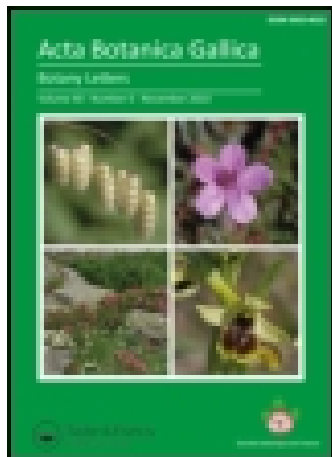


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Acta Botanica Gallica: Botany Letters

Publication details, including instructions for authors and subscription information:
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Ecology and phytosociology of endangered psammophytic species of the *Omphalodes* genus in western Europe

Carlos Neto^a, João Paulo Fonseca^b, José Carlos Costa^c & Frédéric Bioret^d

^a Centre of Geographical Studies, Institute of Geography and Spatial Planning, University of Lisbon, Alameda da Universidade, Lisbon, Portugal

^b Biosciences Center, UIEE-ISPA IU, Lisbon, Portugal

^c Centre for Botany Applied to Agriculture, Instituto Superior de Agronomia, University of Lisbon, Lisbon, Portugal

^d EA 2219 Géoarchitecture, Université de Bretagne occidentale, UFR Sciences et Techniques, Brest, France

Published online: 13 Jan 2015.

To cite this article: Carlos Neto, João Paulo Fonseca, José Carlos Costa & Frédéric Bioret (2015): Ecology and phytosociology of endangered psammophytic species of the *Omphalodes* genus in western Europe, *Acta Botanica Gallica: Botany Letters*, DOI: [10.1080/12538078.2014.981290](https://doi.org/10.1080/12538078.2014.981290)

To link to this article: <http://dx.doi.org/10.1080/12538078.2014.981290>

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Ecology and phytosociology of endangered psammophytic species of the *Omphalodes* genus in western Europe

Carlos Neto^{a*}, João Paulo Fonseca^b, José Carlos Costa^c and Frédéric Bioret^d

^aCentre of Geographical Studies, Institute of Geography and Spatial Planning, University of Lisbon, Alameda da Universidade, Lisbon, Portugal; ^bBiosciences Center, UIEE-ISPA IU, Lisbon, Portugal; ^cCentre for Botany Applied to Agriculture, Instituto Superior de Agronomia, University of Lisbon, Lisbon, Portugal; ^dEA 2219 Géoarchitecture, Université de Bretagne occidentale, UFR Sciences et Techniques, Brest, France

Abstract: *Omphalodes kuzinskyanae* Willk. is an endangered annual plant of the family Boraginaceae, endemic to a narrow coastal area in the Lisbon region (Portugal). *Omphalodes littoralis* Lehm. occurs in northwest Spain (subsp. *gallaecica*) and northwest France (subsp. *littoralis*). Three approaches were used to assess the ecological requirements of *O. kuzinskyanae*: (1) physical and chemical characterization of their habitat soil; (2) phytosociological analysis; (3) comparison of several life history parameters under different light conditions. Germination experiments were conducted to evaluate seed dormancy. The results show that *O. kuzinskyanae* occurs in thin sandy soil with a substantial amount of organic matter and clay, mostly over limestone pavements. Phytosociological analysis shows that *O. kuzinskyanae* occurs both in sciophytic and heliophytic communities. Life history comparisons demonstrated that this plant has a strong preference for sciophytic conditions: under strong shade, plants have a higher survival rate, attain a greater height and width, and produce approximately nine times more seeds than in sunny conditions. In contrast with *O. kuzinskyanae*, published data on *O. littoralis* indicate that this species occurs in heliophytic conditions. This group of *Omphalodes* is possibly limited both in geographical distribution and habitat by its vulnerability to hydric stress. Scenarios are discussed that can explain the extensive gap separating the present ranges of the two species and their ecological differences. We propose two new syntaxa: *Linario arenariae-Omphalodetum littoralis*, *Geranio purpurei-Galietum minutuli omphalodetosum kuzinskyanae*.

Keywords: *Omphalodes kuzinskyanae*; *Omphalodes littoralis*; sciophytes; autecology; biogeography; phytosociology; conservation

Introduction

Omphalodes kuzinskyanae Willk. is a small Boraginaceous therophyte, restricted to a few endangered populations in a narrow coastal area near Lisbon (Albuquerque, Bernardes, and Fonseca 2004). *Omphalodes littoralis* is a close relative, which has a broader geographical distribution, ranging from the southern coast of Galicia to northwestern France (Figure 1). *Omphalodes kuzinskyanae* is classified as endangered (ICN 2006) and is protected by the Berne Convention and listed in Annex II of the Directive (ICN 2006). *Omphalodes littoralis* subsp. *littoralis* is considered as vulnerable in France (Dupont and Lahondère 1995) and endangered in Spain (Moreno-Saiz 2008; Lozano, Rebelo, and Bittman 2012). It is also listed in Annex II of the European Habitats Fauna Flora directive (1992) (Bioret 1993).

Both plants from Portugal and Galicia are morphologically so similar that, until some decades ago, Galician populations were classified as *O. kuzinskyanae*. However, in 1971, Lainz reclassified these populations as belonging to *O. littoralis*, proposing a new subspecies: *O. littoralis* subsp. *gallaecica* M. Lainz, stressing seed morphology (Lainz 1971) (Figure 2). This

taxonomic proposal is consistent with chromosome counts, which are $2n = 24$ for Galician and French populations (Fernández-Casas 1975; Buord 1997, respectively), and $2n = 28$ for the Portuguese populations (Franco 1984). Nowadays, three endemic taxa are recognized within this group (Figure 1 and Table 1): *O. littoralis* subsp. *littoralis* (inhabiting the western and northeastern Atlantic coasts of France and Spain, respectively), *O. littoralis* subsp. *gallaecica* (restricted solely to Galicia, Spain), and *O. kuzinskyanae* (coastal area near Lisbon, Portugal).

In France, *O. littoralis* subsp. *littoralis* presents a typical coastal thermo-Atlantic species: quite frequent on both continental and insular dune systems from the south of Landes up to the Loire estuary, it remains then only in islands off the coast of Brittany: Hoëdic, Houat, Belle-Île, and in the Quiberon peninsula, and reaches its northernmost limit of distribution in the Glénan archipelago (Dupont 1962; Bioret 1989). These insular northern localities correspond to the most thermophytic climatic conditions of the Massif Armoricain: temperature 12°C, precipitation 500–600 mm, characterized by a summer drought (Bioret 1989). Along

*Corresponding author. Email: cneto@campus.ul.pt

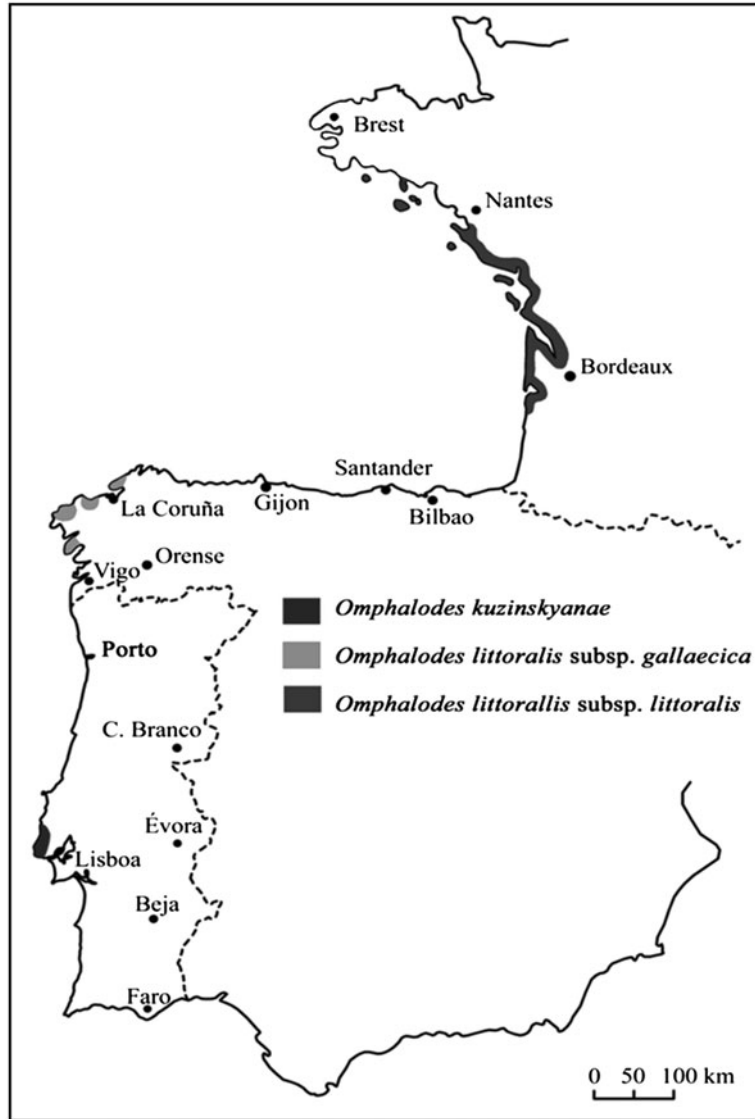


Figure 1. Geographic range of *Omphalodes kuzinskyanae* and *Omphalodes littoralis* (adapted from Dupont and Lahondère 1995; Albuquerque, Bernardes, and Fonseca 2004; Serrano and Carbajal 2004).

