Pak. J. Bot., 43(5): 2323-2330, 2011.

VARIABILITY OF VEGETATION OF TEMPORAL PONDS ALONG GRADIENTS OF STAGNANT WATER AND ALTITUDE IN SOUTH-WEST ANATOLIA

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Abstract

Vegetational zonation within temporal ponds in the western Taurus Mountains of South – West Anatolia, Turkey and changes along altitudinal gradients was studied. Two gradients show different filtering effects and magnitude of influence on the floristic composition of Mediterranenan temporal pools. Classification gave five clusters that represented ecologically meaningful communities according to moisture gradient classified into *Ranunculo argyrei-Tanacetea argentei* (*Sedo nani-Convolvuletalia galactici*), *Stellarietea mediae* (*Thero-Brometalia*) and *Molinio-Arrhentheretea* (*Potentillo-Polygonetalia*). Multivariate analyses were used to explore gradients in the floristic composition and the revealed importance of two groups of explanatory variables: the first is related to mean ground surface elevation (microtopography of the site), clay and carbonate content amount, and the second corresponds to the area of temporal pond and other soil variables. Microtopography (relative elevation within temporal pools) proved to be most important factor influencing species composition.

Introduction

Temporal ponds typically occur in shallow depressions with stagnant water present only for part of the year (Zedler, 2003). Above-ground vegetation is seasonal and consists of ephemeral wetland plants (Deil, 2005). Variability of vegetation is demonstrated in zonation, showing a pattern of more or less concentric zones of different plant species assemblages. Different environmental gradients; seasonal duration of standing water (Zedler, 1987; Bauder 2000), soil chemical and physical factors (Crowe *et al*., 1994), flooding period (Espírito Santo & Arsénio, 2005 etc.) result in series of different plant communities. Extreme habitats are of special interest for vegetation ecologists, specially such self-contained ecosystems as temporary pools (Crowe *et al*., 1994).

In the dolines of Taurus special site conditions appear because of the special topography that allows air at higher elevations to become much heavier than the surrounding air due to night time radiational heat loss. As a result of this, the air sinks downward until it reaches a layer of air cooler than itself or bottoms out against the earth's surface (Çepel, 1990; Atalay, 2004). This movement creates pools of cooler air which are often observed in warm weather as patches of light fog forming over low-lying wetlands, ponds and stream beds or wet vegetation. In cold weather, when the cool air drops below the freezing mark, frost forms on these locations. Such areas are more susceptible to frost than the surrounding terrain. Extreme temperatures do not allow tree species to thrive and bottoms are forest free. Çetik (1974) uses the term cold air lakes for this habitat.

Another reason for the absence of forest vegetation is that water fills these shallow dolines and forms temporal ponds. The wet season (because of long lasting and melting snow, precipitation) appears in winter and spring, and pools desiccate in summer (May-June). We can define these seasonal ponds that fill in winter as brumal pools (Schwartz in Keeley & Zedler, 1998). Heavy clay soils prevail, and soil surfaces are characterized by the presence of rock outcrops and rock fragments, which are products of geochemical, hydrologic and geomorphic process. The rock fragments cover at the soil surface has an ambivalent effect on infiltration. When on the surface it increases infiltration, but while embeded in the soil it seals the surface and inhibits the infiltration (Li *et al*., 2007). According to the habitat typology presented by Deil (2005), such habitats can be classified as seasonal pool habitats or vernal pools in the narrower sense.

The species that thrive in dolines with such ecological conditions form specific patches of vegetation that show spatio-temporal dependence. The vegetation of such extreme habitats is a useful object because of the dynamics and quick species turnovers in short gradients. Microtopography (mean ground surface elevation of the site) determines specific plant species assemblages through the duration of the inundation period. As such dolines exist at different altitudes, another gradient influences plant distribution (Ahmad *et al.*, 2010).

The aims of our study are to answer the following questions: (1) Are there significant differences in species composition and vegetation characteristics between temporary ponds in dolines? What environmental gradients explain these differences? (2) What are the main gradients in the species composition of vegetation that thrive at the bottom of temporary ponds?

