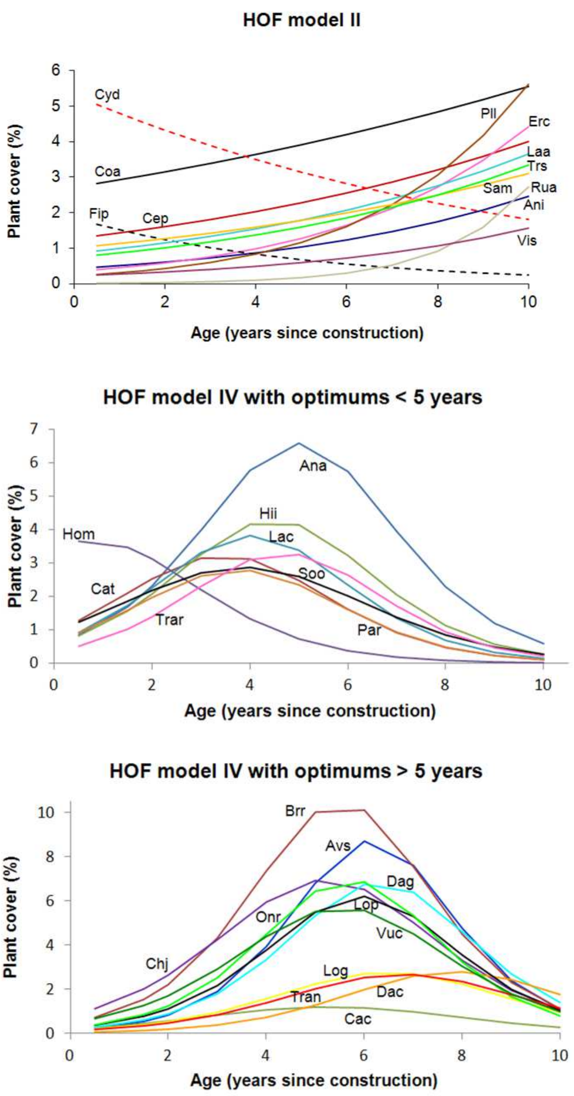

Figure 5. HOF-derived response curves showing the response of the most common species, relative to the time (years) for road slopes on tertiary sediments. Graphs separated for clarity. Species codes in Appendix 1.

Table 2. The optimum cover (µ) and niche widths, for species with unimodal responses in each lithologie. Results are in years and the niche widths are based on 2*t* tolerances (see text for further explanation).

Species	Optimum (*µ*)	2*t*-niche
Tertiary sediments		
Carlina corymbosa	5.30	5.39
Sonchus oleraceus	3.87	5.10
Trifolium angustifolium	6.79	4.83
Logfia gallica	6.49	4.68
Daucus carota	7.84	4.49
Chondrila juncea	5.22	4.47
Hordeum murinum	0.77	4.41
Vulpia ciliata	5.54	4.33
Cardus tenuiflorus	3.47	4.27
Papaver rhoeas	3.76	4.25
Hirchfeldia incana	4.49	4.08
Trifolim arvense	4.68	4.02
Anagallis arvensis	4.99	3.97
Lactuca spp.	4.04	3.97
Lolium perenne	5.94	3.88
Dactylis glomerata	6.31	3.80
Bromus rigidus	5.53	3.69
Ononis repens	5.70	3.64
Avena sterilis	6.15	3.32
Slates		
Dactylis glomerata	7.49	4.46
Carlina corymbosa	5.50	3.86
Andryala integrifolia	4.90	3.67
Bromus rigidus	4.84	3.50
Tolpis barbata	6.39	3.48
Conyza spp.	6.06	2.80
Bromus tectorum	4.40	2.60
Vulpia myuros	3.33	2.25