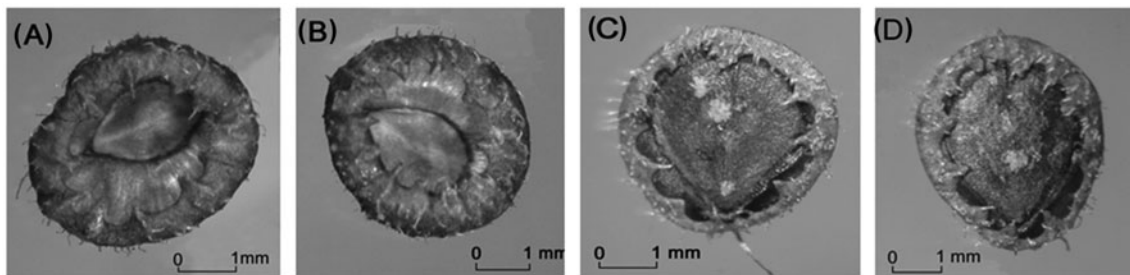


Figure 2. Seeds of *Omphalodes kuzinskyanae* (A, B) and *Omphalodes littoralis* subsp. *gallaecica* (C, D). *Omphalodes kuzinskyanae* have nutlets $3.8\text{--}5.3 \times 2.7\text{--}5.0$ mm, loose, with wing strongly incurved crenate or dentate (with teeth lacking hair), while *O. littoralis* subsp. *gallaecica* have nutlets $3\text{--}4 \times 2.5\text{--}3.5$ mm, densely hirsute, with wings slightly incurved, dentate or lobed (each lobe or tooth ended in a hooked hair).

the French Atlantic coasts, its geographic distribution is similar to that of *Sonchus bulbosus* (Bioret 1989).

As shown in Figure 1, there is a gap between the geographical ranges of *O. kuzinskyanae* and *O. littoralis*

Table 1. Synthetic table summarizing the differences between *Omphalodes kuzinskyanae*, *O. littoralis* subsp. *gallaecica* and *O. littoralis* subsp. *littoralis*.

	<i>Omphalodes kuzinskyanae</i>	<i>Omphalodes littoralis</i> subsp. <i>gallaecica</i>	<i>Omphalodes littoralis</i> subsp. <i>littoralis</i>
Stem	3–15 cm, erect	to 13 cm, prostrate rarely erect	3–15 cm erect
Basal leaves	3.2 × 0.6 cm, spatulate petiolate	3.2 × 0.6 cm, spatulate petiolate	1–2(3) × 0.3–1.1 cm, spatulate long-petiolate
Cauline leaves	2.5 × 0.8 cm, elliptic to ovate sessile	2.2 × 0.7 cm, elliptic to ovate sessile	<2 cm lanceolate sessile
Inflorescence	lax up 6 cm in frutification, bractate at least in part	lax up 5 cm, in frutification, bractate	lax, bractate
Flower	to 3 mm (flower) erect to erect-patent	to 5 mm (flower), erect	1–4 mm (flower), erect
	12 (25) mm (fruit) erect-patent to patent	12(20) (fruit), erect-patent slightly deflexed	10(12) mm (fruit), erect-patent slightly deflexed
	3 mm (flower), 5.5 (fruit)	2–3.5 mm (flower), 4–6.5 (fruit)	3–4 mm (flower), 6 mm (fruit)
	lobes 1 mm, width lanceolate (flower)	lobes 2–3.5 mm width elliptical (flower)	lobes elliptical (flower)
	lobes 3.5 width broadly lanceolate or nearly elliptical (fruit)	lobes 4.5–6.5 width, ovate (fruit)	lobes ovate (fruit)
	6–7.5 mm, blue rarely white	6–7.5 mm, white with blue dye	3–5(6) mm, white
	nutlets 3.8–5.3 × 2.7–5 mm, loosely pilous	nutlets 3–4 × 2.5–3.5 mm, densely hirsute	nutlets densely hirsute
Fruit (see Figure 2)	wing strongly incurved crenate or dentate, with teeth lacking hair	wing slightly incurved, dentate or lobed, each lobe or tooth ended in a hooked hair	wing erect, entire, ciliate and narrow

subsp. *gallaecica*. This gap coincides with an almost continuous sandy coast, between 10 km north of Lisbon and southern Galicia. This gap is due to a particular topoclimate in the Sintra region, with a high number of summer and spring fogs (Daveau 1985). The frequency of fog decreases northward until Aveiro from where the coast is predominantly formed by cliffs. The same gap exists between *O. littoralis* subsp. *gallaecica* and *O. littoralis* subsp. *littoralis* because of the non-existence of suitable habitat for psammophytic *Omphalodes* taxa.

Information on the ecology of *O. kuzinskyanae* appears relevant for its conservation and establishment of a successful management plan. Therefore, soil characteristics, phytosociology and light conditions of its habitats, as well as seed germination rates were studied. Since *O. littoralis* s.l. represents a close relative to *O. kuzinskyanae*, comparative research on habitat preference was performed by means of original and published phytosociological data.

Material and methods

Seed germination rate was determined by the following procedure: two samples comprising 123 and 113 seeds taken from the wild the previous spring were placed in flower pots in October, over two consecutive years. Seedlings were counted in winter and spring and non-germinated seeds were left in the pots until the end of the summer in the following year.

Soil characteristics were determined through the analysis of 20 samples for granulometry and 27 samples for chemical analyses, respectively (Figure 3). Samples were taken at 0–10-cm depth and sampling points were selected to ensure that they fell inside areas occupied by *O. kuzinskyanae*. The chemical analyses and granulometry were performed by a governmental reference laboratory (Laboratório Rebelo da Silva/ Instituto Nacional de Recursos Biológicos, I.P.). Geological bedrock was identified *in situ* and confirmed using Ramalho et al. (1993).

Phytosociological relevés were made according to the sigmatistic approach (Braun-Blanquet 1928; Westhoff and van der Maarel 1973) in the springs of 2007 and 2009. Phytosociological data were compared with the published ones on *O. littoralis* s.l. (Géhu 1964, 1969; Díaz and Navarro 1978). To compose the synoptic table, some relevés were taken from the literature (Rivas Goday 1958; Pinto Silva and Teles 1972; Díaz and Navarro 1978; Rivas-Martínez et al. 1980; Díez-Garretas 1984; Izco, Guitián, and Guitián 1988; Costa, Espírito-Santo, and Lousã 1994; Foucault 1995; Costa, Lousã, and Espírito-Santo 1997; Costa et al. 2000; Neto 2002). A total of 251 relevés were submitted to UPGMA and principal coordinate analysis, with Bray–Curtis coefficient using SYNTAX 2000 software (Podani 2001). New syntaxa follow strictly the rules of the International Code of Phytosociological Nomenclature (Weber, Moravec, and Theurillat 2000). Bioclimatic nomenclature

follows the worldwide bioclimatic classification system (Rivas-Martínez, Rivas-Sáenz, and Penas Merino 2011). The nomenclature of vascular plants follows the works of Castroviejo (1986–2012) and Franco (1984).

Influence of light conditions on phenology, fecundity and survival of *O. kuzinskyanae* was evaluated comparing four developmental parameters: width (maximal possible horizontal distance between leaf tips), height, number of seeds at the onset of senescence, and month of senescence, in three different light conditions: (1) completely shaded sites where plants grow under *Juniperus turbinata* maquis, in sciophytic communities of *Geranio purpurei-Galietum minutuli*; (2) moderately shaded sites under *Cistus ladanifer* shrubs, in sciophytic communities belonging to *Geranio purpurei-Galietum minutuli*, but with the presence of *Euphorbia exigua*, a species characteristic of the heliophytic communities of *Hymenocarpo hamosi-Malcolmion trilobae* and (3) sun-exposed sites, in heliophytic communities of *Hymenocarpo hamosi-Malcolmion trilobae*.

For each light exposure condition, two 1-m² plots were established, one for biometric characterization and another for evaluation of survival. For biometric characterization, about 50 plants in each light condition were examined. Measurements were taken at the beginning of senescence. For estimation of survival rates, about one hundred plants were selected in each light condition. These plants were followed monthly, from February 2007, when we could be reasonably sure that the plants selected were strong enough to survive to maturity, until the end of June, when all plants had died. The number of surviving plants was counted at the end of each month. These data were analysed by Kruskal–Wallis analysis of variance by Rank (Statistica, version 6.0), separately for each of the four parameters (width, height, number of seeds and month of senescence), followed by post-hoc comparisons using Dunn's test.

Results

Germination rate

In both assays high germination rates, about 90% in the first year, were found. None of the remaining seeds germinated in the second year (Table 2).

Sunlight exposure

For all parameters, plants growing in strongly shady places reached greater widths and heights, survived longer, and produced approximately nine times more seeds than plants growing in less shaded habitats (Table 3). Analysis of Table 3 suggests that the same trend holds for most parameters, when comparing plants growing in moderate shade and full sun. However, Dunn's tests only showed significant differences when comparing strong shade with the remaining situations.