Material and Methods

Study sites: The study took place in Elmalı Cedar Research Forest (Antalya/Turkey) in beginning of June 2008. The Elmalı region, at which we carried out the research, includes many frost patches in dolines. It is even called as a mosaic of frost patches (Kantarcı, 1991). The region is shaped by the high mountains reaching up to 3000 m. The range between 1100 and 2000 m is covered by cedar forests standing on steep slopes and includes several frost patches (Kavgaci *et al*., 2010a). The bottom of the frost patches in these forests has a grassland or wetland character, which is mainly formed by non-forest vegetation as a result of the accumulation of cold air, which prevents the regeneration of woody species. The location of dolines in which temporal ponds occur is shown on the map (Fig. 1). More detailed information on some characteristics is presented in Table 1. All flooded dolines in the area were inspected in the range between 1300 and 2000 m above sea level, but some of them were intensively grazed and therefore not sampled.

Fig. 1. Location of frost flat valleys in Elmalı Research forest.

Table 1. Characteristics of dolines within the Cedar Research Forest near Elmalı (Anatolia/Turkey).

Code	Doline	Area (m^2)	Altitude (m)
A	Kalayci	129.741	1610
B	Sarniç	110.198	1298
C	Aliç	81.011	1540
D	Zigircik	19.261	1890
E	Alaşar	63.403	1685
F	Ückuyular 1	10.458	1850
G	Burçak	24.486	1595

The research area lies approximately at latitude 36 ºN and longitude 29 ºE. The altitude of the study area varies between 1050 m (Avlan lake) and 3070 m (Kýzlar Sivrisi). Meteorological data from the station in Çamkuyu (1660 m) were obtained between 1985 and 2000. The mean annual temperature is 7.5 ºC and precipitation is 616.5 mm. The period with large amounts of precipitation is between November and February, while the dry period extends from the beginning of May until the end of September.

The geological structure of the research area consists mostly of aged calcareous rocks which precipitate on the mesosoic old basic rocks (Karaman & Kibici, 1999).

Sampling: Vegetation of temporal ponds develops in a characteristic mosaic pattern. In every doline we inspected the pattern of plant communities, and two relevés were sampled as replicates in the same community to obtain diversity within each community in the particular doline. Sample plots were of standard area (2×2 m). Altogether 59 relevés were sampled. All plant species in a sample plot were recorded. The Braun-Blanquet scale was used for cover estimation and cover was visually estimated. In addition to data on sampling date, cover of herb layer, locality etc., elevation from the lowest point in the frozen hole was recorded for each sampling plot. In every plant community (in one sampling plot) soil samples at a depth of 5 cm were taken.

The relevés were stored in the TURBOVEG database (Hennekens & Schaminée, 2001).

Data analysis

Soil: Soil samples were air dried, ground and sieved from 2 mm for further chemical and physical analysis. After the fine soil was determined by oven drying at 105 ºC for 24 hours, the skeleton and visible coarse woody debris, containing the roots, were hand removed. The soil particle distribution was determined according to the Bouyoucous hydrometer method and the soil texture was outlined with the International Particle Size Distribution triangle. Actual soil pH was determined by glass electrode at the Hannas pH instrument in a suspension of 1:2.5 rate of distilled water which had been left overnight and was then shaken and measured after an hour (Gülçur, 1974). Soil organic carbon was determined by the Walkley-Black method (Gülçur, 1974). The determination of total N was carried out with a modified Kjeldhal method (Jackson, 1962; Gülçur, 1974). Phosphorus content of the soil was detected by the Olsen method and exchangeable K, Ca, Mg and Na levels of the soils were determined by the Ammonium acetate method (Irmak, 1954; Gülçur, 1974).

Statistical analysis: Detrended correspondence analysis (DCA) was used to detect major floristical patterns, and explanatory variables were passively projected onto the biplot to interpret the results. Analysis revealed a long gradient on the first axis; therefore ordination methods for unimodal models were used (Lepš & Šmilauer, 2003).