Species response on the road slopes on slates (Figure 6) could be grouped in a similar manner, although there were many species that showed totally different responses to lithologie. Group 1 (HOF model I), showing no response to age, included seven species mostly dispersed by wind, which were annuals together with more perennial herbs than in tertiary sediments, mainly of the family Asteraceae as in tertiary sediments, but no grasses opposing to tertiary sediments. Their cover was <1%, except for *Chondrila juncea* and *Leontodon taraxacoides* (ca. 3%). Only two species showed the same response to age found on tertiary sediments (Let, Pen). Group 2 contained just one species (Sig) showing HOF model II with decreasing trend and three species (Brr, Brt, Vum) showing HOF model IV with optima before the age of 5 years (Table 2). These species are annuals and mostly anemochorous grasses. Of them, only *Bromus rigidus* endured the same HOF model in both lithologies, while *Bromus tectorum* and *Vulpia myuros* showed no response to age on tertiary sediments and *Silene gallica* was not modeled before. Group 3 included eight species showing HOF model II, with increasing trend, and five showing a unimodal response (HOF model IV) with optima from 5 years of age. This group continued to be dominated by annuals, even more than on the tertiary sediments, although perennial hemicryptophytes were incorporated in the middle and the end of the available temporal gradient, where highlighted *Dactylis glomerata*. Zoochory gained importance, as on tertiary sediments, as well as legumes and composite, which also increased their presence, whereas the number of grasses remained. Of the 13 species of this group, only three (Cac, Dag, Trs) endured the same HOF model in both lithologies, two showed no response to age on tertiary sediments (Hyr, Trc), other two (Cony, Tob) were not modeled before, five showing model II with increasing trend on slates showed model IV on tertiary sediments (Avs, Dac, Soo, Tran, Vuc), and the last one (Ani) showing model IV on slates showed model II with increasing trend on tertiary sediments.

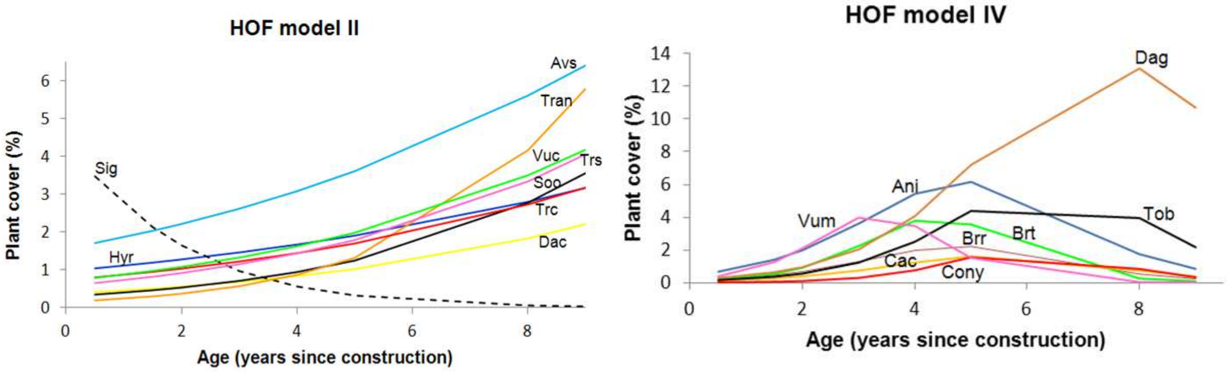

Figure 6. HOF-derived response curves showing the response of the most common species, relative to the time (years) for road slopes on slates. Graphs separated for clarity. Species codes in Appendix 1.

4.- DISCUSSION

4.1.- Relationship between succession and site conditions

The results presented here illustrate clearly that species change in natural revegetation on road slopes in the semi-arid conditions of Spain is affected by at least three major environmental factors: lithologie, surrounding vegetation and proximity between slopes. Indeed, these three factors had a greater effect on the successional trajectories than age itself.