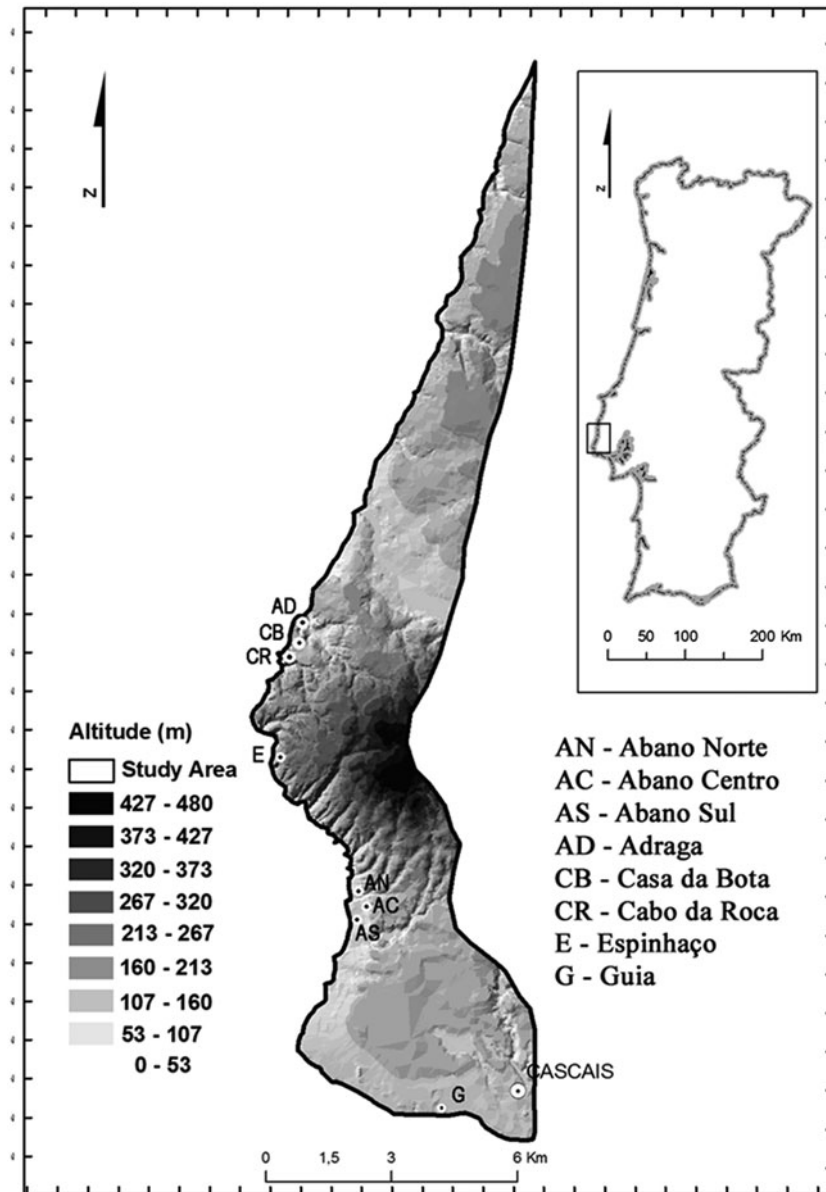


Figure 3. Sampling sites of analysis of soil in habitat of *Omphalodes kuzinskyanae*: AC, Praia do Abano Centre; AD, Adraga; NA, Praia do Abano North; AS, Praia do Abano South; CB, Casa da Bota; CR, Cabo da Roca; E, Espinhaço; G, Guia.

Table 2. Number and rate of germinated seeds.

No. of seeds	Year 1	Year 2
First test, 113 seeds	106 (94%)	0
Second test, 123 seeds	108 (88%)	0

Soil characteristics

Results of granulometric analyses are shown in Figure 4 indicating that the main component of the soils in the *O. kuzinskyanae* habitats, was sand, which exceeded 70%, with just one exception. The second major component was clay, sometimes exceeding 20% of the soil material. Hence, soils in the habitat of *O. kuzinskyanae* can be classified as sand, loamy sand or sandy loam.

The results of the chemical analyses are shown in Table 4 and the sample locations are shown in Figure 3. Analysis of Table 4 shows that the overall pattern of soil composition is characterized by a relatively high content of organic matter (75% of samples displayed values >1.8%), high concentrations of sodium (75% of values >0.43 me/100 g) and iron, adsorbent complex saturated by calcium (80% of values >7.4 me/100 g) and alkaline pH. In most locations, *O. kuzinskyanae* occurred over limestone substrata.

Phytosociological analysis

Populations of *O. kuzinskyanae* contact catenally with scrubland communities or live under shrub canopy. However, although the *O. kuzinskyanae* community

Table 3. Dimensions at beginning of senescence, seed production and survival rates in three light conditions: medians and interquartile differences (Q₃–Q₁).

Sunlight exposure	n	Width (cm)		Height (cm)		N.º seeds		Survival rates at the end of each month. (N = No. of plants at the end of February)		
		Median	Q3–Q1	Median	Q3–Q1	Median	Q3–Q1	Month	Median	Q3–Q1
Strong shade	n = 50	12.8	6.8	7.8	5.0	36.0	33.5	n = 93, Mr: 1; A: 0.99; M: 0.65; Jn: 0.04; JI: 0.00	6.0	1.0
Moderate shade	n = 57	2.5	2.0	2.0	1.3	4.0	4.0	n = 111, Mr: 0.56; A: 0.46; M: 0.00	4.0	2.0
Full sun	n = 58	2.3	1.2	1.6	1.1	4.0	0.0	n = 121, Mr: 0.39; A: 0.39; M: 0.00	3.0	2.0
Kruskal–Wallis d.f. = 2		H = 95.6 p < 0.001		H = 91.8 p < 0.001		H = 103.8 p < 0.001		H = 163.8 p < 0.001		
Dunn's test		F.S. n.s.	p < 0.05	M.S. n.s.	p < 0.05	M.S. n.s.	p < 0.05	F.S. p > 0.05	M.S. p < 0.05	S.S. p < 0.05
		M.S. p < 0.05	p < 0.05	M.S. p < 0.05	p < 0.05	M.S. p < 0.05	p < 0.05	M.S. p < 0.05	M.S. p < 0.05	p < 0.05

Survival rates and month of death: Mr, March; A, April; M, May; Jn, June; JI, July; initial number of plants (n) was counted in February. F.S., full sun; M.S., moderate shade; S.S., strong shade. n.s., non-significant.

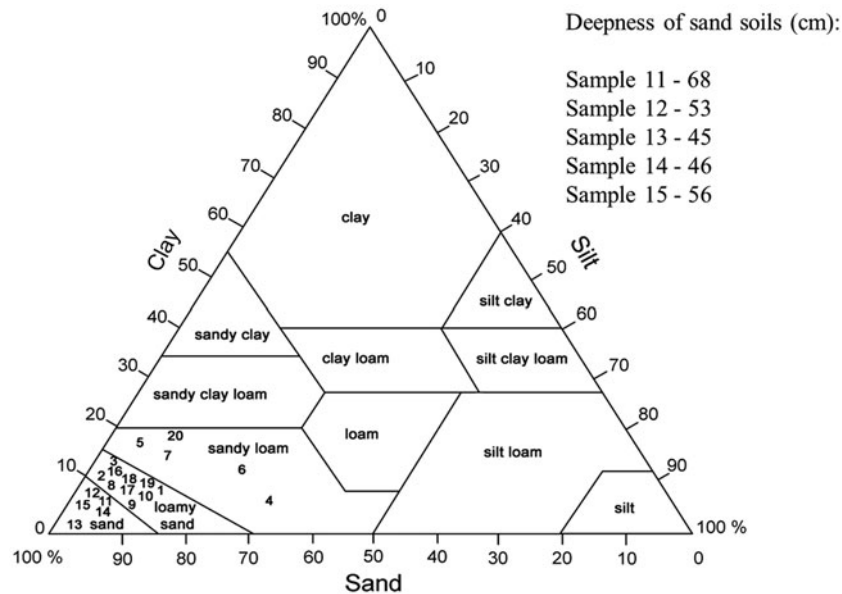


Figure 4. Soil granulometry and deepness of sand soils in habitat of *Omphalodes kuzinskyanae*: 1–4 and 7 (AN); 5 and 6 (AD); 8 (AS); 9–15 (CB); 16–18 (E); 19 and 20 (G) (letters code for the populations displayed in Figure 3).

depends on the presence of a thin layer of sand (15 cm deep), the floristic composition of shrub communities depends on the type of rock substrate. For this reason, it forms a mosaic of different floristic associations that includes: (1) psammophilous chamaephytic communities of *Armerio welwitschii-Crucianelletum maritimae*, (2) psammophilous microphanerophytic communities of *Osyrio quadripartitae-Juniperetum turbinatae*, (3) calcicolous chamaephytic communities of *Salvio sclareoidis-Ulicetum densi* (variant with *Daphne gnidium* var. *maritima* Rozeira); (4) microphanerophytic scrub communities of *Quercus cocciferae-Juniperetum turbinatae*; and (5) acidophilic scrub communities associated with granitic or sienitic rocks of *Quercus cocciferae-Juniperetum turbinatae* or nanophanerophytic communities with *Cistus ladanifer* (Figure 5).

In this vegetation patchwork, *O. kuzinskyanae* can occur in clearings, directly exposed to the sunlight, and also can live under dense bushy vegetation, in shaded places. In these two different situations, *O. kuzinskyanae* is accompanied by different plant communities: in sunny places, the vegetation is dominated by heliophytic therophytes, while the communities that develop under maquis are dominated by sciophytic therophytes.

