

Pedo-climatic and land use preferences of *Gentiana lutea* subsp. *lutea* in central Italy

Andrea Catorci, Karina Piermarteri* & Federico M. Tardella

School of Environmental Sciences, University of Camerino, Via Pontoni, 5 IT-62032 Camerino (MC), Italy

*Author for correspondence: piermarteri.karina@libero.it

Background and aims – *Gentiana lutea* L. is a species of high economic importance threatened in several European countries and included in their Red lists. Nevertheless, there is a dearth of data about its ecology, especially in the Mediterranean mountains, which are the southern part of its distribution area. Our aim was to determine the environmental constraints affecting the distribution and performance of *G. lutea* in the aforesaid context.

Methods – We performed the research on the Sibillini Mountains (central Italy) by assessing the relations between some vegetative traits and types of land use. Using a stratified sampling design, we randomly selected a number of 500 × 500 m cells including one or more populations. Our sampling scheme was based on two different grain sizes: 10 × 10 m plots and individuals level. Data were analysed using descriptive statistics, Mann-Whitney U-test, and Redundancy Analysis.

Key results – *G. lutea* was found on northerly slopes with moderate slope angle, mostly at altitudes ranging from 1450 to 1750 m a.s.l., shifting on southerly aspects at the highest altitudes. Available Water Capacity was the main variable leading the vegetative performances of individuals (optimal values were greater than 50). The relatively low values of soil water deficit (mostly lower than 30 mm yr⁻¹) indicated a very low tolerance of the species to summer water stress. Grassland abandonment was the most suitable land use for the spread of *G. lutea* populations.

Conclusion – This study addressed the dearth of data on the ecology of *G. lutea* providing more information about the main environmental factors affecting its spatial pattern of distribution in central Apennine, providing key data for assessing the land suitability for *G. lutea* cultivation.

Key words – Available Water Capacity, drought stress, grasslands, land suitability, land use, soil water deficit.

INTRODUCTION

Gentiana lutea L. is a perennial herbaceous plant over one meter tall, with rhizomatous and branched roots. Its distribution area extends from the Sierra Nevada to Asia Minor (Lange 1998). In Italy, *G. lutea* is spread on Alps and Apennine ridges, from 900 to 2500 m a.s.l.; central Apennines are near the southern borders of its distribution area (Pignatti 1982). This species has a long winter rest period, preferring cool and sufficiently rainy climates. Soils have to be well-drained and rich in nitrogen, with low content of loam and silt; the optimal soil pH values range from 4.5 to 7.5–8.0 (Aiello & Bezzi 1998).

G. lutea is a competitive species *sensu* Grime (1974), because of its considerable height and the ability of roots and shoots to rapidly monopolize resource capture through spatially-dynamic foraging, with a good ability to spread later-

ally (Grime 2001). The ratio of flowering to vegetative stems ranges from 6 to 23% (Rossi 2012).

The bitter substances contained in the roots of *G. lutea* are used in several European countries to prepare bitters and liqueurs, as well as pharmaceuticals such as anti-inflammatory agents and diuretics (Bellomaria et al. 1981, Carnat et al. 2005, Nastasijević et al. 2012).

These traditional uses led to excessive harvesting of roots and to the decrease in abundance of this species in several sectors of Europe. Because of this, in recent decades *G. lutea* has been added to the Red list of endangered species of many countries, and some nations (e.g. Italy, Spain, Croatia and Bulgaria) have passed legislation protecting the species.

As far as the Italian peninsula is concerned, Gentili et al. (2013) argued that the species is threatened not only by root harvesting but also by global climatic warming, as its distribution mainly regards the upper sectors of the mountains.

Moreover, Kery et al. (2000) demonstrated that the reduction of population size has repercussions in reduced fecundity and decline in offspring performance, thus worsening the problems of species conservation.

For the reasons given above, cultivation may be the best way to preserve the presence of *G. lutea* in natural sites (helping to avoid the illegal harvesting of roots) and, at the same time, to support the economy of mountain areas. This is a key issue because in most parts of Europe the progressive abandonment of the traditional agricultural activities in mountain areas (Antrop 2004) led to homogenization of the landscape (Agnoletti 2007, Geri et al. 2010, Bracchetti et al. 2012) with significant problems for biodiversity and ecosystem services conservation (Metzger et al. 2006, Falcucci et al. 2007). To promote the preservation of a wide number of open areas (croplands), efforts must be made by promoting innovations in agriculture and finding new economic opportunities and livelihoods for mountain dwellers (Catorci et al. 2013b); in this regard, the cultivation of *G. lutea* might be one of the possible innovations for central Italy.

Actually, in recent decades, notwithstanding it is generally considered a fairly difficult plant to cultivate (Galambosi & Galambosi 2010), many countries in central Europe and on Alps, achieved the agronomic knowledge for the cultivation of *G. lutea* (e.g. Desmaret & Derchue 1988, Giovanardi & Barbaro 2009) and experienced in-vitro propagation (Hollobiuc & Catana 2012, Petrova et al. 2006). Contrariwise, in the Italian Apennines the effort to achieve these goals did not give satisfactory results. Indeed, only some small experimental areas are active, while many attempts at cultivation have failed (Menghini et al. 1996).

For the reasons given above, there is a need of knowledge about the ecology of *G. lutea*, especially in the southern part of its distribution area. Indeed, the summer water shortage experienced by plants in the sub-Mediterranean ecosystems, as well as the reduction at the higher altitudes of the growing period (i.e. the time available for plants to complete their vegetative cycle), should be detrimental for the vegetative performances of this competitive species. On the other hand, disturbance due to human activities in mountain agro-ecosystems, e.g. animal grazing and mowing, should be disadvantageous for a competitive species as well (Grime 2001).

As regards the cultivation of *G. lutea*, Gonzalez et al. (2012) found that high altitude and soils with high levels of Mn and K improved the growth and the quality of the roots, while Aiello & Bezzi (1989) generically stated that aridity might be a negative factor for the development of *G. lutea*.

Therefore, improving the knowledge about the ecological needs of *G. lutea* is a key issue to lead the conservation policies. New findings should also give agronomists and farmers information useful for improving techniques for *G. lutea* cultivation and should prove helpful for creating suitability maps (*sensu* Malczewski 2004) for the cultivation of *G. lutea* subsp. *lutea* throughout the Apennine area, by the maintenance of croplands already widespread in the mountain areas which nowadays are largely abandoned (Mazzoleni et al. 2004, Falcucci et al. 2007, Bracchetti et al. 2012).

To analyse the factors affecting the distribution and abundance of *G. lutea*, we selected some macro-environmental

features (i.e. altitude, slope aspect and angle, and type of land form) which shape the distribution of potential vegetation types in Temperate regions at the landscape level (Blasi et al. 2000, Catorci et al. 2012a), and have been used to build models of the realized ecological niche of a species (e.g. Choler & Michalet 2002). Moreover, we assumed that vegetative performances of the *G. lutea* individuals could be affected by fine-scale ecological features (soil water deficit, available water capacity, and pH) as well as by altitude (considered as a proxy for the length of the growing season) and land use.

In particular, we hypothesized that: (i) where drought stress and the length of the growing season are limiting factors for plant survival (i.e. towards the lower and upper boundaries of its elevation range, respectively), the species is restricted to the least stressful conditions; (ii) species vegetative performances are fostered by resource availability (i.e. great available water capacity and low summer water deficit) and lower altitudes; (iii) the species show preference for unmanaged grasslands.