We have used classification to detect major plant community types in vegetation of the dolines in the Cedar Research Forest. Flexible beta (β=-0.25) cluster analysis with Euclidean distance measure was used. Species Indicator Analysis (Dufrene & Legendre, 1997) was applied to detect significant indicators for a particular plant community. Proportional abundance of a particular species in a particular group relative to the abundance in all groups is multiplied by proportional frequency of this species in each group. Values obtained were evaluated by the Monte Carlo method (499 permutations).

Beta diversity is a measure of difference between two or more local assemblages and is influenced by the turnover of species among habitats (Koeleff *et al*., 2003). In our study it was calculated as the mean difference among relevés in the JUICE program (Tichý, 2002). The dataset was partitioned along the gradients of plant communities obtained by classification, and β-diversity was calculated as the mean Whittaker dissimilarity for all pairs of relevés. Confidence intervals were calculated by bootstrap sampling (500 samples) from that partition.

Partial CCA's (pCCA) were performed to detect the effect of each explanatory variable on the species composition of vegetation of flooded dolines. The gross effect is the effect of a particular variable shared with other variables, while the net effect is the effect of a particular variable when the effects of other variables are partialled (factored) out. The significance of both effects was tested with the Monte Carlo test with 999 permutations. We also tested the shared effect of several variables by series of partial CCAs.

The univariate statistical analyses were performed with the software package STATISTICA 8 (StatSoft Inc., 2007). Multivariate statistical analyses (DCA, CCA and pCCA) were done with CANOCO 4.5 programme (ter Braak & Šmilauer, 2002). PC-ORD 5 (McCune & Mefford, 1999) was used for Cluster Analysis and Indicator Species Analysis and the related statistical verifications.

Results

Classification (Fig. 2) results in five clusters that represent ecologically meaningful communities along major gradients: most wet communities in the lowest part of the dolines, further divided into two separate communities along altitudinal gradient (1 and 2), intermediate cluster (3), vegetation community on moderately dry site (4), and the most dry (5) on the edge of the dolines.

Plant communities that result from classification are mostly defined with one dominant and several characteristic species (Table 2). Species Indicator Analysis shows that there occurs one highly significant plant species per community: *Ranunculus argyreus* Boiss., *Tanacetum argenteum* (Lam.) Willd., *Elymus repens* (L.) Gould., *Hordeum geniculatum* All. except for the community that has a relatively ground surface elevation: *Erodium cicutaria* (L.) L'Herit, *Vicia villosa* Roth., *Bromus tomentellus* Boiss., *Trifolium caudatum* Boiss., *Bromus squarrosus* L., *Phlomis armeniaca* Willd.