The shrub vegetation within which the *O. kuzinskyanae* communities are inserted is different from that of heliophytic communities of *O. littoralis* subsp. *littoralis* and *O. littoralis* subsp. *gallaecia* and these differences have some syntaxonomic consequences. While the communities of *O. littoralis* colonize the chamaephytic scrub vegetation of *Roso-Ephedretum* in fixed dunes of France, and *O. littoralis* subsp. *gallaecia* occurs in chamaephytic scrub vegetation of *Iberidetum procumbentis*, *O. kuzinskyanae* occurs in two ecologically distinct situations: (1) in clearings of shrub

vegetation of *Armerio welwitschii-Crucianelletum maritimae* (semi-stabilized dune or grey dune), in clearings Juniper maquis (*Osyrio quadripartitae-Juniperetum turbinatae*) or *Salvio sclareoidis-Ulicetum densi* (Figure 5), and (2) under dense shrub vegetation, in *Juniperus turbinata* subsp. *turbinata*, *Quercus coccifera* subsp. *coccifera*, *Ulex densus* or *Cistus ladanifer* matorrals. In these locations, *O. kuzinskyanae* behaves like a sciophyte.

The relevés conducted in 2007 and 2009 in the Sintra region (mainland Portugal) revealed floristic composition differences compared with the rest of the Iberian Peninsula and French similar communities with *O. littoralis*. Consequently, we have described in 2011 a new association belonging to *Tuberarietea guttatae* (heliophytic communities), *Omphalodo kuzinskyanae-Evacetum ramosissimae* (Costa et al. 2011, 2012) and we propose a new subassociation, sciophytic, belonging to *Cardaminetea hirsutae* (Table 5).

In the first case, floristic relevés reveal an original composition relative to other littoral therophytic communities of *Hymenocarpo hamosi-Malcomion trilobae*. Besides *O. kuzinskyanae*, we identified as characteristic species: *Evax pygmaea* subsp. *ramosissima*, *Erodium cicutarium* subsp. *bipinnatum*, *Pimpinella villosa*, *Ornithopus pinnatus*, *Ornithopus sativus isthmocarpus*, *Rumex bucephalophorus* subsp. *hispanicus*, *Jonopsidium acaule*, *Tuberaria guttata*, *Ononis dentata* and *Ononis broteriana* (Costa et al. 2011).

Under dense scrub vegetation, in shady places *O. kuzinskyanae* occurs in a sciophytic community belonging to *Cardaminetea hirsutae* (*Geranio purpurei-Galietum minutuli*). This association was first described by Rivas-Martínez et al. (1980) in Juniper maquis from

Table 4. Chemical analysis of soil in habitat of *Omphalodes kuzinskyanae* (locations in Figure 3).

Sampling sites	AC1	AC2	AC3	AD1	AD2	AN1	AN2	AN3	AS1	AS2	AS3	AS4	AS5	AS6	CB1	CB2	CB3	CB4	CB5	CR1	CR2	E1	E2	E3	G1	G2	G3	
Depth (cm)													0-10															
Organic matter (%)	0.6	2.2	2.1	8.1	6.7	2.9	3.4	0.7	2.5	2.1	1.8	0.9	1.2	1.8	3.7	2.8	<0.3	1.7	0.8	3.9	6.2	4.1	3.4	4.9	5	4.5	5.1	
pH (H ₂ O)	6.5	6.7	8.2	7.6	7.8	7.6	7.9	7.5	8.2	8.3	8.2	8.3	8.2	8.3	7.7	7.6	8.1	7.7	7.9	8.3	5.5	8.3	8.9	8.5	8.2	8.6	8.4	
P ₂ O ₅ (ppm)	<8	8	<8	10	12	19	13	15	137	122	240	136	145	<8	71	9	27	<8	41	123	255	123	240	225	35	132	87	
K ₂ O (ppm)	360	176	145	400	675	196	184	159	119	94	86	125	117	393	240	224	270	143	51	393	220	240	364	400	397	285	400	
Mg (ppm)	770	220	190	755	720	248	228	205	320	240	113	145	115	328	320	297	313	183	100	465	507	462	492	492	725	800	915	
Fe (ppm)	26	62	92	113	81	75	83	42	97	128	149	81	94	80	86	51	60	42	29	96	200	87	72	70	102	71	83	
Mn (ppm)	13	38	60	167	145	67	52	46	47	66	52	84	75	209	110	69	95	44	23	96	200	192	30	149	132	81	166	
Zn (ppm)	0.7	0.9	1.1	2.7	2.2	6.8	3.4	1.5	11	11	6.6	5	6.9	2.1	11	2.2	1.2	0.6	2.2	5.8	8	2.8	3.3	6	12	16	6.4	
Cu (ppm)	0.1	0.4	2.8	1.2	0.6	1.6	1.5	0.8	1.6	1.8	1.1	1.6	2.1	0.5	1	0.3	0.6	0.3	2.6	1.2	1.5	0.3	1.5	1.2	1.3	2.4	2	
S (ppm)	28	6	9	11	9	11	7	4	12	14	21	8	12	5	9	7	10	9	16	15	17	10	11	18	14	11	11	
CaCO ₃ (%)	n	n	n	n	Ve.	n	Ve.	N	7.7	7.8	4.8	6.9	13	n	n	n	2	n	n	3	0.2	1.8	7.3	4.8	1	n	n	
mS/cm 25°C	0.4	0.2	0.2	0.2	0.2	0.2	0.2	0.1	0.3	0.3	0.2	0.3	0.3	0.2	0.2	0.2	0.2	0.1	0.1	0.3	0.3	0.3	0.3	0.5	0.8	0.3	0.5	
Exchangeable bases																												
Ca (me/100 g)	3.5	2.8	15	9.3	13	8.6	8.7	1.8	8.4	8.5	7.9	7.5	9	8.9	11	5.1	12	4.5	4.9	13	10	12	11	13	11	11	9.7	
Mg (me/100 g)	4.8	1.3	4.5	1.4	4.2	1.5	1.4	1.3	1.9	1.5	0.7	1	1	2.4	2.1	1.9	2	1.2	0.6	3	3	3.2	2.6	3.2	4.9	4.4	5.2	
K (me/100g)	0.7	0.3	0.9	0.3	1.1	0.4	0.3	0.3	0.2	0.2	0.1	0.2	0.2	0.8	0.5	0.4	0.5	0.3	0.1	1	0.5	0.5	0.7	0.8	0.9	0.6	1.1	
Na (me/100g)	1.6	0.6	0.9	0.4	0.9	0.5	0.5	0.7	0.7	0.5	0.2	0.4	0.4	0.8	0.6	0.7	0.4	0.3	0.1	1.2	1.2	0.9	1.6	1.5	2.8	1.7	2.9	
Exchangeable acid																												
me/100g	0.9	0.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
(TEB) me/100 g	11	5.1	21	11	19	11	11	4	12	11	9	9.1	11	13	14	8.2	14	6.3	5.6	18	15	16	16	18	20	17	19	
(CEC) me/100 g	11	5.7	21	11	19	11	11	4	12	11	9	9.1	11	13	14	8.2	14	6.3	5.6	18	20	16	16	18	20	17	19	
(BSR) %	92	89	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	74	100	100	100	100	100	100	100

TEB, Total Exchangeable Bases; CEC, Cation Exchange Capacity; BSR, Base Saturation Ratio; Ve., Vestigial; n, Not detected. Locations: AC, Praia do Abano; AD, Adraga; AN, Praia do Abano/North; AS, Praia do Abano/South; CB, Casa da Botã; CR, Cabo da Roca; E, Espinhaço; G, Guia.

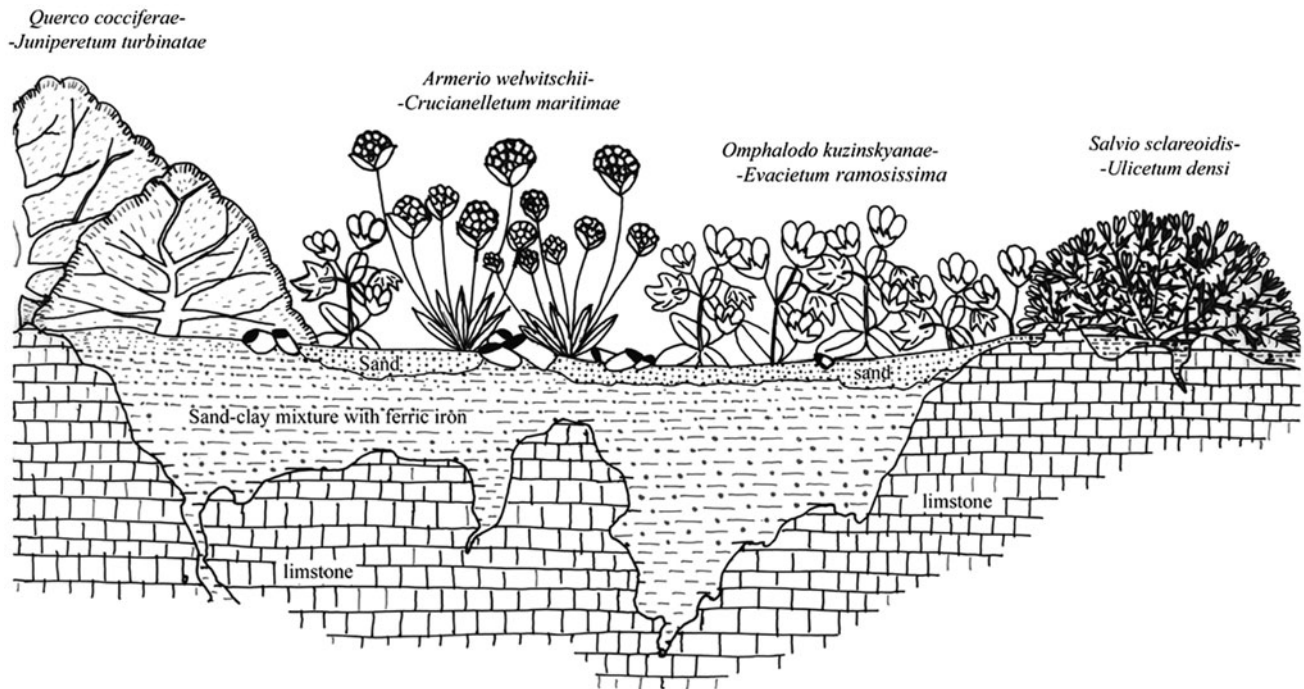


Figure 5. Patchworks of plant communities on limestone at Cabo Raso (Cascais). In the thin sandy layer overlapping limestone or “terra rossa”, there are therophytic communities dominated by *Omphalodes kuzinskyanae*, and chamephytic communities dominated by *Armeria welwitschii*. In the places with “terra rossa”, the communities are dominated by *Juniperus turbinata* or *Ulex densus*.