MATERIAL AND METHODS

Study area

The study area is in the Monti Sibillini National Park, located in the central Apennines, between the Marche and Umbria regions (42°49'26"N 13°16'32"E). This area, of about 70000 hectares, is mainly characterised by limestone bedrock (Regione Marche 1991). The lowest altitude is about 400 m, while the highest peak is 2476 m a.s.l. The plant landscape consists of forest ecosystems belonging to *Quercetalia pubescenti-petraeae* Klika 1933, mostly found below 1000 m a.s.l., and *Fagetalia sylvaticae* Pawlowski in Pawlowski, Sokolowski & Wallisch 1928, growing on slopes ranging from 1000 to 1700 m a.s.l. Instead, grassland communities predominate in the upper sectors of the mountains (from 1200–1300 to 2470 m a.s.l.) and belong to *Brometalia erecti* Br.-Bl. 1936, *Seslerietalia tenuifoliae* Horvat 1930, *Nardetalia strictae* Oberdorfer ex Preising 1949, *Caricetalia davaliana* Br.-Bl. 1949 and *Arrhenatheretalia elatioris* Tüxen 1931. The timberline is at 1800–1900 m a.s.l. (Catorci et al. 2011a).

The bedrock's geochemical features and glacial or post-glacial erosion processes contributed to the formation of rough land forms with extremely steep slopes carved by gorges, valleys and rocky walls. Such geomorphological and historical-climatic features as well as the past land use with pastoralism and forestry contributed to the erosion of the most superficial soil layer. Currently, the soils underling the pastoral ecosystems are shallow (< 30–50 cm), with acid/sub-acid to alkaline pH, high content of organic matter and sandy to sandy-loam texture (Giovagnotti et al. 2003).

Regarding climatic features, the study area lies within the Temperate region, near the border of the Mediterranean region, thus it can be referred to the so called "sub-Mediterranean bioclimate", which is a bioclimatic variant of the Temperate macrobioclimate, characterized for having intermediate features between Temperate and Mediterranean climatic conditions (Blasi 1994, Rivas-Martínez et al. 2007).

Table 1 – The main bioclimatic features in the study area.
The main climatic features of the bioclimatic belts of the study area (Blasi 1994, Biondi & Baldoni 1995, Orsomando et al. 2000).

Climatic features	Bioclimatic belt			
	Upper Mesotemperate	Lower Supratemperate	Upper Supratemperate	Orotemperate
Altitudinal range (m a.s.l.)	600–900	900–1400	1400–1900	1900–2300
Average annual temperature (°C)	11–13	9–11	7–9	5–7
No. of months with t < 0°C	0	2	4	6
Drought stress (no. of months)	1	0	0	0
Cold stress (no. of months)	3	4	5–6	6–7
Summer drought stress	0–20	0	0	0
Winter cold stress	210–230	260–280	280–300	290–310
Growing period (no. of days with t > 6 °C)	210–180	180–150	150–120	< 120
Average annual prec. (mm)	850–1100	1100–1300	1300–1500	1200–1400
Summer precipitation (mm)	165–195	180–195	200–240	225–240
Average soil water regime	Xeric	Ustic	Ustic	Udic

Indeed, it is characterised by alternation of winter cold stress and summer drought stress with different intensities, depending on the elevation gradient and land form factors such as slope aspect and angle (Rivas-Martínez & Rivas-Saenz 1996–2009). Because of this, the summer drought stress is generally present in the lower bioclimatic belts and reduced to the south-facing slopes at the higher altitudes. The protected area is part of four bioclimatic belts (Blasi 1994, Biondi & Baldoni 1995, Orsomando et al. 2000), whose main features are shown in table 1.

Experimental design and data collection

After consulting bibliographic (Ballelli et al. 1981, 2005, 2010, Costanzo et al. 2009) and unpublished data to gain a first draft of the *G. lutea* subsp. *lutea* distribution, we interviewed the rangers of the National Park and conducted a field survey of the *G. lutea* populations along transects which followed mountain roads and pathways. We indicated the results of this survey on a topographic map on a scale of 1: 50000, and then overlaid it with a grid with cells corresponding to 500 × 500 m units. Using a stratified sampling design, we divided the altitudinal range of *G. lutea* into six 200 meter-wide altitude classes (from 1200, as the lowest stations were found at about 1280 m a.s.l., to 2400 m a.s.l.) and in each of them we randomly selected a number of cells including one or more populations. The number of cells chosen in each altitude class was proportional to the number of cells where *G. lutea* occurred.

In each selected square, we laid one transect along the major axis of each area covered by a *G. lutea* population. In each transect we laid one or more 10 × 10 m plots (55 in all). Consecutive plots were 10 m from each other; the first one was placed at the border of the area covered by the population. In each plot we collected data on altitude (m a.s.l.), aspect (azimuth degrees), slope angle (vertical degrees), cover percentage of the herb layer and of *G. lutea* (based on

visual estimates), pH (measured five times per plot using a pH-meter), and soil depth (measured using a graduated pole; five measurements per plot were taken). Soil samples, each of which was a mixture of samples collected in five locations inside the plot, were collected as well. Data on conditions of land use, categorized as mowing, grazing and abandoned, were recorded by visual observation and confirmed by interviews with farmers. Land forms were categorized as: slope, concave water drainage surface (hereafter named impluvium), and convex surface straddling a watershed (hereafter named watershed).

To collect data on *G. lutea* individuals, we followed the major axis of the area covered by the *G. lutea* population and laid another transect using a string, along which we chose, every five meters, the individual of *G. lutea* closest to the string (we considered the farthest individual within the buffer of 1 meter from the string). For each of the 96 sampled individuals (all composed of all the leafy and/or flowering shoots arising from the rhizome) we collected data on vegetative traits, namely plant height (m), surface area (m²) covered by leaves (based on visual estimates), and number of stems, number and dry weight of leaves and bracts of the inflorescence (considered as proxies for the vegetative strength and the reproductive performance of the individuals). Slope aspect (azimuth degrees), slope angle (vertical degrees), pH, and soil depth were measured next to each individual. One soil sample was collected as well.

The aboveground part of each selected individual was cut and then oven-dried for 48 h at 90°C. Finally, the dry weight (g) of leaves and bracts was measured.

Data were collected between mid July and mid August 2013, when *G. lutea* was in full bloom.

Data on precipitation were gathered from the maps of average precipitation reported in Amici & Spina (2002). Data on average monthly temperatures (°C) of the last thirty years were collected from Pintura di Bolognola (1445 m a.s.l.) and

Table 2 – Main descriptive statistics of the environmental features concerning the analysed plots.

Descriptive statistics of environmental features of plots ($n = 55$). Aspect azimuth degree was converted from the 0–360 compass scale to a linear (0–180) scale, giving northerly aspect a value approaching 0 and southerly aspect a value approaching 180, and then shifted to a minimum on north-north-east slopes (22.5°) and a maximum on south-south-west slopes (202.5°).