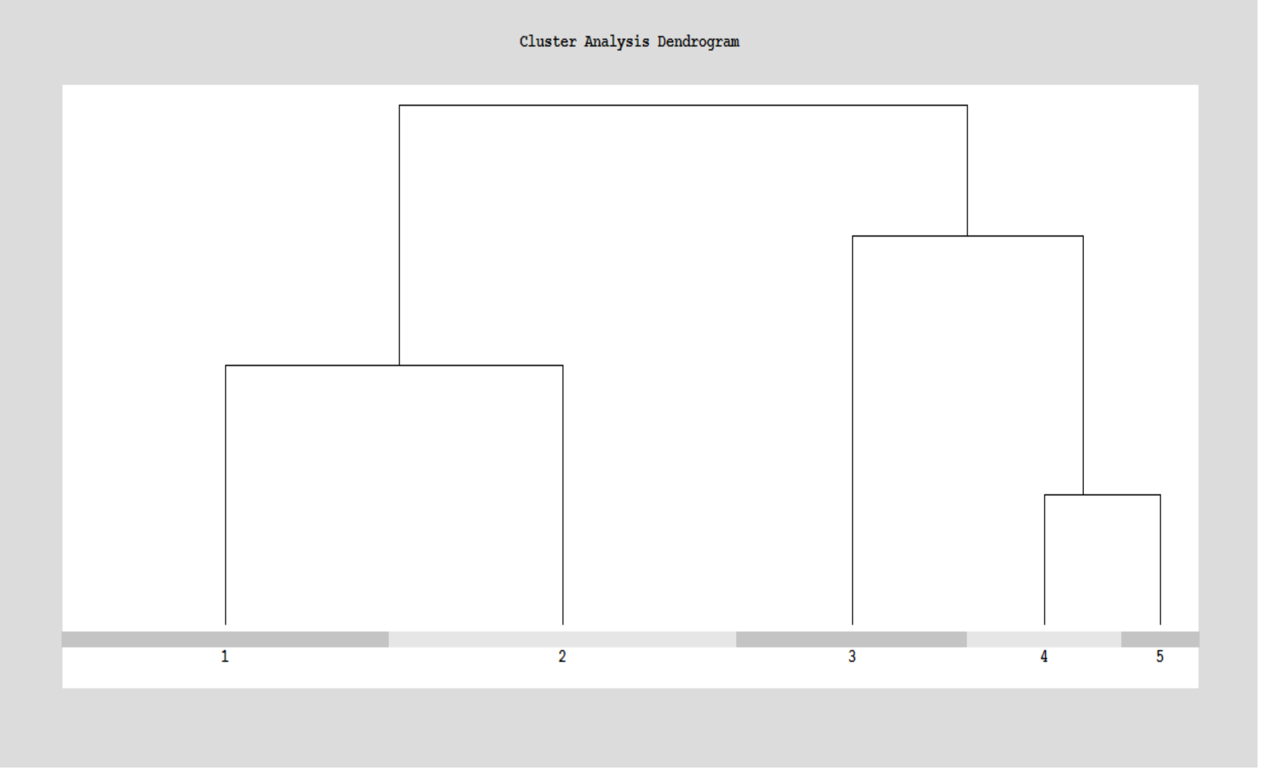

Fig. 2. Classification of sample plots into communities. Numbers refer to groups presented in Tables 2 and 3.

Table 2. Species characteristic of different plant communities from classification as a result of species indicator analysis. Only significant species are presented.

Species	Number of cluster	Observed indicator value	p
Ranunculus argyreus Boiss.	1	84.2	***
Eleocharis quinqueflora (Hartmann) O. Schwarz	1	65.4	**
Sedum nanum Boiss.	1	65.8	**
Tanacetum argenteum (Lam.) Willd.	2	68.8	***
Aira elegantisima Schur.	2	45.4	**
Elymus repens (L.) Gould	3	99.8	***
Myosotis ramosissima Rochel ex Schultes	3	33.3	*
Erophila verna (L.) Cheval	3	25	*
Alopecurus vaginatus (Willd.) Boiss.	3	33.3	*
Taraxacum aleppicum Dahlst.	3	32.1	*
Ornithogalum lanceolatum Labill.	3	27.2	*
Poa bulbosa L.	3	27.2	*
Hordeum geniculatum All.	4	77.2	***
Ranunculus arvensis L.	4	46.9	**
Convolvulus arvensis L.	4	32.6	*
Cerastium fragillimum Boiss.	4	37.2	*
Lotus corniculatus L.	4	32.2	*
Erodium cicutaria (L.) Cheval.	5	90	***
Vicia villosa Roth.	5	97.1	***
Bromus tomentellus Boiss.	5	73.4	***
Trifolium caudatum Boiss.	5	81.4	***
Bromus squarrosus L.	5	67.5	***
Phlomis armeniaca Willd.	5	65.9	***
Falcaria vulgaris Bernh.	5	50	**
Valerianella turgida (Stev.) Betche.	5	50	**
Aegilops umbellulata Zhuk.	5	50	**
Astragalus pinetorum Boiss.	5	42	*
Taeniatherum caput-medusae (L.) Nevski	5	44.8	*
Anthemis wiedemanniana Fisch. & Mey.	5	35.3	*
Cardaria draba (L.) Desv.	5	39.2	*
Crepis foetida L.	5	30.9	*
Trisetum flavescens (L.) P. Beauv.	5	30	*

p= ***<0.0001, **<0.001, *<0.01

In the lowest part of the temporal pond appear communities of the *Ranunculo argyrei-Tanacetea argenteae*. Next in the zonation is the therophytic vegetation of the *Stellarietea mediae*, and in the most upper part is periodically flooded grassland of the *Molinio-Arrhenatheretea* (syntaxonomic scheme according to Kavgaci *et al*., 2010b).