Table 5. *Geranio purpurei-Galietum minutuli omphalodetosum kuzinskyanae* Neto, J.P. Fonseca and J.C. Costa subass. nova hoc loco.

Numerical order	1	2	3	4
Minimal area	2	4	4	1
Characteristics				
<i>Omphalodes kuzinskyanae</i> (dif. subass.)	3	3	1	1
<i>Galium murale</i>	2	3	2	3
<i>Centranthus calcitrapae</i>	2	1	2	2
<i>Galium minutulum</i>	1	1	+	.
<i>Geranium purpureum</i>	.	+	2	1
<i>Geranium molle</i>	1	+	1	.
<i>Geranium rotundifolium</i>	+	.	.	+
<i>Cardamine hirsuta</i>	.	.	1	.
<i>Anthriscus caucalis</i>	.	.	.	+
Companions				
<i>Anagallis arvensis</i>	1	+	+	+
<i>Centaurium erythraea</i>	+	+	.	+
<i>Chamaemelum nobile</i> var. <i>discoideum</i>	1	2	.	.
<i>Lepidophorum repandum</i>	+	+	.	.
<i>Euphorbia exigua</i>	+	.	+	.
<i>Senecio gallicus</i>	.	+	.	+
<i>Plantago coronopus</i>	.	+	.	+
<i>Lagurus ovatus</i>	.	.	1	.
<i>Polycarpon tetraphyllum</i>	+	.	.	.
<i>Cistus ladanifer</i>	+	.	.	.
<i>Polypogon maritimus</i>	.	+	.	.
<i>Poa annua</i>	.	+	.	.
<i>Senecio vulgaris</i>	.	+	.	.
<i>Avena barbata</i>	.	.	+	.
<i>Ononis dentata</i>	.	.	+	.
<i>Juniperus turbinata</i> (pl.)	.	.	.	+

Locations: 1, 2 Abano (Cascais), 3 Guia (Cascais), 4 between Ursa and Adraga (Sintra).

Doñana (Andalucia), and is present in coastal Juniper maquis of Tróia – southwest Portugal (Neto 2002). The relevés made in shady places (in the distribution area of *O. kuzinskyanae*) present an original floristic composition within the *Geranio purpurei-Galietum minutuli*. Therefore, we consider this phytocoenosis as a new subassociation named *omphalodetosum kuzinskyanae* Neto, J.P. Fonseca and J.C. Costa subass. nov. hoc loco (holotypus relevé no. 2, Table 5), in which *O. kuzinskyanae* is the differential species (Table 5).

For the Houat and Hoëdic islands in western France, Géhu (1964) proposed the syntaxa *Roso-Ephedretum omphalodetosum littoralis*, for which *O. littoralis* is differential of subassociation. In these islands, the fixed dune community is relatively homogeneous, and a separation between the *Roso-Ephedretum* and a therophytic community is purely theoretical and does not respond to any ecological difference.

In the Glénan archipelago (northwest France), fixed dunes are characterized by a strong dominance of therophytes in the clearings in shrub vegetation. Hence, for this archipelago, we propose a new therophytic association *Linario arenariae-Omphalodetum littoralis* Bioret, Neto and J.C. Costa ass. nova hoc loco (Table 6, holotypus relevé no. 9) for the clearing in the shrub vegetation (grey dunes) from which *O. littoralis* is characteristic. Besides *O. littoralis*, the following species are characteristic of the new association: *Phleum arenarium*, *Arenaria serpyllifolia*, *Vulpia membranacea*, *Cerastium diffusum* subsp. *diffusum*, *Mibora minima*, *Medicago littoralis*, *Asterolinum linum-stellatum*, *Bromus*

Table 6. *Linario arenariae-Omphalodetum littoralis* Bioret, Neto and J.C. Costa ass. nova hoc loco.

Numerical order	1	2	3	4	5	6	7	8	9	10	11	12	Σ
Surface (m ²)	15	6	20	10	20	10	100	10	10	15	50	35	
Vegetation cover (%)	95	99	90	90	80	70	35	50	50	20	100	35	
No. of species	28	22	33	32	34	34	22	18	16	14	26	11	
Characteristic species													
<i>Omphalodes littoralis</i> *	.	1	+	+	1	1	1	3	3	1	+	+	V
<i>Mibora minima</i>	1	2	1	1	1	1	1	2	3	1	+	.	V
<i>Cerastium diffusum</i>	+	1	+	+	+	1	1	.	+	1	+	.	V
<i>Arenaria serpyllifolia</i> *	1	1	1	1	2	1	.	+	.	.	1	.	IV
<i>Linaria arenaria</i> *	+	+	.	.	+	.	1	.	+	1	1	+	IV
<i>Saxifraga tridactylites</i> *	1	+	.	+	1	+	1	.	.	.	1	.	III
<i>Catapodium rigidum</i>	.	.	+	.	+	1	+	+	1	.	+	.	III
<i>Phleum arenarium</i> *	1	.	.	+	.	+	+	+	1	.	.	.	III
<i>Viola kitaibeliana</i>	+	.	.	+	+	+	.	.	+	.	+	.	III
<i>Vulpia membranacea</i>	.	.	1	+	.	.	.	+	.	+	+	.	III
<i>Asterolinon linum-stellatum</i>	+	1	.	.	1	.	+	+	III
<i>Myosotis ramosissima</i>	.	.	.	+	1	+	+	.	II
<i>Bromus hordeaceus</i> subsp. <i>ferronii</i>	1	.	.	1	.	+	II
<i>Vicia lathyroides</i> *	+	+	.	.	+	II
<i>Euphorbia exigua</i>	.	1	+	I
<i>Aira praecox</i>	.	+	.	+	I
<i>Aphanes microcarpa</i> *	1	+
<i>Aira caryophyllea</i>	.	+	+
Companion species													
<i>Carex arenaria</i>	2	2	2	2	3	3	1	1	+	+	1	2	V
<i>Sedum acre</i>	1	2	+	1	1	1	1	+	+	+	1	2	V
<i>Euphorbia portlandica</i>	1	+	+	1	1	1	1	+	+	+	1	2	V
<i>Erodium cicutarium</i> var. <i>dunense</i>	+	.	2	+	2	+	2	2	+	1	2	3	V
<i>Lagurus ovatus</i>	2	2	2	.	1	1	2	+	+	+	4	+	V
<i>Aetheorhiza bulbosa</i>	3	2	1	3	1	2	2	.	.	+	1	.	IV
<i>Geranium molle</i>	+	+	+	+	+	+	.	+	+	.	+	.	IV
<i>Anagallis arvensis</i>	.	.	.	+	+	+	1	+	.	+	+	+	IV
<i>Eryngium campestre</i>	+	.	1	1	+	+	r	.	.	.	1	r	IV
<i>Asparagus prostratus</i>	2	.	+	1	.	+	1	.	2	r	.	.	III
<i>Raphanus raphanistrum</i> subsp. <i>landra</i>	2	2	+	.	.	.	+	2	.	+	.	1	III
<i>Leontodon taraxacoides</i>	+	.	+	2	+	2	2	III
<i>Veronica arvensis</i>	+	1	+	.	+	+	+	.	III
<i>Valerianella</i> sp.	+	.	.	.	+	+	+	+	.	.	+	.	III
<i>Cochlearia danica</i>	.	.	+	+	+	+	.	+	.	.	+	.	III
<i>Allium sphaerocephalum</i>	.	2	2	.	+	.	.	1	1	.	.	.	III
<i>Galium arenarium</i>	r	.	1	1	3	+	III
<i>Senecio vulgaris</i> var. <i>radiatus</i>	+	+	.	+	.	+	+	.	III
<i>Calystegia soldanella</i>	1	.	1	+	.	1	II
<i>Crepis capillaris</i>	.	.	1	.	3	1	+	.	II
<i>Armeria maritima</i>	.	.	2	.	+	+	.	2	II
<i>Rumex acetosella</i>	.	.	.	1	.	+	2	II
<i>Festuca rubra</i>	.	.	2	1	+	.	.	.	II
<i>Trifolium occidentale</i>	.	.	+	1	.	+	II
<i>Lotus corniculatus</i>	.	.	+	+	.	1	II
<i>Sherardia arvensis</i>	.	1	+	.	I
<i>Potentilla reptans</i>	.	.	+	.	+	I
<i>Senecio jacobaea</i>	.	.	2	.	r	I
<i>Plantago lanceolata</i> fo.	+	+	I
<i>Plantago coronopus</i>	.	.	.	2	.	+	I
<i>Poa bulbosa</i>	.	.	+	+
Lichens	3	.	2	2	3	.	2	.	.	.	2	.	III
Bryophytes	2	.	3	+	2	II

Location: all relevés come from the islands of the Glénan archipelago (Finistère, Brittany): Saint-Nicolas, Le Loc'h and Penfret.

hordeaceus subsp. *ferronii*, *Linaria arenaria*, *Hypochoeris glabra*, *Aira praecox*, *Trifolium campestre*, *Trifolium arvense*, *Silene conica* subsp. *conica*, *Jasione montana*, *Saxifraga tridactylites*, *Catapodium rigidum* subsp. *rigidum*, *Viola kitaibeliana*, *Vicia lathyroides*, *Aphanes microcarpa* (Tables 6 and 7).