Environmental features	Min	Max	Mean	SD	Median	1 st quartile	3 rd quartile
Altitude (m a.s.l.)	1278.00	2236.00	1610.36	254.47	1520.00	1488.50	1742.50
Aspect (azimuth degree)	0.00	157.50	65.05	48.54	45.00	22.50	112.50
Slope (vertical degree)	0.00	35.00	16.96	8.97	20.00	10.00	20.00
Soil depth (cm)	7.20	62.00	46.31	14.27	50.00	37.67	58.00
pH	4.25	7.21	5.96	0.88	6.20	5.19	6.70
Skeleton (%)	0.00	42.86	9.26	13.48	4.76	0.00	8.61
Sand (%)	38.10	82.20	63.99	11.83	65.40	55.88	72.80
Loam (%)	9.40	51.10	24.18	9.30	22.10	19.43	27.25
Clay (%)	1.20	30.20	11.83	5.99	10.80	7.58	15.83
Available Water Capacity	5.82	136.79	69.34	29.33	71.69	53.04	91.43
Water deficit (mm yr ⁻¹)	0.00	42.00	8.69	11.06	4.45	0.00	12.80

Monte Terminillo (1750 m a.s.l.), the closest meteorological stations to the study area placed above 1000 m a.s.l. To individuals and plots were assigned the thermometric values from the station closest in altitude to the relevé sites. The thermometric data were interpolated according to Cerquetti & Cruciani (1987), who assert that in the Umbria-Marche Apennines, temperatures decrease by 0.43°C for every 100 meter increase in altitude.

Data analysis

Soil samples were analysed by the Marche Region agro-chemical analysis and research laboratories, according to the methodological standards established by Italian Ministerial Decree 13 Sep. 1999. The parameters determined were percentage of skeleton and texture (percentage of sand, loam, and clay). Soil nitrogen content was not assessed owing to the generally high amount of nutrient in these kinds of soils (Pieruccini 2007) and because some authors have indicated that the nitrogen content and enrichment of soils is not a key factor for the *G. lutea* cultivation (Franz & Fritz 1978).

Following Warren (2008), aspect azimuth was firstly converted from the 0–360 compass scale to a linear (0–180) scale, giving northerly aspect (the shadiest one) a value approaching 0 and southerly aspect (the sunniest one) a value approaching 180, a useful conversion for linear or linearized models. This transformation also converted East and West azimuth degrees so that they were equally distant from North. Moreover, as south-south-west-facing slopes are the warmest aspect (Orsomando et al. 2000), the aspect azimuth was shifted to a minimum on north-north-east slopes (22.5°) and a maximum on south-south-west slopes (202.5°).

We calculated the pH and soil depth mean value for each plot as well as the dry weight of leaves and bracts for each individual of *G. lutea*.

Climatic data (mean monthly temperatures and mean monthly precipitation), latitude, aspect and slope angle served to estimate potential evapotranspiration; soil texture and soil depth data of each individual and of each plot were used to calculate available water capacity (AWC) and soil water reserve. These data were processed using the software developed in Microsoft Office Excel 2000 by Armiraglio et al. (2003), to calculate soil water deficit (mm yr⁻¹), namely the difference between potential and actual evapotranspiration in a given site. This method allows estimation of the available water capacity and of the summer water deficit of the soil, so that the resulting values can be used for making comparisons among sites within homogeneous macro-environmental conditions (Catorci et al. 2011b). As AWC and summer water deficit are key factors to understand the ecological needs of the species, we represented their frequency distribution using box-plots, to search for the possible presence of outliers to be excluded in the definition of the optimal range for the species.

For each environmental variable collected in the plots we calculated basic statistics (mean $\pm$ standard deviation, minimum, maximum, median, 1st and 3rd quartile) that could be used to identify threshold values in view of the drawing of land suitability maps.

To assess the spatial distribution of *G. lutea* stations, the data were divided into two altitudinal classes (below and above 1520 m a.s.l., i.e. the median altitude value). For the two subsets, we calculated again the basic statistics for aspect and slope angle. As data did not meet the assumptions

for parametric tests, we compared median values using the Mann-Whitney U-test.

To analyze the relationships between the data on herb cover and *G. lutea* cover collected in the 10×10 m plots and the environmental variables examined (altitude, aspect, slope, land form, and land use), we performed canonical redundancy analysis (RDA) of the “plot-by-*G. lutea* and herb cover %” matrix, constrained by topographic characteristics (quantitative variables) and by land form and land use types (factorial variables).

To identify the relations between response variables measured for the individuals (dry weight of leaves and bracts, height, leaf cover, number of leaves and bracts and total number of stems) and the explanatory variables (altitude, pH, water deficit, available water capacity, and land use) we performed another RDA of the “plot-by-*G. lutea* individual-variables” matrix. Prior to this RDA, both explanatory quantitative variables and response variables were standardized (variables were rescaled using standard deviation, to have a mean of zero and a standard deviation of one). We ran a global test of RDA results by 1000 permutations; then we calculated the proportion of variance explained by the overall RDA models and by each variable and checked the correlations between response and explanatory variables. Adjusted R-square values (*adj. R*²) were calculated to produce unbiased estimates of the contributions of the independent variables to the explanation of the response variables.

Prior to RDAs we ran detrended correspondence analyses (DCAs) to decide (on the basis of the gradient lengths depicted by axis 1 of DCA) whether the linear or unimodal

model was more appropriate in the subsequent multivariate analyses. DCA results on the data matrices (“plot-by-*G. lutea* and herb cover %” matrix and “plot-by-*G. lutea* individual-variables” matrix) showed short gradients (0.529 S.D., 0.630 S.D., respectively), suggesting that an ordination technique based on the linear model, such as Redundancy analysis, could be used (ter Braak 1995).

To perform statistical elaborations we used the R software (R core team 2013, Oksanen et al. 2013), and *vegan* R-package (version 2.0.9; <http://cran.r-project.org/web/packages/vegan>).

RESULTS

The lowest stations of *G. lutea* were placed at about 1280 m a.s.l., while the highest at about 2240 m a.s.l. *G. lutea* was found on the cooler slopes with moderate slope angle, mostly at altitudes ranging from 1450 to 1750 m. The soil pH varied from sub-acid to neutral (5.2–6.7). The soil depth for the most part exceeded 40 cm. The dominant soil texture was sandy with low percentage of loam, clay and skeleton (table 2). The AWC values within the interquartile range varied from 53 to 91, while those of summer water deficit from 0 to 12.80 mm yr⁻¹ (fig. 1). As shown in table 3, there were some differences between the two altitudinal classes, i.e. below and above 1520 m a.s.l.: the former was linked to northerly aspects, the latter shifted to southerly ones ($P = 0.035$). Moreover, at altitudes higher than 1520 m, slope angle had greater values than at the lower ones ($P < 0.001$).

The proportion of variability of *G. lutea* and herb cover explained by the environmental variables was 26.2% of the total variance. The RDA model was significant ($P = 0.046$). The first RDA axis ($P = 0.001$) (fig. 2) explained 16.7% of the total variability (63.6% of the constrained variance), while the second axis ($P = 0.003$) explained the remaining 9.5% (36.3% of the constrained variance). Slope angle explained the 12.06% ($P = 0.001$) of the total variance (*adj. R*²), altitude the 8.30% ($P = 0.009$). Herb cover was negatively related to slope angle (*adj. R*² = 0.1821, $P < 0.001$) and altitude (*adj. R*² = 0.1327, $P = 0.004$), while *G. lutea* cover was correlated to the type of land form (*adj. R*² = 0.2067, $P < 0.001$), and particularly linked to impluviums.