Differences in characteristics of particular vegetation communities of dolines are presented in Table 3 and Fig. 3.

Detrended Correspondence Analysis (DCA) (Fig. 4) was used to explore gradients in the floristic composition of vegetation samples and revealed the importance of two groups of explanatory variables separating sample plots in two perpendicular directions. The first gradient more corresponding to the first axis, comprises relative elevation (microtopography of site), clay and carbonate amount in soil. The second group of explanatory variables corresponds to the area of doline and other soil variables. Samples from particular dolines are grouped within an envelope and show differences between sample plots along relative altitude within the doline, while dolines are lined along altitude and intercorrelated variables.

As already visible from the DCA scatter diagram, two major groups of explanatory variables influence species composition and there are also large intercorrelations between factors. Altitude and amount of silt in the soil have the largest gross effects, but after a series of partial CCA analyses the relative elevation of the sample plot proved to be the most influential for species composition.

Mean ground surface elevation (microtopography) proved to be most significant explanatory variable to influence species composition of flooded dolines (Table 4).

Table 3. Comparison of vegetation and soil characteristics of five different communities along gradient of microtopography and altitude of dolines in Cedar Research Forest.

		Wet high (1)	Wet low (2)	Intermediate (3)	Dry (4)	Most dry (5)
	Mean	7.30	9.27	7.57	14.25	16.92
Species number	Min	5.00	7.00	6.00	6.00	11.00
	Max	9.00	13.00	10.00	23.00	29.00
	Mean	78.00	56.00	76.00	85.00	83.89
Plant cover (%)	Min	50.00	25.00	50.00	50.00	60.00
	Max	100.00	90.00	90.00	95.00	95.00
	Mean	31.86	26.36	32.74	35.74	29.78
Sand (%)	Max	25.61	21.06	22.62	28.77	27.54
	Min	38.25	37.08	54.37	46.40	37.37
	Mean	26.54	32.97	27.51	31.55	35.82
Silt (%)	Max	21.71	28.36	24.80	25.73	32.01
	Min	28.86	37.76	31.99	35.04	38.63
	Mean	41.61	40.67	39.75	32.71	34.40
Clay(%)	Max	33.94	33.33	19.92	21.89	30.62
	Min	48.58	44.80	52.57	39.63	36.91
	Mean	5.50	5.65	6.20	6.19	6.14
pH	Max	5.08	5.39	5.47	5.86	5.76
	Min	6.05	5.97	6.73	6.62	6.66
	Mean	2.58	3.03	2.61	2.21	2.41
$CaCO_3$	Max	1.89	1.89	2.52	1.89	1.89
	Min	3.15	3.77	3.15	2.52	3.77
	Mean	6.87	5.33	5.40	6.21	4.57
Organic matter	Max	4.97	4.85	3.55	4.59	3.29
	Min	8.08	6.46	8.08	9.88	6.91
	Mean	0.34	0.26	0.27	0.31	0.23
N	Max	0.25	0.24	0.18	0.23	0.16
	Min	0.40	0.32	0.40	0.49	0.35
	Mean	0.15	0.13	0.17	0.15	0.11
Cations	Max	0.10	0.10	0.09	0.03	0.10
	Min	0.21	0.17	0.30	0.29	0.12
	Mean	41.80	32.82	36.43	36.17	33.33
Na	Max	33.00	29.00	31.00	28.00	30.00
	Min	49.00	40.00	52.00	42.00	38.00
	Mean	781.70	808.18	692.29	741.83	654.83
K	Max	540.00	540.00	368.00	380.00	324.00
	Min	1020.00	927.00	928.00	1200.00	800.00
	Mean	4766.00	4092.73	5008.57	4671.67	4405.00
Ca	Max	3860.00	3850.00	3470.00	3910.00	3770.00
	Min	6160.00	4610.00	6040.00	5810.00	5720.00
	Mean	353.30	321.27	322.29	294.67	301.00
Mg	Max	312.00	284.00	202.00	236.00	235.00
	Min	399.00	364.00	480.00	382.00	393.00
	Mean	66.82	109.07	76.96	62.13	70.70
P	Max	21.80	55.40	14.60	32.00	32.80
	Min	100.00	168.50	121.50	118.00	98.00
	Mean	9.13	4.12	21.67	58.25	62.29
Relative elevation (cm)	Max	0.00	0.00	0.00	19.59	21.65
	Min	24.42	12.72	48.57	90.15	106.59