The influence of lithologie was expected given the recognized importance of soil starting material in restoration (Bradshaw, 1983), as found for Martínez-Ruiz and Marrs (2007) on uranium wastes. Lithologie can determine differences in the starting quality of substrates inducing changes in the plant communities' development and affecting the speed of succession.

The surrounding vegetation was also decisive in the spontaneous colonization of the slopes, which depends largely on the presence and distance to a source of propagules (Kirmer and Mahn, 2001; Novák and Prach, 2003; Bochet *et al*., 2007a; Martínez-Ruiz and Marrs, 2007). Several studies have shown that the probability that the seeds reach a particular area is inversely proportional to the distance to the source of seed (Wilson, 1993; Bochet *et al.,* 2007a; Bochet *et al.*, 2011) and that the effectiveness of spontaneous colonization from nearby vegetation areas can be high (Matesanz *et al.,* 2006; Martínez-Ruiz and Marrs, 2007; Martínez-Ruiz *et al.*, 2007). In this sense, our results are fully consistent, being the proximity of woody vegetation ('Dehesa' of *Quercus ilex* spp. *ballota*, pine woodlands and shrublands) one of the considered environmental factors which most determines the species composition of our slopes.

The proximity between slopes was another of the most influential factors in the processes of colonization and natural dynamics of the slopes under study. Our results show a clear differentiation between the floristic composition of the road slopes located on the east and west of the province of Salamanca, although primarily related to the marked geological differences between the two sides of the province. However, higher floristic similarity between slopes can be due to the shorter physical distance between them, even when they differ in other characteristics such as aspect (Martínez-Ruiz and Fernández-Santos, 2005) or lithologie.

The age of road slopes was also shown to be important, of course. Many studies have found a clear age gradient of species turnover from early-successional stages to late-successional ones on different types of restored sites in Central Europe (Prach *et al.,* 2007), on reclaimed coal wastes in the USA or Spain (Holl and Cairns, 1994; Moreno de las Heras *et al.,* 2008; Alday *et al.*, 2011), or on reclaimed uranium wastes under semi-arid Mediterranean conditions (Martínez-Ruiz *et al.*, 2001; Martínez-Ruiz and Fernández-Santos, 2005; Martínez-Ruiz and Marrs, 2007). However, the age influence was not equally evident on all lithologies. Indeed, for the whole data set, age was correlated with CCA3, being therefore the age gradient more distinguishable within two of three lithologies (tertiary sediments and slates). On both lithologies, axis 1 showed a clear age gradient, although more orderly on tertiary sediments suggesting that succession is faster than on slates. Furthermore, we observe significant differences in floristic composition between tertiary sediments and slates within the same successional stage (on slates there were 21 species no present on sediments), possibly due to differences in the surrounding vegetation, that is consistent with our results in which this variable was significant. On the other hand, since the dynamics of succession is strongly influenced by soil dynamics (Tilman, 1988), the slow rate of soil formation on granites probably swamps the effect of time since road slope construction that may influence floristic composition sooner on a more suitable substrate (tertiary sediments or slates). Consequently, longer and continuous temporal series are needed in order to find differences in floristic composition according to the age on hard substrates such as granites.

Other influential factors on vegetation dynamics when lithologie is considered separately were steepness, and height and type of slope. Our results showed that vegetation cover and species diversity experienced a decrease with increasing road-slopes steepness and height (two variables closely related), confirming the results of previous studies in a wide range of environments (Bochet and García-Fayos, 2004; Cantón *et al*., 2004; Desta *et al*., 2004; Warren, 2008). In these studies, differences in species composition were attributed to the higher degree of erosion and the increased likelihood of seed removal by drag or gravity (García-Fayos and Cerdà, 1997), in addition to the reduced availability of water in the soil as described for other semi-arid Mediterranean areas (García-Fayos *et al.,* 2000; Bochet *et al.,* 2007b; Bochet *et al.,* 2010a; Mola *et al*., 2011).