With ecologically similar traits to the new French association, Díaz and Navarro (1978) have described two associations for Asturias (north Spain). Both were positioned in the *Thero-Airon* alliance: *Asterolino lini stellati-Rumicetum bucephalophori* T.E. Díaz and F. Navarro 1978 and *Petrorrhagio-Trifolietum arvensis* T.E.

Table 7. Synthetic table of communities of *Omphalodes kuzinskyanae*, *Omphalodes littoralis gallaecica* and *Omphalodes littoralis littoralis*.

Order number	1	2	3	4	5	6	7	8
Number of relevés	7	7	4	6	13	22	12	40
Characteristics and differentials								
<i>Myosotis personii</i>	.	II
<i>Ranunculus parviflorus</i>	II
<i>Viola kitabiliana</i>	II	III	I
<i>Urtica membranacea</i>	II	V
<i>Myosotis ramosissima</i>	V	V	II	.
<i>Cardamine hirsuta</i>	IV	III	1
<i>Geranium rotundifolium</i>	I	.	2
<i>Galium minutulum</i>	V	V	3
<i>Geranium purpureum</i>	V	V	3
<i>Geranium molle</i>	III	III	3	I	.	.	IV	.
<i>Centranthus calcitrapae</i>	III	V	4	IV
<i>Galium murale</i>	II	.	4	IV
<i>Anthriscus caucalis</i>	.	.	1
<i>Omphalodes kuzinskyanae</i>	.	.	4	IV
<i>Evax ramosissima</i>	.	.	.	V
<i>Pimpinella villosa</i>	.	.	.	V
<i>Ononis dentata</i>	.	.	1	III
<i>Jonopsidium acaule</i>	.	III	.	II
<i>Erodium bipinnatum</i>	.	III	.	V	IV	.	.	.
<i>Euphorbia exigua</i>	.	.	2	IV	.	.	I	.
<i>Rumex hispanicus</i>	.	.	II	IV	+	.	.	.
<i>Ononis broteriana</i>	.	.	.	IV
<i>Ornithopus pinnatus</i>	.	.	.	III
<i>Coronilla repanda</i>	.	.	.	III
<i>Silene scabriflora</i>	.	.	.	III
<i>Ornithopus isthmocarpus</i>	.	.	.	II
<i>Scorpiurus muricatus</i>	.	.	.	II
<i>Ononis diffusa</i>	.	.	.	I
<i>Ornithopus sativus</i>	.	.	.	I
<i>Linaria spartea</i>	.	.	.	I
<i>Polycarpon alsinifolium</i>	.	.	.	I
<i>Micropyrum tenellum</i>	.	.	.	I
<i>Vulpia membranacea</i>	.	.	.	IV	.	IV	III	V
<i>Tuberaria guttata</i>	.	.	.	IV	.	I	.	.
<i>Trifolium arvense</i>	.	.	.	I	.	II	.	r
<i>Medicago littoralis</i>	.	.	.	IV	.	II	.	.
<i>Omphalodes gallaecica</i>	+	.	.	.
<i>Viola henriquesii</i>	II	.	.	.
<i>Silene littorea</i>	V	.	.	.
<i>Pseudorlaya pumila</i> var. <i>microcarpa</i>	IV	.	.	.
<i>Sedum arenarium</i>	II	.	.	.
<i>Polycarpon diphyllosum</i>	I	.	.	.
<i>Cerastium pumilum</i>	+	.	.	.
<i>Malcolmia ramosissima</i>	+	.	.	.
<i>Ononis diffusa</i>	+	.	.	.
<i>Romulea clusiana</i>	+	.	.	.
<i>Asterolinon linum-stellatum</i>	.	.	.	I	I	II	III	.
<i>Cerastium diffusum</i>	III	III	V	III
<i>Mibora minima</i>	II	IV	V	IV
<i>Omphalodes littoralis</i>	IV	V	.
<i>Linaria arenaria</i>	II	IV	.
<i>Bromus hordeaceus</i>	III	II	.
<i>Aira caryophyllea</i>	I	+	.
<i>Logfia minima</i>	I	.	.
<i>Aphanes microcarpa</i>	+	.
<i>Phleum arenarium</i>	V	III	V
<i>Arenaria serpyllifolia</i>	III	IV	V
<i>Trifolium campestre</i>	III	.	II
<i>Catapodium rigidum</i>	III	III	IV
<i>Aira praecox</i>	II	I	r

(Continued)

Table 7. (Continued).

Order number	1	2	3	4	5	6	7	8
<i>Silene conica</i>	II	.	IV
<i>Vicia lathyroides</i>	II	r
<i>Saxifraga tridactylites</i>	I	III	IV
<i>Trifolium scabrum</i>	I	.	I
<i>Cerastium semidecandrum</i>	I	.	V
<i>Veronica arvensis</i>	I	.	III	IV
<i>Hornungia petraea</i>	IV
<i>Bupleurum baldense</i>	II
<i>Erophila verna</i> subsp. <i>praecox</i>	I
<i>Minuartia hybrida</i>	I
<i>Medicago minima</i>	I
Principal companions								
<i>Juniperus turbinata</i> (pl.)	V	.	1	II
<i>Stellaria media</i>	V	IV
<i>Senecio sylvaticus</i>	II
<i>Poa annua</i>	III	.	1
<i>Vicia peregrina</i>	III
<i>Arabidopsis thaliana</i>	I	I
<i>Euphorbia peplus</i>	I
<i>Cerastium glomeratum</i>	I	I	.	I
<i>Mercurialis ambigua</i>	.	II
<i>Galium verrucosum</i>	.	I
<i>Oxalis pes-caprae</i>	.	I
<i>Scrophularia sublyrata</i>	.	I
<i>Aetheorhiza bulbosa</i>	.	I	.	.	.	II	IV	.
<i>Anagallis arvensis</i>	.	.	4	IV	+	III	IV	.
<i>Centaurium erythraea</i>	.	.	3	IV
<i>Chamaemelum discoideum</i>	.	.	2	2
<i>Lepidophorum repandum</i>	.	.	2
<i>Senecio gallicus</i>	.	.	2	II	+	.	.	.
<i>Lagurus ovatus</i>	.	.	1	III	+	III	V	.
<i>Polycarpon tetraphyllum</i>	.	.	1	II
<i>Polypogon maritimus</i>	.	.	1	I
<i>Senecio vulgaris</i>	.	.	1	III	.	.	II	.
<i>Paronychia argentea</i>	.	.	.	III	+	.	.	.
<i>Anagallis microphylla</i>	.	.	.	III
<i>Cistus salviifolius</i>	.	.	.	III
<i>Narcissus bulbocodium</i>	.	.	.	III
<i>Lobularia maritima</i>	.	.	.	II
<i>Armeria welwitschii</i>	.	.	.	II
<i>Centaurea sphaerocephala</i>	.	.	.	I
<i>Malcolmia littorea</i>	I	.	.	.
<i>Vulpia alopecuros</i>	I	.	.	.
<i>Papaver rhoeas</i>	I	.	.	.
<i>Catapodium maritimum</i>	I	.	.	.
<i>Sonchus oleraceus</i>	I	.	.	.
<i>Dianthus gallicus</i>	V	.	.
<i>Helichrysum stoechas</i>	V	.	.
<i>Koeleria albescens</i>	V	.	.
<i>Carex arenaria</i>	V	.	.
<i>Eryngium campestre</i>	V	IV	.
<i>Euphorbia portlandica</i>	V	V	.
<i>Sedum acre</i>	V	V	.
<i>Asperula cynanchica</i>	V	.	.
<i>Asparagus prostratus</i>	IV	III	.
<i>Plantago lanceolata</i>	IV	I	.
<i>Leontodon taraxacoides</i>	IV	III	.
<i>Allium sphaerocephalum</i>	IV	III	.
<i>Ephedra distachya</i>	IV	.	.
<i>Herniaria ciliolata</i>	IV	.	.
<i>Cladonia rangiformis</i>	IV	.	.
<i>Tortula ruralis</i>	IV	.	.
<i>Corynephorus canescens</i>	III	.	.
<i>Rosa pimpinellifolia</i>	III	.	.

(Continued)

Table 7. (Continued).