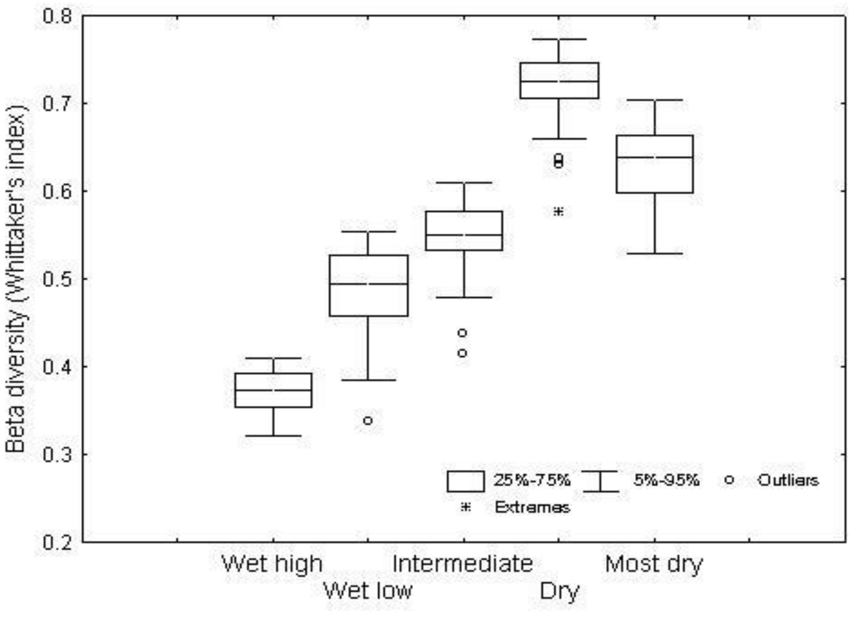

Fig. 3. Box-and-whiskers plot of beta diversity (Whittaker's index of dissimilarity) of different plant communities along the gradient of microtopography.