Finally, our results also reflected the influence of the type of slope into the vegetation dynamics, at least on slates, coinciding with findings in other studies also in Mediterranean environments (Bochet *et al.,* 2010a; Bochet *et al.,* 2010b); despite most of our road slopes were cutslopes. The abiotic conditions of cutslopes are much less favorable for the establishment of vegetation than those of embankments (Bochet *et al.,* 2011), as seen in several studies in which higher levels of organic matter and nitrogen were found in the latters (Bochet *et al.*, 2010a; Mola et al., 2011). Moreover, the level of soil compaction is much higher in cutslopes (Bochet et al., 2010a), which can reach the threshold that determines the ability of the roots of many uncultivated herbaceous species to penetrate a substrate (Basset *et al.*, 2005; Monsalve *et al.*, 2010). Engineering measures, more than ecological ones should be considered in these cases (Bochet *et al.,* 2010a) in order to reduce the steepness and length of slopes, or to create areas of lower compaction soil (Bochet *et al*., 2011). Probably on tertiary sediments with better soils is not so noticeable the influence of type of slope, as if the substrate is very severe as in the granites. It seems therefore that differences in species composition between the two types of slopes (cutslopes and embankments) in the province of Salamanca are evident only for intermediate quality situations of original material (slates). Although this result is not conclusive since the number of embankments analyzed in this study was very low.

Surprisingly, aspect did not appear as a key factor in the dynamics of vegetation on these road slopes of the Salamanca province, contrary to found by other authors in different degraded areas, as slopes of linear infrastructures (Bochet *et al.,* 2009; Bochet *et al.,* 2010b) or mine wastes (Martínez-Ruiz *et al.*, 2001; Martínez-Ruiz and Fernández-Santos, 2005; Martínez-Ruiz and Marrs, 2007) under semi-arid Mediterranean conditions. Since these studies have shown that aspect introduces qualitative and/or quantitative changes in floristic composition, but after a certain age, probably longer temporal series would be analyzed for future studies in the study area to find some aspect influence on vegetation dynamics.

4.2.- Species composition trajectories

Although lithologie was influential, some general trends in species responses to successional change were found by considering species traits. On both lithologies (tertiary sediment and slates) most species showing no temporal change were dispersed by wind, mainly grasses and therophytes on tertiary sediments whereas on slates hemicriptophytes from *Asteraceae* family were more numerous and no grasses were found. The presence of many annual species in all lithologies could be explained by the greater numbers of stress-tolerators compared to ruderals in these xeric habitats (Madon and Médail, 1997). In more productive habitats a decline in therophytes with time would be due to their inability to compete with late-successional competitive dominants (Down, 1973; Prach *et al.,* 1997). In contrast, irregular rainfall distribution (Madon and Médail, 1997) and the apparent lack of long-term persistent seed banks in unproductive communities (van Dijk and Sykora, 1982; Zobel *et al.*, 1998) could explain the absence of response to age of several species (not only annuals) in the study area (Martínez-Ruiz and Marrs, 2007). Here, persistence of the species in the community depends on re-establishment, and therefore dispersal into the site (van Andel *et al.*, 1993) and safe site availability (Zobel *et al.*, 1998), rather than persistence of individuals through competition. The high turnover in the species-rich target communities found by Garañeda (2001) implies that species are re-establishing more or less continuously (Bakker *et al.,* 1996; Zobel *et al.,* 1998). In these circumstances, having long-range dispersal mechanisms (mainly anemochory at early succession; Houssard *et al.*, 1980; Hodgson and Grime, 1990) gives them a great advantage.