The proportion of variability of *G. lutea* characteristics (dry weight of leaves and bracts, height of the individual, leaf cover, total number of stems, number of leaves and bracts) explained by the explanatory variables was 15.6% of the total variance. The RDA model was significant ($P = 0.002$). The first RDA axis ($P = 0.001$) explained 12.9% of the total variability (82.6% of the constrained variance); the second axis ($P = 0.127$) explained the remaining 1.7% (11.1% of the constrained variance). The greatest amount of the total variance was explained by AWC (*adj. R*² = 0.0430, $P = 0.005$) and land use (*adj. R*² = 0.0350, $P = 0.046$). Most of the response variables displayed positive correlation with AWC and abandoned condition and inverse correlation with the grazing condition (fig. 3). Altitude exerted a significant negative effect on plant height (*adj. R*² = 0.0319, $P = 0.045$), bract number (*adj. R*² = 0.0522, $P = 0.014$) and bract weight (*adj. R*² = 0.0357, $P = 0.036$), while water deficit and pH had no effect on species performance. The percentages of vari-

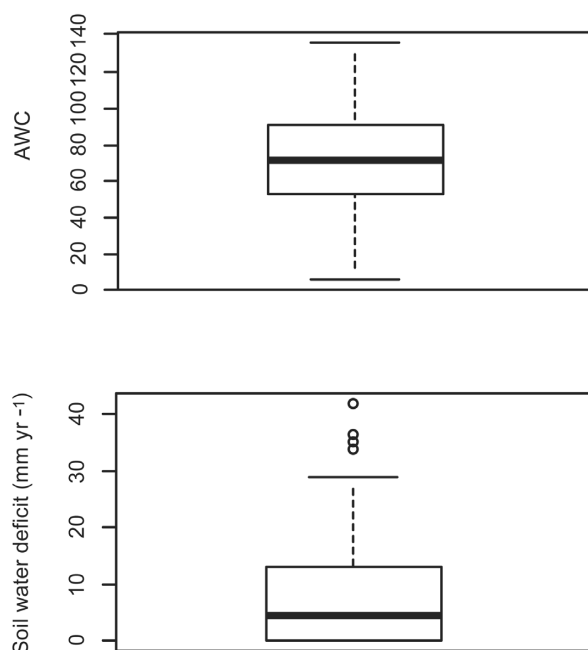


Figure 1 – Box plot diagrams of AWC and soil summer water deficit values referred to 10×10 m plots.

Table 3 – Descriptive statistics of environmental features into two altitudinal classes.

Descriptive statistics of environmental features of plots below 1520 m (1) and above 1520 m a.s.l. (2). Aspect azimuth degree was converted from the 0–360 compass scale to a linear (0–180) scale, giving northerly aspect a value approaching 0 and southerly aspect a value approaching 180, and then shifted to a minimum on north-north-east slopes (22.5°) and a maximum on south-south-west slopes (202.5°). Sig.: significance of differences between the two altitudinal classes after Mann-Whitney U-test.

Environmental features	Altitudinal class	Min	Max	Mean	SD	Median	1 st quartile	3 rd quartile	Sig.
Aspect (azimuth degree)	1	0.00	157.50	51.75	38.36	45.00	22.50	67.50	0.035
	2	0.00	157.50	81.00	55.11	67.50	45.00	135.00	
Slope (vertical degree)	1	0.00	30.00	13.07	7.65	11.00	10.00	20.00	< 0.001
	2	1.00	35.00	21.64	8.28	20.00	15.00	30.00	

ance explained by each explanatory variable in the two RDA models, as well as the correlations between response and explanatory variables are indicated in table 4.

DISCUSSION

Our results revealed that the main driving force influencing *G. lutea* growth and vegetative features in the study area was Available Water Capacity which positively affected vegetative parameter values such as dry matter, height of the individual, number of leaves and total number of stems (fig. 3, table 4). This is a finding in line with the observation of Aiello & Bezzi (1989). The key role played by soil water resources was also emphasised by the fact that the observed soil water deficit (mostly lower than 30 mm yr⁻¹, fig. 1) have relatively low values, thus indicating a very low tolerance of the species to summer water stress. Since AWC depend on soil features as well as topographic characteristics (Armiraglio et al. 2003), one can also understand why the topographic (i.e. altitude, slope aspect, and land form) and pedological conditions (e.g. sand percentage and soil depth) emerged as key factors in shaping the distribution and abundance of *G. lutea*. Indeed, the sub-Mediterranean regions are characterised by summer drought stress with different intensities, de-

pending on the elevation gradient and land form factors such as slope aspect and angle (Rivas-Martínez & Rivas-Saenz 1996–2009). The main ecological factor behind these variables is the total solar radiation amount per unit area (Biondi et al. 2011). Light radiation is not only a beneficial resource, but can also be a detriment, as it determines evaporative water demand and the potential for drought stress (Pausas & Austin 2001). In fact, on south-facing slopes, the greater radiation in summer dramatically reduces the soil water content (Joffre & Rambal 1993), posing one more stress factor faced by plants in mountain areas (Catorci et al. 2013c).

These constraints strongly affect the composition and distribution of plant communities, leading to the dominance of xerophyllous species on south-facing slopes and of mesophilous species on the north-facing slopes (Burrascano et al. 2013, Catorci et al. 2012b). Moreover, the most mesophilous conditions were found on the bottom of flat valleys (Blasi et al. 2012) and this may explain why impluvium (with deeper soils and consequent greater availability of water) emerged as the most suitable land form for the spread of *G. lutea*.

The combination of different landscape attributes also explains the change in the preferential slope aspect between the lower (less than 1520 m a.s.l.) and the upper slopes, that is, the rotation of the distribution area of the *G. lutea* popu-

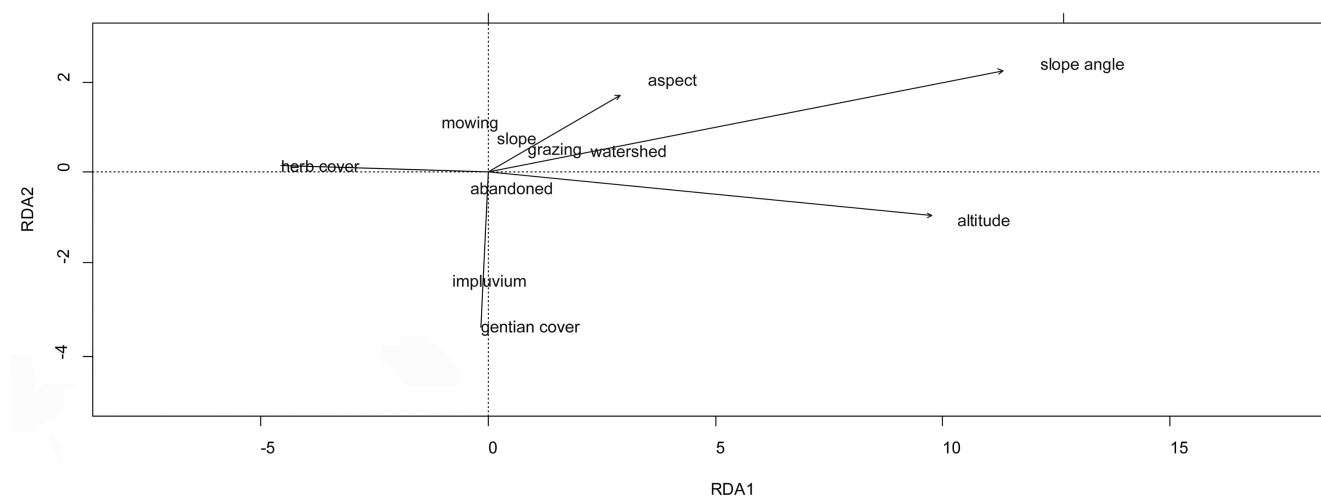


Figure 2 – Redundancy analysis ordination graph for *G. lutea* and herb cover data set (10 × 10 m plots) using topographic variables (aspect, slope angle, altitude), land form (impluvium, slope, watershed) and land use types (mowing, grazing and abandoned conditions).