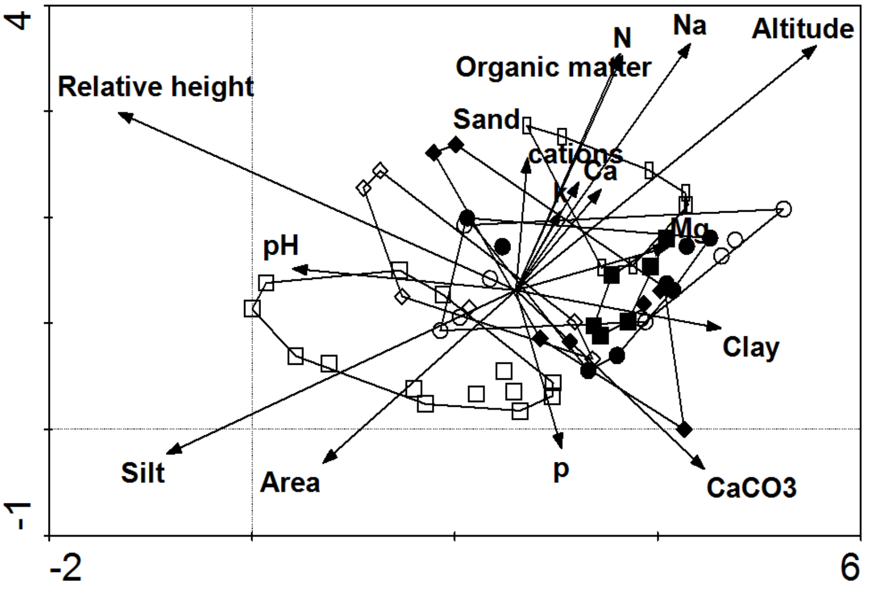

Fig. 4. DCA biplot with passively projected explanatory variables. Different symbols linked by line represent sample plots of a particular doline (empty quadrat- Sarniç, empty circle- Kalayci, empty diamond- Aliç, full diamond- Burçak, full circle- Alaşar, full quadrat- Ückuyular 1, empty rectangular- Zigircik).

Discussion

Altitudinal distribution: The study compares two different gradients (altitude and elevation (microtopography)), their filtering effect and magnitude of influence on the floristic composition of flooding dolines. The altitudinal gradient of temporal pools was seldom researched. Johnson & Rogers (2003) mention altitudinal range of turfs in New Zealand, while Rudner (2005) mentions zonation of plant communities according to altitude in the Iberian Peninsula.

An altitudinal range of 600 m seemed the most important variable of the site, but it turned out that the variable altitude intercorrelates with many other variables (e.g. organic matter, N, Na, area etc.) and its influence is indirect. Organic matter decomposes slowly at higher altitudes as temperatures are more severe (Ahmad *et al.*, 2011). It is recognized that climate (especially temperature and precipitation) is the most important factor regulating soil organic matter (Alvarez & Lavado, 1998). With higher temperatures, carbon content in the soil decreases because of more intense organic matter mineralization (Kirschbaum, 1995). The fraction of sand particles is also larger at higher altitudes, while there is more silt in the soil in temporal pools at lower altitude.

Zonation: It was shown that elevation (microtopography) of the sample plot has a far greater influence than altitude. The period of inundation (rain water and melting snow) of the site is essential in determining the pattern of floristic composition. Several studies (Bauder, 2000; Barbour *et al.*, 2005) have shown that inundation as a function of elevation and topography of site, controls species composition. Species that can withstand longer inundation colonize the bottom of the dolines, and more terrestrial species occupy the margins. Small scale zonation is more evident when using the cover of plant species (Crowe *et al.*, 1994), because presence/absence data show the range of many plant species along the whole elevation gradient. In our case, distinct plant communities are seen with boundaries between groups of species. The mean species number increases towards the edge of the doline that is less inundated, and the number of characteristic species per community also increases. Less severe conditions enable generalist species to thrive. In ephemeral wetlands in other parts of the world more specialized species occur (Deil, 2005), and in California even pronounced endemism is known for vernal pools (Barbour *et al*., 2005). On the other hand, the lack of specialists for ephemeral wetlands could be explained by nocturnal cooling in frost hollows.

Table 4. Explained variation (%) by particular explanatory variables. Gross effect includes explained variation by a particular variable shared with others, while net effect includes explained variation after shared variation was partialled out. F-values of the permutation tests and p-values are presented for pCCA's, when net effects of explanatory variables were calculated.

Variable	Gross effects (%)	Net effects (%)	F	p
Relative height	7.94	4.95	4.66	0.001
pH	4.74	3.57	3.36	0.001
N	4.91	3.51	3.30	0.001
Organic	4.83	3.49	3.29	0.001
K	3.45	3.39	3.18	0.001
Sand	2.90			
Silt	9.22	2.95	2.75	0.001
Clay	4.14			
Ca	2.93	2.36	2.22	0.002
Mg	3.39	2.19	2.07	0.001
$CaCO_3$	4.62	1.99	1.87	0.016
Cations	2.57	1.96	1.85	0.026
Altitude	9.11	1.90	1.79	0.025
Area	5.71	1.86	1.75	0.036
Na	5.29	1.80	1.70	0.023
P	2.61	1.73	1.64	0.040
All	13.19			