Species with greatest cover at the start of the seres and decreasing with time and those with optima below 5 years were mainly annuals and anemochorous on both litologies, of the *Asteraceae* family on tertiary sediments and grasses on slates. Among species with greatest cover at the end of the seres and those with optima above 5 years, on tertiary sediments perennial grasses and legumes herbs (mainly hemicryptophytes) gained in importance, and even one woody species was found (*Ononis repens*), whereas on slates this group continued to be dominated by annuals, although perennial hemicryptophytes were incorporated in the middle and the end of the available temporal gradient, gaining in importance legumes and *Asteraceae*, as on tertiary sediments, whereas the number of grasses remained. Therefore, there was a tendency for life-form replacement during succession, as found on uranium wastes (Martínez-Ruiz and Marrs, 2007), although more clear on the tertiary sediments than on slates; the no so clear trend in the life-form replacement over time on slates is mainly due to species that increased through time are mostly annuals. Hemicryptophythes have been shown to be important in colliery spoil reclamation (Down, 1973; Prach *et al.*, 1997). They often have long tap roots enabling them to extract water from depth during summer drought, which directly improves their survivability (Torbert, 1990; Volaire and Lelièvre; 2001). Their increasing presence within the available temporal range on a better substrate such as sediments may indicate a faster rate of successional dynamics than on a rockier one such as slates, as these stony soils limit water availability and speed of plants growth (van Wesemael *et al*., 2000; Josa *et al*., 2012). On the other hand, woody species were more prevalent on tertiary sediments than on slates, confirming that their establishment tended to be easier under moderate environmental conditions (Martínez-Ruiz and Marrs, 2007) and retarded in extreme habitats such as very dry, very wet or very acidic ones (Prach and Pyšek, 1994).

There was also a replacement during succession for the main taxonomical groups but in opposite direction for both lithologies: from *Asteraceae* to grasses on tertiary sediments and on the contrary on slates. However legumes gained in importance with time in both lithologies, the fact that in our temporal sere *Poaceae* and *Asteraceae* species were dominant is interesting for restoration, since the former have a fast growing development thus helping to cover and stabilize the soil (Chambers, 2000), whereas the latter are great colonisers as shown by other restoration studies of mined areas (Martínez-Ruiz and Marrs, 2007). It is also important the increase, in richness and cover, of legumes from the age of 5 years in our temporal sere, since they presumably improve the recovery process by fixing atmospheric nitrogen in the soil, producing a large amount of soil organic matter and increasing nitrogen mineralisation (Palaniappan *et al.,* 1979), thus facilitating the establishment and development of late-successional species (Palmborg *et al.*, 2005; Walker and del Moral, 2009; Pallavicini, 2013), which is supported by several studies performed in mines (Holl, 2002; Alday *et al*., 2011) and suggests that the direct introduction of legume species could accelerate successional development (Walker and del Moral, 2009) by improving soil conditions and erosion control of degraded areas (Le Houérou *et al.,* 1992).

As for the type of dispersion, although anemochory was still significant at the end of the short available temporal range, dispersion through animals increased with transition from ectozoochory towards endozoochory along the temporal gradient on both lithologies. This is consistent with the results obtained in other studies of primary (Martínez-Ruiz and Marrs, 2007) or secondary (Bonet and Pausas, 2004) succession in semi-arid Mediterranean environments, and of primary succession under sub-humid Mediterranean climate (González-Alday and Martínez-Ruiz, 2007; Alday *et al.*, 2011), in which anemochory and zoochory were the more frequent dispersal mechanisms in the early stages of succession. However, it is possible that the role of wind dispersal will be replaced by animal dispersal during succession, as literature predicts (Houssard *et al.*, 1980; Huston and Smith, 1987; Rydin and Borgegård, 1988), whether a longer temporal sere is analyzed.

The variation range of niche widths for the species with unimodal response is similar on both lithologies. The extraordinarily wide niches of most species with unimodal response, although no so higher than on uranium wastes (Martínez-Ruiz and Marrs, 2007), are typical of early-successional species that occupy disturbed habitats with variable and changing environments (Lawesson and Oksanen, 2002). In contrast, the niches for many species are close together, indicating potential species co-existence (Lawesson and Oksanen, 2002) and hence the importance of between species interactions in the structuring plant communities in semi-arid environments (Pugnaire and Luque, 2001).