Table 4 – Proportion of variance (*adj. R*²) of the two response variable data sets.
Data collected along transects in 10 × 10 m plots and for single individuals of *Gentiana lutea* subsp. *lutea* explained by each explanatory variable, and adjusted squared correlation coefficients (*adj. R*²) between response and explanatory variables in the two RDA models (* = *P* < 0.05; ** = *P* < 0.01; *** = *P* < 0.001; n.s.= not significant).

		Response variable	Explanatory variable				
			Altitude	Aspect	Slope angle	Land form	Land use
10 × 10 m plots	Proportion of variance explained (<i>adj. R</i> ²)		0.0830**	-0.0082 ^{n.s.}	0.1206***	0.060 ^{n.s.}	0.0005 ^{n.s.}
	Correlation coefficients (<i>adj. R</i> ²)	<i>Gentiana lutea</i> cover	-0.0184 ^{n.s.}	-0.0128 ^{n.s.}	-0.0049 ^{n.s.}	0.2062***	-0.0091 ^{n.s.}
		Herb layer cover	0.1327**	-0.0060 ^{n.s.}	0.1821***	-0.0112 ^{n.s.}	0.0053 ^{n.s.}
			Altitude	pH	AWC	Water deficit	Land use
Individuals of <i>Gentiana lutea</i> subsp. <i>lutea</i>	Proportion of variance explained (<i>adj. R</i> ²)		0.0143 ^{n.s.}	0.0173 ^{n.s.}	0.0430**	-0.0020 ^{n.s.}	0.0350*
	Correlation coefficients (<i>adj. R</i> ²)	Plant height	0.0319*	0.0450*	0.0647**	0.0093 ^{n.s.}	0.0540*
		No. of stems	-0.0101 ^{n.s.}	-0.0081 ^{n.s.}	0.0399*	-0.0096 ^{n.s.}	0.0050 ^{n.s.}
		Leaf cover	-0.0096 ^{n.s.}	0.0019 ^{n.s.}	0.0022 ^{n.s.}	0.0137 ^{n.s.}	-0.0012 ^{n.s.}
		Leaf number	-0.0098 ^{n.s.}	-0.0064 ^{n.s.}	0.0460*	-0.0104 ^{n.s.}	0.0273 ^{n.s.}
		Leaf weight	0.0010 ^{n.s.}	0.0096 ^{n.s.}	0.0687**	-0.0036 ^{n.s.}	0.0466*
		Bract number	0.0522*	0.0227 ^{n.s.}	0.0260 ^{n.s.}	-0.0030 ^{n.s.}	0.0523*
		Bract weight	0.0357*	0.0564*	0.0534*	-0.0102 ^{n.s.}	0.0612*

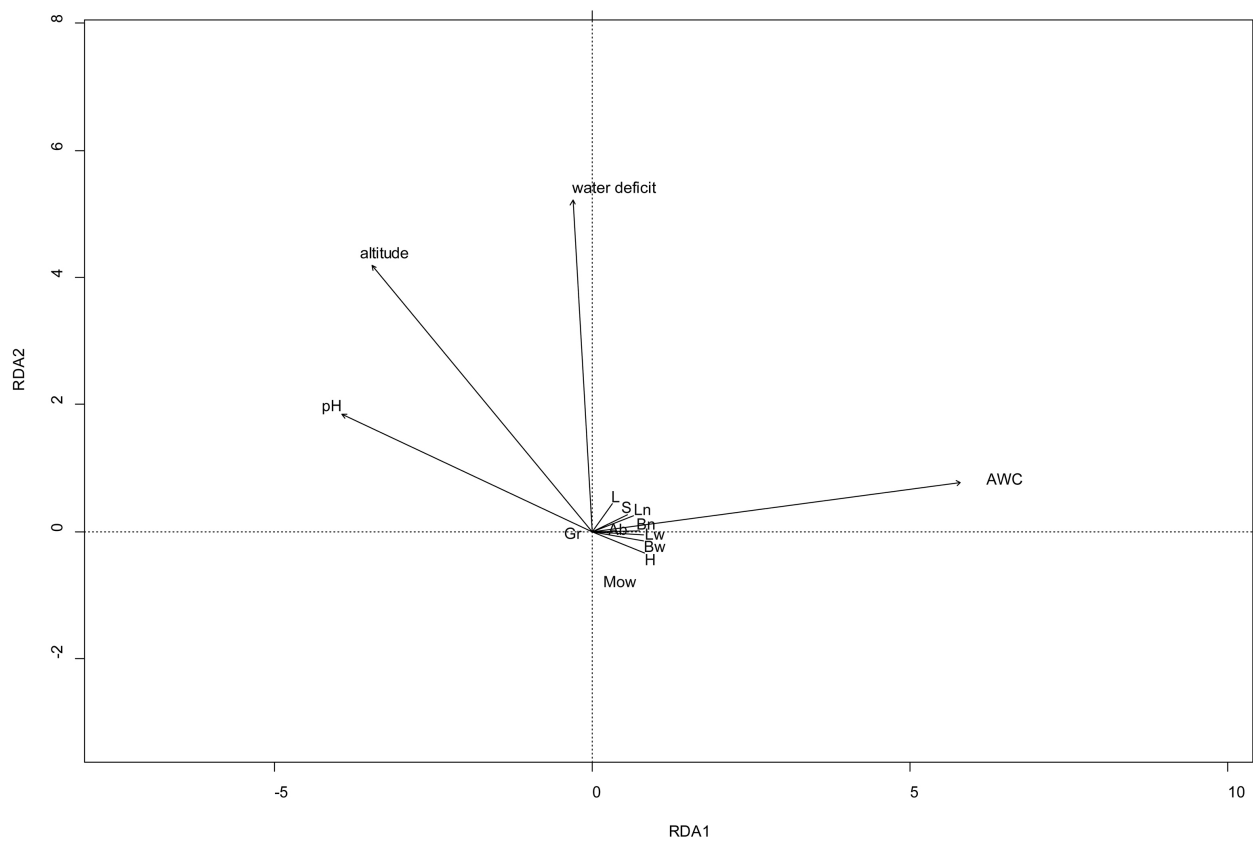


Figure 3 – Redundancy analysis ordination graph for leaves weight (Lw), bracts weight (Bw), height of the individual (H), leaf cover (L), number of leaves (Ln), number of bracts (Bn) and total number of stems (S) using altitude, pH, water deficit, available water capacity (AWC) and land use types, i.e. mowing (Mow), grazing (Gr) and abandoned (Ab) conditions, as explanatory variables.

lations from north-facing to south-facing slopes, following an altitudinal gradient, as shown in figure 2. This is consistent with the general trend of vegetation and species distribution in the sub-Mediterranean mountains (Orsomando et al. 2000). In terms of *G. lutea* cultivation, it follows that the lower the altitude of the farming property the more important it is to choose wet and cool conditions such as those found on impluvium on north-facing slopes.

These factors may also explain the regional distribution of *G. lutea*, which is absent in the mountains situated at north of the Sibillini Mountains (Ballelli & Pedrotti 1992), though their average altitudes (1400–1500 m a.s.l.) should allow the growth of this species. Indeed, the rainfall in these mountains is 200–300 mm yr⁻¹ less than that in the Sibillini (Amici & Spina 2002), thus it may be hypothesized that the greater summer water stress in these mountains hinders the spread of *G. lutea*.

Climatic change projections for the Mediterranean basin predict a long-term downward trend in rainfall and an increase in temperature, especially during the hot season (Kutiel & Maheras 1998), which should cause greater aridity during the summer (Giorgi & Lionello 2008, Savo et al. 2012). The results of our study, as well as the projections for climate change in this area, confirm the opinion of Gentili et al. (2013) that *G. lutea* is threatened by the global warming, and indicate that the distribution of the species will probably shrink progressively, withdrawing to higher altitudes and a more limited set of land forms; i.e. at lower altitudes, species should be restricted to slightly steep slopes, concave land forms, and northerly shady aspects.

