Plant traits as predictors of species response to succession in Mediterranean rangelands

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Abstract

The objective of this paper was to identify plant traits that can predict plant response to succession in Mediterranean rangelands. Research was done in the Lagadas county of Thessaloniki, N. Greece. Four different vegetation states, with four replicates each, were studied: abandoned arable field, grassland, open shrubland and dense shrubland, representing various stages of secondary succession following grazing extensification. Seventeen plant traits (leaf, stem and whole plant traits) were measured or collected from the literature for the most abundant species of each plot. Species frequency was also measured on the herbaceous layer in order to quantify species response to vegetation succession. Vegetative plant height, life cycle and the life form of therophytes were the traits with the highest predictive capacity over species response to succession as single predictors, but their coefficients of determination were low. When more traits were combined their predictive capacity was increased. The combination of vegetative plant height, life cycle, leaf dry matter content, pollination mode and specific leaf area provided the best prediction for species response to succession. It is concluded that plant traits can capture species response to vegetation succession after grazing extensification in Mediterranean rangelands.

Key words: Vegetative plant height, life form, life cycle, secondary succession.

Introduction

Mediterranean rangelands are closely related to grazing activities for many years. Over the last decades however, grazing extensification combined with cessation of firewood cutting has led to the invasion of shrubs in grasslands and resulted in their succession to woody communities (Papanastasis and Chouvardas 2005, Zarovali et al. 2007). Predicting plant species response to successional changes is of great interest for theoretical and practical purposes. Plant traits, especially the easily measured plant characteristics (soft traits) (Weiher et al. 1999), could be a useful tool towards this direction. Traits that could predict species response to grazing have been identified by Diaz et al. (2001) and de Bello et al. (2005) but not to vegetation succession. The objective of this paper was to identify plant traits that can predict plant response to succession in Mediterranean rangelands.

Material and Methods

Research was done in the Lagadas county of Thessaloniki, N. Greece. Four different vegetation states, with four replicates each, were studied: abandoned arable field, grassland, open shrubland and dense shrubland, representing various stages of secondary succession following grazing extensification. Seventeen plant traits (Table 1) were measured or collected from the literature for the most abundant species according to Zarovali et al. (2007) following the protocols of Cornelissen et al. (2003).

Table 1. List of traits. Abbreviations and units/ categories used are presented.

Clon: Clonality (non clonal, clonal)	LPC: leaf phosphorus concentration
Def: defences (no defences, defences)	OnFl: onset of flowering (Jul. Day)
Disp: dispersal mode (unassisted, wind, animal, launching)	Phot. pathway: photosynthetic pathway (C_3, C_4) Pol: pollination mode (insect, wind)
LC: life cycle (annual, perennial)	RPH: reproductive plant height (cm)
LCC: leaf carbon concentration (mg/g)	SLA: specific leaf area (mm^2/mg)
LDMC: leaf dry matter content (mg/g)	SM: seed mass (mg)
LF: life form (therophytes, hemicryptophytes, chamaephytes)	StDMC: stem dry matter content (mg/g) VPH: vegetative plant height (cm)
LNC: leaf nitrogen concentration (mg/g)	

Species frequency on the herbaceous layer was also measured, in order to quantify species response to vegetation succession. For this purpose a canonical correspondence analysis (CCA) was carried out on species frequency (response variable) in which vegetation succession was used as the only explanatory variable (values 1 to 4, from early to late successional stages). Species' scores on the ordination axis constrained by vegetation succession were used as their response. Downweighting of rare species and Monte Carlo permutation test (999 permutations) were used (Leps and Smilauer 2003). The relationship between species response to succession (dependent variable) and species traits (independent variable) was investigated by applying the best fit method of regression analysis. Furthermore, a stepwise regression was carried out in the same data set in order to determine the trait combination with the best prediction over species response to succession. A trait was included in the model if $p \leq 0.05$ and removed if $p \geq 0.10$. Traits with more than two categories were expressed as dummy variables (Tabachnick and Fidell 2001). All analyses were carried out using the software packages CANOCO 4.5 and PASW Statistics 18.0.

Results and Discussion

Species response to vegetation succession ranged from -2.48 to 3.39 (values on the constrained axis of CCA). Positive values indicated positive response to succession.

Plant traits that produced a significant regression model with species response to succession are presented in table 2. The linear, quadratic and cubic model of the vegetative plant height had the highest coefficients of determination than the models of all other traits. The differences in coefficients among the three models were very small, indicating that the linear model was enough for predicting species response, since the complexity of the other two models was not compensated by an increase in their explaining capacity. Life cycle could predict species response with three regression models. Each one explained 27.5% of the dependent variable, indicating that the linear model was enough for this trait, too. The life form of therophytes and hemicryptophytes and clonality produced each a significant linear model with species response to succession explaining 27.5%, 11.3% and 21.9% of the variance in species response respectively. Plant height, life cycle, hemicryptophytes and clonal species increased with succession, while therophytes decreased. Similar results have been reported by other researchers (e.g. Prach et al. 1997, Kahmen and Poschlod 2004, Castro et al. 2010).