Order number	1	2	3	4	5	6	7	8
<i>Festuca rubra</i>	III	II	.
<i>Galium arenarium</i>	III	III	.
<i>Calystegia soldanella</i>	III	II	.
<i>Sanguisorba minor</i>	III	.	.
<i>Tortella flavovirens</i>	III	.	.
<i>Pleurochaete squarrosa</i>	III	.	.
<i>Coincya eurocastrum</i>	III	.	.
<i>Erodium dunense</i>	II	V	.
<i>Hypochaeris glabra</i>	III	.	II
<i>Scilla autumnalis</i>	II	.	.
<i>Jasione montana</i>	II	.	.
<i>Pancreatium maritimum</i>	II	.	.
<i>Medicago marina</i>	II	.	.
<i>Pteridium aquilinum</i>	II	.	.
<i>Rumex acetosella</i>	II	II	.
<i>Vincetoxicum officinale</i>	I	.	.
<i>Cynodon dactylon</i>	I	.	.
<i>Sedum anglicum</i>	I	.	.
<i>Anthoxanthum odoratum</i>	I	.	.
<i>Teedalia nudicaulis</i>	I	.	.
<i>Ononis repens</i>	I	.	.
<i>Raphanus raphanistrum</i> subsp. <i>landra</i>	III	.
<i>Cochlearia danica</i>	III	.
<i>Armeria maritima</i>	II	.
<i>Crepis capillaris</i>	II	.
<i>Trifolium occidentale</i>	II	.
<i>Lotus corniculatus</i>	II	.
<i>Sherardia arvensis</i>	I	.
<i>Potentilla reptans</i>	I	.
<i>Bromus hordeaceus</i> subsp. <i>thominei</i>	V
<i>Moenchia erecta</i>	I

Geranio purpurei-Galietum minutuli: 1, Rivas-Martínez et al. 1980 tab. 39; 2, Neto 2002 tab. 43; 3 *Geranio purpurei-Galietum minutuli omphalodetosum kuzinskyanae*; 4, *Omphalodo kuzinskyanae-Evacetum ramosissimae* Costa et al. 2011 tab. 4; 5, *Violo henriquesii-Silenetum littoreae* Izo, Guitián and Guitián 1988 tab. 1; 6, *Roso-Ephedretum omphalodetosum littoralis* Géhu 1964 tab. 3; 7: *Linarion arenariae-Omphalodetum littoralis*; 8 *Hornungio petraeae-Phleetum arenarii* Foucault 1995 tab. 4

Díaz and F. Navarro 1978 (Díez-Garretas and Asensi 2002). However, Foucault (1999) integrated these communities in the *Sileno conicae-Vulpion membranaceae* alliance as suggested by the two performed analyses (UPGMA and principal coordinate analysis) (Figures 6 and 7). This alliance is characterized by *Cerastium diffusum*, *Cerastium semidecandrum*, *Erodium cicutarium*, *Hornungia petraea*, *Medicago littoralis*, *Mibora minima*, *Minuartia hybrida* subsp. *hybrida*, *Petrorhagia polifera*, *Phleum arenarium*, *Saxifraga tridactylites*, *Trifolium arvense*, *Veronica arvensis* L. and *Vulpia membranacea* (Foucault 1999).

The two Asturian communities (*Asterolino lini stellati-Rumicetum bucephalophori* and *Petrorhagio-Trifolietum arvensis*) and the French ones (*Linarion arenariae-Omphalodetum littoralis* and *Hornungio petraeae-Phleetum arenarii*) have in common the following characteristic species: *Aira praecox*, *Cerastium diffusum*, *Asterolino linum-stellatum*, *Mibora minima*, *Trifolium arvense*, *Arenaria serpyllifolia*, *Phleum arenarium*.

The differential species of the new association compared with the Asturian ones are: *Omphalodes*

littoralis, *Arenaria serpyllifolia*, *Petrorhagia prolifera*, *Saxifraga tridactylites*, *Bromus ferronii*, *Linarion arenaria*, *Silene conica*, *Vicia lathyroides*, *Aphanes microcarpa*.

The principal coordinate analysis ordination (Figure 6) separated the relevés of *Linarion pedunculatae* (relevés 1–123), *Hymenocarpus hamosi-Malcolmion trilobae* (relevés 124–212), *Sileno conicae-Vulpion membranaceae* (relevés 213–247) and *Parietarium lusitanico-mauritanicae* (relevés 248–251). These four alliances represent all those in which the studied psammophilous *Omphalodes* communities are inserted. The *Linarion pedunculatae* alliance (*Cutandietalia maritima* order) is distributed in the west and northwest of the Iberian Peninsula and north of Morocco in the grey dunes (semi-fixed dunes), submitted to salt spray. In the *Linarion pedunculatae* alliance, *Omphalodes* genus (i.e. *O. littoralis*) occurs only in the *Violo henriquesii-Silenetum littoreae* (Table 6). This association colonizes the grey dunes from Aveiro (Portugal) to Galiza (Spain). Its southernmost distribution (Aveiro) corresponds to the biogeographic

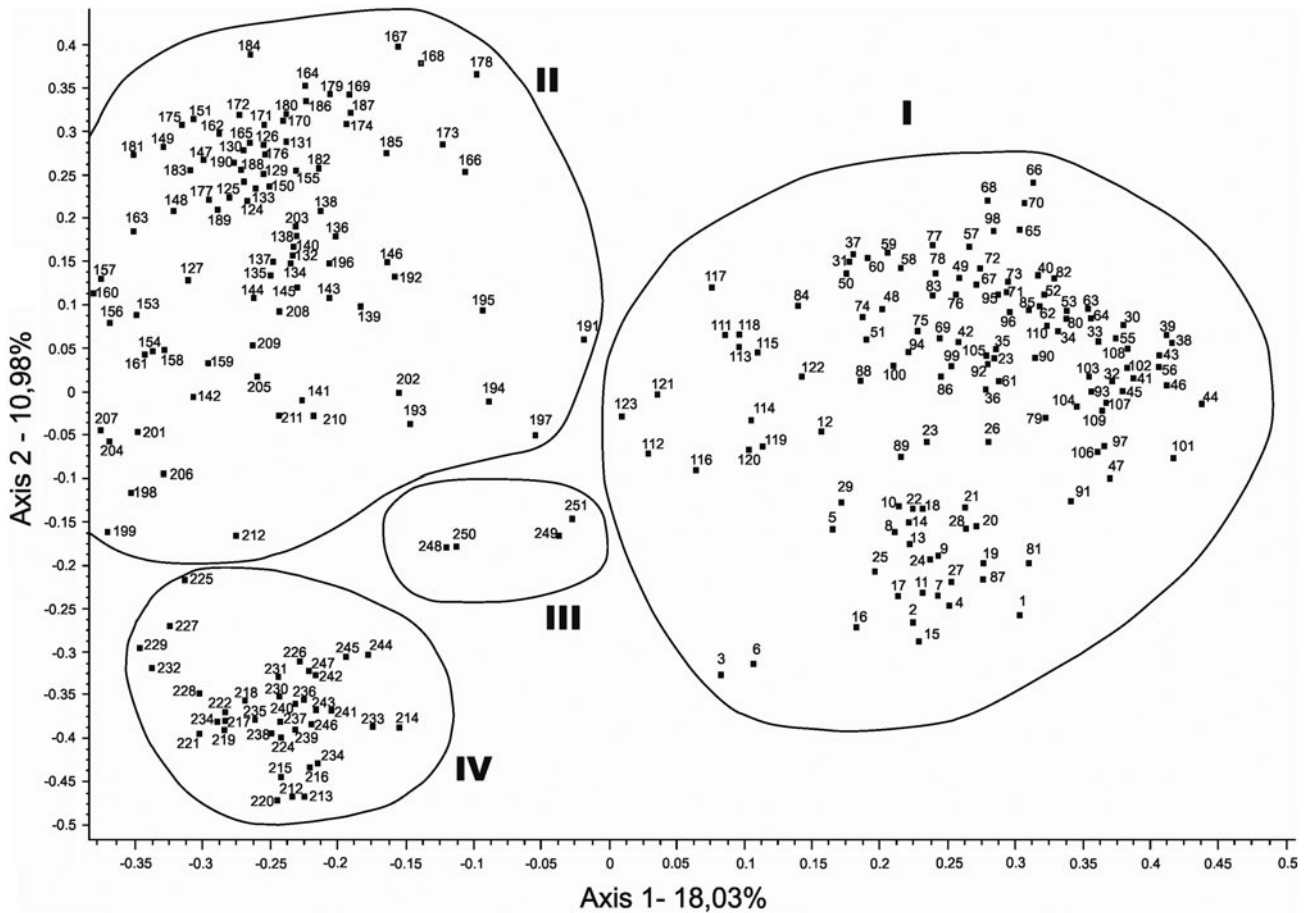


Figure 6. Principal coordinate analysis using Bray–Curtis coefficients from a total of 251 relevés belonging to 14 associations of the four psammophilous alliances that comprise all the annual plant communities from Iberian Peninsula and western France: I, *Linaria pedunculatae* Díez Garretas, Asensi, and Esteve in Díez Garretas 1984 (relevés 1–123); II, *Sileno conicae-Vulpion membranaceae* Foucault, 1999 (relevés 124–212); III, *Parietaron lusitanico-mauritanicae* Rivas-Martínez and Cantó 2002 (relevés 248–251); IV, *Hymenocarpus hamosi-Malcolmion trilobae* Rivas-Goday 1958 em. Rivas-Martínez 1978 nom. mut. (relevés 124–212).