Data on land use showed that abandonment is the most suitable condition for the spread of *G. lutea*. Indeed, as shown in the RDA graph, abandoned grasslands host populations of *G. lutea*, with a higher number of individuals, with greater values of vegetative traits than in the other land use typologies. This is the typical behaviour of a competitive and dominant species (Grime 2001) and is consistent with the findings of many authors (e.g. Andersen et al. 1990, Grime 2001, Huhta et al. 2001, Catorci et al. 2014) in explaining how abandonment affects dominant tall species.

In conclusion, as we identified the critical importance of soil water capacity in southern European mountain systems, one can argue that this factor may be the main constraint to be considered aiming the cultivation of *G. lutea*. In fact, some authors indicated that the nitrogen content and enrichment of soils is not a key factor (Franz & Fritz 1978) as well as the soil pH value, considering the variety of ecotypes in which the species grows (Bezzi et al. 1996).

Assuming that interquartile range as a proxy to identify the optimal growth conditions, the optimal altitudinal interval ranges from 1488 to 1742 m, encompassing the north-facing slopes (from North-East to South-East or from West to North) and the flat bottom of impluviums. Within this range of topographic conditions, the optimal soil features are sandy soils (from 55 to 72%) with depth higher than 40 cm and pH values between 5.2 and 6.7. Moreover, considering the altitude distribution range, and especially its lower boundary (1280 m), joint to our results and the rainfall features of the study area (Amici & Spina 2002), we can in-

fer that the species thrives when the annual rainfall exceeds 1000–1100 mm, with not less than 250–260 mm in summer, while, as highlighted in figure 1, the AWC should be higher than 50–55, and the summer water deficit should not exceed 28–30 mm yr⁻¹. These water deficit values may be considered as a threshold value for summer drought stress, which in turn could be useful for calibrating the realised niche breadth (Lawesson & Oksanen 2002, Smart et al. 2010) and land suitability for this species.

CONSERVATION AND MANAGEMENT PROSPECTS

The quantitative assessment of the variables affecting *G. lutea* distribution in the climatic context of sub-Mediterranean mountains should prove valuable for future applied research to define the suitability of a territory for *G. lutea* cultivation. Indeed, in the context of land suitability analysis the main goal is to identify the best sites for some activities, given a set of potential or feasible sites. In this type of inquiry, the main challenge is to rank or rate the suitability of alternative sites for a given activity, and to define their boundaries (Malczewski 2004). This ranking is achieved by assessing how well the characteristics of the sites meet specific requirements, preferences, or predictors of success for some activity (Collins et al. 2001). With this object in view, our research provides the basic quantitative data needed for such future analysis.

Finally, an interesting paradox emerges from our finding, on one hand, that pasture abandonment is a positive factor enhancing *G. lutea* spread, and the well known observation, on the other hand, that grazing and mowing act as a driving force in determining and preserving the biodiversity of pastoral ecosystems (MacDonald et al. 2000, Kahmen et al. 2002, Peco et al. 2006, Catorci et al. 2011a, 2013a). How are decision makers to act, then, to conserve both the presence of *G. lutea* and grassland biodiversity, especially in protected areas? On the basis of our research, we suggest a management plan that allows some partially abandoned lands (where the spread of *G. lutea* is facilitated) to remain free of mowing and grazing, with only minimal intervention to counter shrub invasion.

ACKNOWLEDGEMENTS

This research was funded by the European Union's "Green Mountain Project" (<http://www.greenmountain-see.eu>), part of the South East Europe Transnational Cooperation Programme (Lead Partner: Province of Macerata). The authors wish to thank Marco Tavoloni, Nicola Postiglione, Riccardo Pennesi and Luca Malatesta for their help in field data collection, and Sheila Beatty for editing the English usage of the manuscript.

REFERENCES

- Agnoletti M. (2007) The degradation of traditional landscape in a mountain area of Tuscany during the 19th and 20th centuries: Implications for biodiversity and sustainable management. *Forest Ecology and Management* 249: 5–17. <http://dx.doi.org/10.1016/j.foreco.2007.05.032>