p= ***<0.0001. **<0.001. *<0.01

Zonation within dolines is also correlated with the area of the doline. In larger dolines the inundation gradient is longer and diversity of plant communities is higher. The selective role of inundation and drying in correlation with the area of temporal pond (size and shape) was pointed out by Keeley & Zedler (1998). On the other hand, area is negatively correlated with altitude. In higher altitudes smaller dolines with temporal ponds are found. Weathering and corrosion are less intense at higher altitudes in forming dolines. Soil reaction and amount of $CaCO_3$ are in correlation with the mean elevation in a temporal pond (Table 5).

Temporal ponds in high mountains offer "steep" environmental gradients over relatively short distances, which provide a useful model for studying the variability of vegetation and factors contributing to it.

Table 5. Species with the highest correlation with relative mean ground elevation within dolines. Species with a fit higher than median are presented.

Species	Ax1 score	Fit	Species	Ax1 score	Fit
Falcaria vulgaris Bernh.	-2.07	0.29	*Crepis foetida* L.	-0.64	0.0642
Aegilops umbellulata Zhuk.	-2.07	0.29	*Velezia quadridentata* (Stev.) Betche.	-0.38	0.0492
Valerianella turgida (Stev.) Betche.	-2.07	0.285	*Ranunculus argyreus* Boiss.	-0.34	0.0457
Papaver argemone L.	-2.07	0.1447	*Convolvolus arvensis* L.	0.27	0.0527
Alyssum szowitsianum Fisch. & Mey.	-2.07	0.1447	*Hordeum geniculatum* All.	0.46	0.0881
Camelina rumelica Vel.	-2.07	0.1447	*Filago aegeae* Wagenitz	0.48	0.0498
Trigonella spruneriana Boiss.	-2.07	0.1447	*Trifolium caudatum* Boiss.	0.48	0.0491
Eryngium campestre L.	-2.07	0.1447	*Galium verum* L.	0.53	0.0413
Turgenia latifolia (L.) Hofm.	-2.07	0.1447	*Poa bulbosa* L.	0.54	0.1014
Scabiosa rotata Bieb.	-2.07	0.1447	*Potentilla recta* L.	0.69	0.0587
Tragopogon pterodes Panc.	-2.07	0.1447	*Capsella bursa-pastoris* (L.) Medik.	0.89	0.0427
Rostraria cristata (L.) Tzvelev	-2.07	0.1447	*Trisetum flavescens* (L.) P. Beauv.	0.93	0.1414
Achillea phrygia Boiss. & Bal.	-2.07	0.136	*Muscari tenuiflorum* Tausch.	1.11	0.0642
Galium tricornutum Dandy	-2.07	0.136	*Verbena supine* L.	1.14	0.1035
Xanthium annuum Georgi	-2.07	0.136	*Taraxacum aleppicum* Dahlst.	1.14	0.0857
Picris echioides L.	-2.07	0.136	*Bromus tomentellus* Boiss.	1.28	0.1366
Androsace maxima L.	-1.19	0.0554	*Cuscuta* sp.	1.34	0.0411
Lactuca serriola L.	-1.05	0.065	*Herniaria incana* Lam.	1.48	0.0669
Scorzonera cana (C. A. Mayer) Hoffm.	-0.81	0.0564	*Silene* sp.	1.69	0.059
Polygonum belardii All.	-0.80	0.0707	*Sanguisorba minor* Scop.	2.21	0.1233

Acknowledgement

Alan McConnell-Duff kindly checked our English. We are particularly grateful to I. Gokhan Deniz for determination of some species. This work was supported by a grant from ARRS P1-0236 and bilateral grant SLO-TR-2-2006-2009 and TUBITAK-TOVAG-(Slovenya 106O487). We also thank to Southwest Anatolia Forest Research Institute for logistic support.

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(Received for publication 12 May 2009)