Curiously, only six of all modelled species showed the same trend along time in both lithologies (*Bromus rigidus, Carlina corymbosa, Dactylis glomerata, Leontodon taraxacoides, Petrorhagia nanteuilli, Trifolium striatum*), which are as therophytes as hemicryptophytes. Nevertheless, the trajectories of most modelled species varied with lithologie, suggesting an interaction with mico-climatic conditions (Tilman, 1988; Martínez-Ruiz and Marrs, 2007). Such species included annual therophytes mostly dispersed by wind, which change between models II and IV mainly.

5.- CONCLUSIONS

Lithologie, surrounding vegetation and proximity between slopes had a great effect on the floristic composition of plant communities during succession. The age influence was not equally evident on all lithologies, as the steepness, and height and type of slope, only significant when lithologie is considered separately, and no influential on the hard lithologie (granites) where succession was slower. Therefore, the maintenance of areas of natural vegetation in the vicinity of the slopes during the execution of the constructions that act as seed sources can be an inexpensive tool that improves the results of restoration projects.

Some trends in species responses to successional change were found by considering species traits. There was a tendency for life form replacement (from therophytes to hemicryptophytes) during succession, clearly on the tertiary sediments than on slates. A dispersal-mode replacement sequence was found from anemochory to zoochory, although anemochory continues to be important at the end of the short temporal gradient analyzed (early stages of succession). There was also a replacement during succession for the main taxonomical groups but in opposite direction for both lithologies (tertiary sediments and slates), and the role of legumes in restoration is emphasized.

Finally, our results showed highly variable patterns in changes through time of species with the same life-form (therophytes). This fact emphasises the importance of improving natural colonisation by providing suitable substrate for the restoration of similar semi-arid ecosystems if an adjacent seed source is present in remnant patches of natural vegetation. Although comparisons between habitats are subject to limitations and are not directly comparable, our results agree with those obtained in other studies (Valladares *et al.,* 2004; Tena, 2006; García-Palacios *et al.,* 2010) and indicate that in a relatively short time, vegetation communities spontaneously installed on road slopes are rich in species, which questions the necessity of introducing allochthonous species as those usually selected for hydroseeding. Moreover, this diversity increases progressively with time (Tena, 2006; García-Palacios *et al.,* 2010). The result would be more diverse vegetation, dominated by annual species, capable of responding to year-to-year variation in weather conditions that characterise those environments.

Furthermore, in case of still needed other measures to incorporate seeds, as hydroseeding, studies of this type (Prach, 2003; Tinsley *et al.,* 2006) show that the use of local species able to establish themselves on the slopes is a better alternative for hydroseeding, besides being highly recommended for its geomorphological and ecological benefits, such as preservation of genetic integrity, conservation of local diversity and compatibility with other local species (Petersen *et al.,* 2004; Tinsley *et al.*, 2006; Steinfeld *et al.,* 2007).

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Appendix 1. Family, life span, life form, dispersal mode and temporal response pattern of main species in tertiary sediments (T) and slates (ST).