- Aiello N., Bezzi A. (1989) La coltivazione di *Gentiana lutea* L. in ambienti semiaridi del Trentino meridionale e dell'Appennino settentrionale e centrale: *Annali dell'Istituto sperimentale per l'assessamento forestale e per l'apicoltura* 9: 237–264.
- Aiello N., Bezzi A. (1998) *Genziana maggiore* (*Gentiana lutea* L.): aspetti biologici, qualitativi e riproduttivi. *Agricoltura Ricerca* 176: 8–17.
- Amici M., Spina R. (2002) Campo medio della precipitazione annuale e stagionale sulle Marche per il periodo 1950–2000. *Macerata, Centro di Ecologia e Climatologia, Osservatorio Geofisico Sperimentale Macerata*.
- Andersen H., Bakker J.P., Brongers B., Heydemann B., Irmeler U. (1990) Long-term changes of salt marsh communities by cattle grazing. *Vegetatio* 89: 137–148. <http://dx.doi.org/10.1007/BF00032166>
- Antrop M. (2004) Landscape change and the urbanization process in Europe. *Landscape and Urban Planning* 67: 9–26. [http://dx.doi.org/10.1016/S0169-2046\(03\)00026-4](http://dx.doi.org/10.1016/S0169-2046(03)00026-4)
- Armigliano S., Cerabolini B., Gandellini F., Gandini P., Andreis C. (2003) Calcolo informatizzato del bilancio idrico del suolo. *Natura Bresciana, Annali Museo Civico Scienze Naturali, Brescia* 33: 209–216.
- Ballelli S., Pedrotti F. (1992) Le emergenze botanico-vegetazionali della Regione Marche. *Ancona, Regione Marche*.
- Ballelli S., Biondi E., Brilli-Cattarini A.J.B., Cortini Pedrotti C., Francalancia C., Orsomando E., Pedrotti F. (1981) Schede delle aree floristiche delle Marche. *Regione Marche, Italy*.
- Ballelli S., Lucarini D., Pedrotti F. (2005) *Catalogo dell'Erbario dei Monti Sibillini di Vittorio Marchesoni*. Camerino. *Braun Blanquetia* 38: 3–257.
- Ballelli S., Cesaretti S., Gatti R., Montenegro B.F., Vitanzi A., Catorci A. (2010) *Catalogo bibliografico della flora vascolare dei Monti Sibillini: (Appennino centrale - Italia)*. Camerino. *Braun Blanquetia* 47: 5–127.
- Bellomaria B., Salvucci M., Valentini G. (1981) Morfologia, principi attivi e distribuzione di *Gentiana lutea* nelle Marche e nell'Umbria. *Acta biologica* 58: 57–75.
- Bezzi A., Vender C., Scartezzini F. (1996) Dati morfologici rilevati su coltivazioni di *Gentiana lutea* (1981–1994). In: *Atti del Convegno "Genziana e specie amaro-aromatiche. Ricerche ed Applicazioni"* Camerino 8–10 giugno 1995. *L'uomo e l'ambiente* 19: 35–56.
- Biondi E., Baldoni M. (1995) A possibile method for geographic delimitation of phytoclimate of the Marche region of Italy. *Documents phytosociologiques* 15: 15–28.
- Biondi E., Casavecchia S., Pesaresi S. (2011) Phytosociological synrelevés and plant landscape mapping: From theory to practice. *Plant Biosystems* 145: 261–273. <http://dx.doi.org/10.1080/11263504.2011.572569>
- Blasi C. (1994) Fitoclimatologia del Lazio. *Fitosociologia* 27: 151–175.
- Blasi C., Carranza M., Frondoni R., Rosati L. (2000) Ecosystem classification and mapping: a proposal for Italian landscape. *Applied Vegetation Science* 3: 233–242. <http://dx.doi.org/10.2307/1479002>
- Blasi C., Tilia A., Rosati L., Del Vico E., Copiz R., Ciaschetti G., Burrascano S. (2012) Geographical and ecological differentiation in Italian mesophilous pastures referred to the alliance *Cynosurion cristati* Tx. 1947. *Phytocoenologia* 41: 217–229. <http://dx.doi.org/10.1127/0340-269X/2011/0041-0504>
- Bracchetti L., Carotenuto L., Catorci A. (2012) Land-cover changes in a remote area of central Apennines (Italy) and management directions. *Landscape and Urban Planning* 104: 157–170. <http://dx.doi.org/10.1016/j.landurbplan.2011.09.005>
- Burrascano S., Anzellotti I., Carli E., Del Vico E., Facioni L., Pretto F., Sabatini F.M., Tilia A., Blasi C. (2013) Drivers of beta-diversity variation in *Bromus erectus* semi-natural dry grasslands. *Applied Vegetation Science* 16: 404–416. <http://dx.doi.org/10.1111/avsc.12021>
- Carnat A., Fraisse D., Carnat A.P., Felgines C., Denis D., Lamaison J.L. (2005) Influence of drying mode on iridoid bitter constituent levels in gentian root. *Journal of the Science of Food and Agriculture* 85: 598–602. <http://dx.doi.org/10.1002/jsfa.2011>
- Catorci A., Ottaviani G., Ballelli S., Cesaretti S. (2011a) Functional differentiation of Central Apennine grasslands under mowing and grazing disturbance regimes. *Polish Journal of Ecology* 59: 115–128.
- Catorci A., Vitanzi A., Tardella F.M. (2011b) Variations in CSR strategies along stress gradients in the herb layer of submediterranean forests (central Italy). *Plant Ecology and Evolution* 144: 299–306. <http://dx.doi.org/10.5091/plecevo.2011.621>
- Catorci A., Foglia M., Tardella F.M., Vitanzi A., Sparvoli D., Gatti R., Galli P., Paradisi L. (2012a) Map of changes in landscape naturalness in the Fiastra and Salino catchment basins (central Italy). *Journal of Maps* 8: 97–106. <http://dx.doi.org/10.1080/17445647.2012.668769>
- Catorci A., Ottaviani G., Vitasović Kosić I., Cesaretti S. (2012b) Effect of spatial and temporal patterns of stress and disturbance intensities in a sub-Mediterranean grassland. *Plant Biosystems* 146: 352–367. <http://dx.doi.org/10.1080/11263504.2011.623192>
- Catorci A., Cesaretti S., Gatti R. (2013a) Effect of long-term abandonment and spring grazing of floristic and functional composition of dry grasslands in a Central Apennine farmland. *Polish Journal of Ecology* 61: 505–518.
- Catorci A., Cesaretti S., Tardella F.M. (2013b) The geosynphyto-sociological approach as a tool for agriculture innovation: the study case of saffron (*Crocus sativus* L.) cultivation suitability assessment in the Macerata district (central Italy). *Plant Sociology* 50: 79–91.
- Catorci A., Tardella F.M., Cutini M., Luchetti L., Paura B., Vitanzi A. (2013c) Reproductive traits variation in the herb layer of a submediterranean deciduous forest landscape. *Plant Ecology* 214: 737–749. <http://dx.doi.org/10.1007/s11258-013-0203-0>
- Catorci A., Antolini E., Tardella F.M., Scocco P. (2014) Assessment of interaction between sheep and poorly palatable grass: a key tool for grassland management and restoration. *Journal of Plant Interactions* 9: 112–121. <http://dx.doi.org/10.1080/17429145.2013.776706>
- Cerquetti F., Cruciani G. (1987) *Caratterizzazione climatologia del territorio marchigiano. Un'analisi dei parametri climatici della Regione*. Roma, Osservatorio geofisico di Macerata, ENEA.
- Choler P., Michalet R. (2002) Niche differentiation and distribution of *Carex curvula* along a bioclimatic gradient in the southwestern Alps. *Journal of Vegetation Science* 13: 851–858. <http://dx.doi.org/10.1111/j.1654-1103.2002.tb02114.x>
- Collins M.G., Steiner F.R., Rushman M.J. (2001) Land use suitability analysis in the United States: historical development and promising technological achievements. *Environmental Management* 28: 611–621. <http://dx.doi.org/10.1007/s002670010247>
- Costanzo E., Furnari F., Tomaselli V. (2009) A phytosociological survey of the main plant community types of alpine and sub-alpine belt in the Sibillini Mountains (Central Apennines, Italy). *Lazaroa* 30: 219–250.