On the other hand, leaf nitrogen concentration predicted species response with a cubic model (Table 2), which is non-linear, in contrast to Garnier et al. (2004) who have found that leaf nitrogen concentration decreases during succession. This could be attributed to the low values of leaf nitrogen concentration that some forbs had in the early stages of succession and to the presence of legumes in all successional stages (Papadimitriou et al. 2004). Onset of flowering had the lowest coefficients of determination, explaining 16.2% and 17.4% of species response with the quadratic and the cubic models respectively. Kahmen and Poschlod (2004) found that species flowered later at the advanced stages of succession than the ones in the early stages. *Chondrilla juncea*, a forb of the early successional stages that flowers at the end of July, seemed to be the reason for the unimodal response of species in our data set. When this species was omitted from the analysis, then onset of flowering produced a significant linear model with species response (R^2=0.131, p=0.030).

Table 2. Regression models of plant traits (X) and species response to succession (Y). Only traits with a significant model are presented.

Plant traits	Regression model	R^2	p.
VPH	Linear: $Y = -1.301 + 0.100x$	0.311	0.000
	Logarithmic: $Y = -3.024 + 1.305\ln(X)$	0.249	0.002
	Quadratic: $Y = -1.420 + 0.116x - 0.0004x^2$	0.312	0.002
	Cubic: $Y = -1.7 + 0.179x - 0.004x^2 + 0.00006x^3$	0.313	0.006
Life cycle[1]	Linear: $Y = -3.123 + 2.092x$	0.275	0.001
	Logarithmic: $Y = -1.031 + 3.018\ln(X)$	0.275	0.001
	Inverse: $Y = 3.153 - 4.184/X$	0.275	0.001
Therophytes[2]	Linear: $Y = 1.061 - 2.092x$	0.275	0.001
Hemicryptophytes[3]	Linear: $Y = -0.305 + 1.252x$	0.113	0.041
Clonality[4]	Linear: $Y = -0.722 + 1.791x$	0.219	0.003
LNC	Cubic: $Y = -33.952 + 5.340x - 0.260x^2 + 0.004x^3$	0.216	0.043
Onset of flowering	Quadratic: $Y = -30.235 + 0.383x - 0.001x^2$	0.162	0.049
	Cubic: $Y = -21.817 + 0.209x - 0.000003x^3$	0.174	0.039

[1]Life cycle 1: Annual, 2: Perennial; [2]Therophyte 0: No, 1: Yes;
[3]Hemicryptophyte 0: No, 1: Yes; [4]Clonality 0: No clonal, 1: Clonal;

Therefore, vegetative plant height, life cycle and the life form of therophytes were the traits with the higher predictive capacity as single predictors. Similar results have been found by Diaz et al. (2001) and de Bello et al. (2005) in relation to grazing. It should be noted though, that even for those traits the coefficients of determination were low.

When more traits were combined their predictive capacity was increased compared with the models of single traits. The stepwise regression showed that the combination of vegetative plant height, life cycle, leaf dry matter content, pollination mode and specific leaf area provided the best prediction for species response to succession (Table 3). These traits together explained 59.6% (Adj. R^2) of the variance in species response to succession. The combination of similar traits (plant height, life cycle and leaf mass) have been also found to give the best prediction over species response to grazing by Diaz et al. (2001).

Table 3. Stepwise regression of plant traits (independent variable) and species response to succession (dependent variable).

Plant traits	B	Std. error	Beta (β)	t	Sig.	Model
(Constant)	-6.618	1.532		-4.318	0.000	R=0.808 R^2=0.652 Adj. R^2=0.596 Std. error=1.176 F=11.624 Sig. = 0.000
VPH	0.069	0.021	0.383	3.262	0.003	
Life cycle[1]	1.892	0.500	0.474	3.785	0.001	
LDMC	0.014	0.003	0.485	3.981	0.000	
Pollination[2]	-1.740	0.478	-0.462	-3.636	0.001	
SLA	0.069	0.033	0.252	2.067	0.047	

[1]Life cycle 1: Annual, 2: Perennial; [2]Pollination mode 1: Insects, 2: Wind

Conclusions

Vegetative plant height, life cycle and the life form of therophytes are the traits with the higher predictive capacity of species response to succession as single predictors, but their coefficients of determination are low. When more traits are combined their predictive capacity is increased. It is concluded that plant traits can capture species response to vegetation succession after grazing extensification in Mediterranean rangelands.

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