						Temporal response pattern	
Code	Species names	Family	Life span	Life form	Dispersal mode	T	SL
Aet	*Aegilops triuncialis* L.	P	A	T	ec	I	
Ana	*Anagallis arvensis* L.	Pri	A	T	au	IV	
Ani	*Andryala integrifolia* L.	A	P	H	a	II↑	IV
Avs	*Avena sterilis* L.	P	A	T	a	IV	II↑
Brh	*Bromus hordeaceus* L.	P	A	T	a	I	
Brr	*Bromus rigidus* Roth	P	A	T	a	IV	IV
Brt	*Bromus tectorum* L.	P	A	T	a	I	IV
Cat	*Carduus tenuiflorus* Curtis	A	A	T	a	IV	
Cac	*Carlina corymbosa* L.	A	P	H	a	IV	IV
Cep	*Centaurea paniculata* L.	A	B	H	a	II↑	
Chj	*Chondrila juncea* L.	A	P	H	a	IV	I
Coa	*Convolvulus arvensis* L.	Con	P	H	a	II↑	
Con	*Conyza* spp. Less.	A	A	T	a		IV
Cyd	*Cynodon dactylon* (L.) Pers	P	P	H	a	II↓	
Dag	*Dactylis glomerata* L.	P	P	H	a	IV	IV
Dac	*Daucus carota* L.	Umb	A	H	ec	IV	II↑
Erc	*Erodium cicutarium* (L.) L'Hér.	Ger	A	T	ec	II↑	
Fip	*Filago pyramidata* L.	A	A	T	a	II↓	
Hii	*Hirschfeldia incana* (L.) Lagréz-Fossat	Cru	A	H	au	IV	
Hom	*Hordeum murinum* L.	P	A	T	a	IV	
Hyr	*Hypochoeris radicata* L.	A	P	H	a	I	II↑
Lac	*Lactuca* spp. L.	A	A	T	a	IV	
Laa	*Lathyrus angulatus* L.	F	A	T	b	II↑	
Let	*Leontodon taraxacoides* (Vill.) Mérat	A	P	H	a	I	I
Log	*Logfia gallica* (L.) Cosson & Germ	A	A	T	a	IV	I
Lop	*Lolium perenne* L.	P	P	H	ec	IV	
Onr	*Ononis repens* L.	F	W	Ch	b	IV	
Par	*Papaver rhoeas* L.	Pap	A	T	a	IV	
Pen	*Petrorhagia nanteuilli* (Burnat) Ball & Heywood	Car	A	T	a	I	I
Pll	*Plantago lanceolata* L.	Pla	P	H	a	II↑	I
Rua	*Rumex acetosella* Scop	Pol	P	H	a	II↑	
Sam	*Sanguisorba minor* L.	Ros	P	H	en	II↑	I
Sig	*Silene gallica* L.	Car	A	T	b		II↓
Soo	*Sonchus oleraceus* L.	A	A	H	a	IV	II↑
Tob	*Tolpis barbata* (L.) Gaertner	A	A	T	a		IV
Tran	*Trifolium angustifolium* L.	F	A	T	ec	IV	II↑
Trar	*Trifolium arvense* L.	F	A	T	en	IV	
Trc	*Trifolium campestre* Schreb.	F	A	T	en	I	II↑
Trg	*Trifolium glomeratum* L.	F	A	T	en		I
Trs	*Trifolium striatum* L.	F	A	T	en	II↑	II↑
Vis	*Vicia sativa* L.	F	A	T	en	II↑	
Vuc	*Vulpia ciliata* Dumort.	P	A	T	a	IV	II↑
Vum	*Vulpia myuros* (L.) C.C. Gmelin	P	A	T	a	I	IV

Abbreviations.
Family: A, *Asteraceae*; Car, *Caryophyllaceae*; Con, *Convolvulaceae*; Cru, *Cruciferae*; F, *Fabaceae*; Ger, *Geraniaceae*; Pap, *Papaveraceae*; Pla, *Plantaginaceae*; P, *Poaceae*; Pol, *Polygonaceae*; Pri, *Primulaceae*; Ros, *Rosaceae*; Umb, *Umbelliferae*.
Life span: A, annual; B, biennial; P, perennial; W, woody.
Life form: Ch, chamaephyte; H, hemicrytophyte; T, therophyte.
Dispersal mode: a, anemochory; au, autochory; b, barochory; ec, ectozoochory; en, endozoochory.
Temporal response pattern: I (HOF model I), II↑ (HOF model II, increasing trend), II↓ (HOF model II, decreasing trend), IV (HOF model IV).