- Desmarest P., Derchue D. (1988) La culture de la gentiane jaune en France. Techniques de production et amelioration. In: Sixieme Colloque International consacré aux plantes médicinales et substances d'origine naturelle, Angers, 3 et 4 juin 1988: 33–40. Angers, Université d'Angers.
- Falcucci A., Maiorano L., Boitani L. (2007) Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. *Landscape Ecology* 22: 617–631. <http://dx.doi.org/10.1007/s10980-006-9056-4>
- Franz C., Fritz D. (1978) Cultivation aspects of *Gentiana lutea* L., Spice and Medicinal plants. *Acta Horticulturae* 73: 307–314.
- Galambosi B., Galambosi Zs. (2010) Seedling quality and seed yield of *Gentiana lutea* L. *Acta Horticulturae* 860: 255–258.
- Gentili R., Ardenghi N.M.G., Armiraglio S., Bacchetta G., Bartolucci F., Cogoni D., Conti F., Fenu G., Fisogni A., Galloni M., Gigante D., Maneli F., Parolo G., Rossi M., Santangelo A., Selvaggi A., Wagensommer R.P. (2013) *Gentiana lutea* L. s.l. *Informatore Botanico Italiano* 45: 115–193.
- Geri F., Rocchini D., Chiarucci A. (2010) Landscape metrics and topographical determinants of large-scale forest dynamics in a Mediterranean landscape. *Landscape and Urban Planning* 95: 46–53. <http://dx.doi.org/10.1016/j.landurbplan.2009.12.001>
- Giorgi F., Lionello P. (2008) Climate change projections for the Mediterranean region. *Global and Planetary Change* 63: 90–104. <http://dx.doi.org/10.1016/j.gloplacha.2007.09.005>
- Giovagnotti, C., Calandra, R., Leccese, A., Giovagnotti, E. (2003) I Paesaggi Pedologici e la Carta dei Suoli dell'Umbria. Perugia, Camera di Commercio, Industria, Artigianato e Agricoltura di Perugia.
- Giovanardi R., Barbaro M. (2009) Sviluppo della Filiera produttiva della Genziana Maggiore in Friuli Venezia Giulia. Verona, Forum.
- Gonzales O., Mayo S., Rodriguez A., Casquero P.A. (2012) Effect of soil in the growth of *Gentiana lutea* radical system in North Mountain of Leon (Spain). *Acta Horticulturae* 955: 281–286.
- Grime J.P. (1974) Vegetation classification by reference to strategies. *Nature* 250: 26–31. <http://dx.doi.org/10.1038/250026a0>
- Grime J.P. (2001) Plant strategies, vegetation processes and ecosystem properties. Chichester, Wiley.
- Holobiuc I., Catana R. (2012) Recurrent somatic embryogenesis in long-term cultures of *Gentiana lutea* L. as a source for synthetic seed production for medium-term preservation. *Archives of Biological Sciences* 64: 809–817. <http://dx.doi.org/10.2298/ABS1202809H>
- Huhta A.P., Rautio P., Tuomi J., Laine K. (2001) Restorative mowing on an abandoned semi-natural meadow: short-term and predicted long-term effects. *Journal of Vegetation Science* 12: 677–686. <http://dx.doi.org/10.2307/3236908>
- Joffe R., Rambal S. (1993) How tree cover influences the water balance of Mediterranean rangelands. *Ecological Society of America* 74: 570–582. <http://dx.doi.org/10.2307/1939317>
- Kery M., Matthies D., Spilman H.H. (2000) Reduced fecundity and offspring performance in small populations of the declining grassland plants *Primula veris* and *Gentiana lutea*. *Journal of Plant Ecology* 88: 17–30. <http://dx.doi.org/10.1046/j.1365-2745.2000.00422.x>
- Kahmen S., Poschlod P., Schreiber K. (2002) Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. *Biological Conservation* 104: 319–328. [http://dx.doi.org/10.1016/S0006-3207\(01\)00197-5](http://dx.doi.org/10.1016/S0006-3207(01)00197-5)
- Kutiel H., Maheras P. (1998) Variations in the temperature regime across the Mediterranean during the last century and their relationship with circulation indices. *Theoretical and Applied Climatology* 61: 39–53. <http://dx.doi.org/10.1007/s007040050050>
- Lange D. (1998) Europe's medicinal and aromatic plants: their use, trade and conservation. Cambridge, TRAFFIC International.
- Lawesson J.E., Oksanen J. (2002) Niche characteristics of Danish woody species as derived from coenoclines. *Journal of Vegetation Science* 13: 279–290. <http://dx.doi.org/10.1111/j.1654-1103.2002.tb02048.x>
- MacDonald D., Crabtree J.R., Wiesinger G., Dax T., Stamou N., Fleury P., Lazpita J.G., Gibon A. (2000) Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *Journal of Environmental Management* 59: 47–69. <http://dx.doi.org/10.1006/jema.1999.0335>
- Malczewski J. (2004) GIS-based land-use suitability analysis: a critical overview. *Progress in Planning* 62: 3–65. <http://dx.doi.org/10.1016/j.progress.2003.09.002>
- Mazzoleni S., Di Pasquale G., Mulligan M., Di Martino P., Rego F. (2004) Recent dynamics of the Mediterranean vegetation and landscape. Chichester, Wiley & Sons. <http://dx.doi.org/10.1002/0470093714>
- Menghini, A., Pocceschi N., Matteini G.M. (1996) Un quinquennio di coltivazione sperimentale di *Gentiana lutea* L. in provincia di Rieti. In: Genziana e specie amaro-aromatiche. Ricerche e Applicazioni. Camerino, 8–10 giugno 1995. L'uomo e l'ambiente 19: 163–166.
- Metzger M.J., Rounsevell M.D.A., Acosta-Michlik L., Leemans R., Schröter D. (2006) The vulnerability of ecosystem services to land use change. *Agriculture, Ecosystems & Environment* 114: 69–85. <http://dx.doi.org/10.1016/j.agee.2005.11.025>
- Nastasićević B., Lazarević-Pašti T., Dimitrijević-Branković S., Pašti I., Vujačić A., Joksić G., Vasić V. (2012) Inhibition of myeloperoxidase and antioxidative activity of *Gentiana lutea* extracts. *Journal of Pharmaceutical and Biomedical Analysis* 66: 191–196. <http://dx.doi.org/10.1016/j.jpba.2012.03.052>
- Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Wagner H. (2013) Vegan: Community Ecology Package. R package version 2.0-9. Available from <http://cran.r-project.org/web/packages/vegan> [accessed 20 Mar. 2014].
- Orsomando E., Catorci A., Pitzalis M., Raponi M. (2000) The phytoclimate of Umbria. *Parlatorea* 6: 5–24.
- Pausas J.G., Austin M.P. (2001) Patterns of plant species richness in relation to different environments: an appraisal. *Journal of Vegetation Science* 12: 153–166. <http://dx.doi.org/10.2307/3236601>
- Peco B., Sánchez A.M., Azcárate F.M. (2006) Abandonment in grazing systems: Consequences for vegetation and soil. *Agriculture, Ecosystems & Environment* 113: 284–294. <http://dx.doi.org/10.1016/j.agee.2005.09.017>
- Petrova M., Zagorska N., Tasheva K., Evstatieva L. (2006) In vitro propagation of *Gentiana lutea* L. *Genetics and Breeding* 35: 63–68.
- Pieruccini P. (2007) Suoli e geomorfologia delle praterie montane dell'Appennino umbro-marchigiano. *Braun-Blanquetia* 42: 19–36.
- Pignatti S. (1982) Flora d'Italia. Bologna, Edagricole.
- Regione Marche (1991) L'ambiente fisico delle Marche. Geologia, geomorfologia e idrogeologia. Regione Marche, Giunta Regionale, Assessorato Urbanistica e Ambiente. Ancona, Italy.
- Rivas-Martínez S., Rivas-Saenz S. (1996–2009) Worldwide Bioclimatic Classification System, Phytosociological Research Cen-

- ter, Spain. Available from <http://www.globalbioclimatics.org> [accessed 20 Mar. 2013].
 - Rivas-Martínez S., Asensi A., Díez-Garretas B., Molero J., Valle F., Cano E., Costa M., López M. L., Díaz T.E., Prieto J.A.F. et alii (2007) Mapa de series, geoseries y geopermaseries de vegetación de España. Parte I. *Itinera Geobotanica* 17: 5–436.
 - Rossi M. (2012) Taxonomy, phylogeny and reproductive ecology of *Gentiana lutea* L. PhD thesis, Bologna, Italy.
 - R Core Team (2013) R: A language and environment for statistical computing, version 3.0.2. R Foundation for Statistical Computing, Wien, Austria. Available from <http://www.R-project.org> [accessed 20 Mar. 2014].
 - Savo V., De Zuliani E., Salvati L., Perini L., Caneva G. (2012) Long-term changes in precipitation and temperature patterns and their possible impacts on vegetation (Tolfa-Cerite area, central Italy). *Applied Ecology and Environmental Research* 10: 243–266.
 - Smart S.M., Scott W.A., Whitaker J., Hill M.O., Roy D.B., Critchley C.N., Marini L., Evans C., Emmett B.A., Rowe E.C., Crowe A., Le Duc M., Marrs R.H. (2010) Empirical realised niche models for British higher and lower plants – development and preliminary testing. *Journal of Vegetation Science* 21: 643–656. <http://dx.doi.org/10.1111/j.1654-1103.2010.01173.x>
 - ter Braak C.J.F. (1995) Ordination. In: Jongman R.H.G., ter Braak C.J.F., van Tongeren O.F.R. (eds) *Data Analysis in Community and Landscape Ecology*: 91–173. New York, Cambridge University Press.
 - Warren R.J. II (2008) Mechanisms driving understory evergreen herb distributions across slope aspects: as derived from landscape position. *Plant Ecology* 198: 297–308. <http://dx.doi.org/10.1007/s11258-008-9406-1>
- Manuscript received 9 Jan. 2014; accepted in revised version 24 Mar. 2014.
- Communicating Editor: Elmar Robbrecht.