frontier between Eurosiberian and Mediterranean regions in Portuguese sand dunes (also in salt marshes) (Costa et al. 2000, 2009). *Omphalodes littoralis* does not occur in the Portuguese sector of the *Viola henriquesii-Silenetum littoreae*, but only in Galicia. The order *Malcolmietalia* was proposed by Rivas Goday in 1958 for the pioneer therophytic communities with spring flowering, on deep unconsolidated sandy soils and palaeodunes, not directly subjected to the influence of salt spray (Díez-Garretas and Asensi 2002; Costa et al. 2011, 2012). In the western part of the Iberian Peninsula, the order *Malcolmietalia* is represented by the *Hymenocarpus hamosi-Malcolmion trilobae* alliance, which comprises the sandy coastal communities not subjected to the influence of salt spray occurring in the bush and woodland clearings in thermo-Mediterranean to lower meso-Mediterranean euoceanic bioclimate and with a Coastal Lusitanian Andalusian biogeographical province distribution (Neto et al. 2007; Costa et al., 2012). The therophytic communities of this alliance integrate some of the most important annual psammophilic communities of the Portuguese stabilized

sand dunes not submitted to salt spray. Many of these communities are included in annex II of Natura 2000 Network because of the presence of a high number of Lusitanian endemic taxa. In the Olissiponense district, in upper thermo-Mediterranean and upper dry belt, in dunes on calcareous or syenitic platforms, the *Omphalodo kuzinskyanae-Evacetum lusitanicae* alliance occurs (Table 6). The *Sileno conicae-Vulpion membranaceae* alliance (*Stipo capensis - Brachypodietea distachyi*) occurs in thermo-Atlantic calcareous sand dunes in northern Spain and western France. The *Parietaron lusitanico-mauritanicae* alliance (*Cardaminetea hirsutae*) comprises the ephemeral annual semi-shaded, slightly nitrified fringe communities that develop in spring and summer in the western Mediterranean with thermo-meso-Mediterranean bioclimate (Costa et al. 2012). In this alliance, the *Geranio purpurei-Galietum minutuli* corresponds to the annual subnitrophyllous plants that colonize the shady habitats under Juniper maquis dominated by *Juniperus turbinata* (*Osyrio quadripartitae-Juniperetum turbinatae*) with a coastal Lusitanian-Andalusian province distribution (southwest

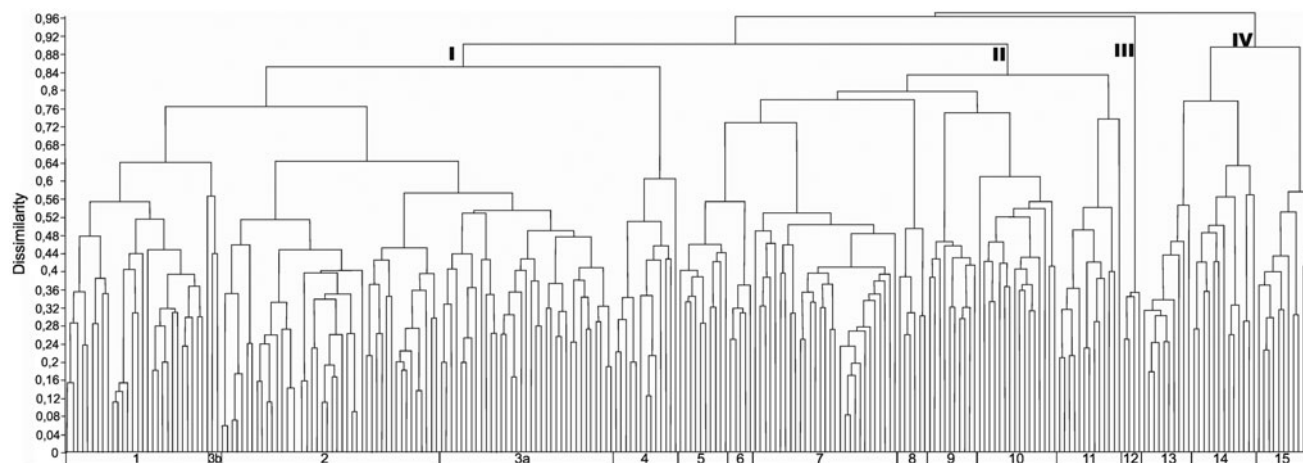


Figure 7. UPGMA with Bray–Curtis coefficient of the main annual psammophilous plant communities in the Iberian Peninsula and occidental coast of France: Alliances: I, *Linaria pedunculatae* Díez Garretas, Asensi, and Esteve in Díez-Garretas 1984; II, *Sileno conicae-Vulpion membranaceae* Foucault, 1999; III, *Parietarium lusitanico-mauritanicae* Rivas-Martínez and Cantó 2002; IV, *Hymenocarpus hamosi-Malcolmion trilobae* Rivas-Goday 1958 em. Rivas-Martínez 1978 nom. mut. Associations (the relevés numbers are the same as shown in Figure 6): 1, *Ononido variegatae-Linaria pedunculatae* Díez-Garretas ex Izco, P. and J. Guitián 1988 [relevés 1–11 (Garretas et al. 1984), relevés 12–29 (Costa et al. 1996)]; 2, *Herniario algarvicae-Linaria ficulhoanae* Díez Garretas 1984 [relevés 30–36 (Garretas et al. 1984), relevés 37–51 (Costa et al. 1994), relevés 52–73 (Neto 2002)]; 3(a and b), *Pseudorhago minusculae-Polycarpum alsinifolium* J.C. Costa, Neto, Capelo and Lousã 2011 [relevés 74–99 (3b, 81 and 87) inéd., relevés 100–110 (Costa et al. 2000)]; 4, *Viola henriquesii-Silenetum littoreae* Izco and Guitián 1988 [relevés 111–123, (Izco, Guitián, and Guitián 1988)]; 5, *Hymenostemmo pseudanthemidis-Arenarium emarginatae* Rivas Goday 1958 [relevés 124–133 (Rivas Goday 1958)]; 6, *Anthyllido hamosae-Malcolmion patulae* Rivas Goday 1958 [relevés 147–151 (Rivas Goday 1958)]; 7, *Corynephoru macrantheri-Arenarium algarbiense* P. Silva and Teles ex Rivas-Martínez and Izco 2002, [relevé 162 (Teles and Pinto da Silva 1972), relevés 163–190 (Neto 2002)]; 8, *Omphalodo kuzinskyanae-Evacetum lusitanicae* Neto, Monjardino, E. Pereira, Neto, Monjardino, E. Pereira, Lousã and J.C. Costa in J.C. Costa, Neto, Capelo and Lousã 2011 [relevés 191–196 (Costa et al. 2011)]; 9, *Tolpido barbatae-Tuberarium bupleurifoliae* J.C. Costa in J.C. Costa, Lousã and Espírito-Santo 1997, [relevés 152–161 (Costa, Lousã, and Espírito-Santo 1997)]; 10, *Cerastio diffusi-Vulpium fontqueranae* J.C. Costa, Neto, Capelo and Lousã 2011 [relevés 197–212, (Costa et al. 2011)]; 11, *Linaria arenariae-Omphalodetum littoralis* Bioret, Neto, J.C. Costa ass. nova (relevés 236–247); 12, *Geranio purpurei-Galietum minutuli* Rivas Martínez, Costa, Castroviejo and E. Valdés 1980 *omphalodetosum kuzinskyanae* Neto, J.P. Fonseca and J.C. Costa subass. nova (relevés 248–251); 13, *Asterolino lini-stellati-Rumicetum bucephalophori* T.E. Díaz and Navarro 1978 [relevés 213–222, (Díaz et al. 1978)]; 14, *Petrorhagio proliferae-Trifolium arvensis* T.E. Díaz and F. Navarro 1978 [relevés 223–235 (Díaz et al. 1978)].

of the Iberian Peninsula) in the thermo-Mediterranean bioclimate. In the Sintra region, this association is enriched with *Omphalodes kuzinskyanae* which led to the description (made above) of the new syntaxa *omphalodetosum kuzinskyanae*.

The performed cluster analysis UPGMA showed a segregation of the psammophilic annual plant communities from southwest, west, northwest and north of Iberian Peninsula and western France. It also shows a clear differentiation between the four alliances and the integration of the Asturian communities into the *Sileno conicae-Vulpion membranaceae* alliance.

Syntaxonomic scheme

TUBERARIETEA GUTTATAE (Br.-Bl. in Br.-Bl., Roussine and Nègre 1952) Rivas Goday and Rivas-Martínez 1963 em. Rivas-Martínez 1978 nom. mut.

Malcolmietalia Rivas Goday 1958

Hymenocarpus hamosi-Malcolmion trilobae Rivas Goday 1958 em. Rivas-Martínez 1978 nom. mut.

Omphalodo kuzinskyanae-Evacetum lusitanicae Neto, Monjardino, E. Pereira, Neto, Monjardino, E. Pereira, Lousã and J.C. Costa in J.C. Costa, Neto, Capelo and Lousã 2011

STIPO CAPENSIS - BRACHYPODIETEA DISTACHYI (Br.-Bl. 1947) Brullo 1985

Phleo arenarii-Cerastietalia semidecandri (Glowacki, 1998) Foucault 1999

Sileno conicae-Vulpion membranaceae Foucault 1999

Linaria arenariae-Omphalodetum littoralis Bioret, Neto, J.C. Costa ass. nova hoc loco

CARDAMINETEA HIRSUTAE Brullo in Brullo and Marceno 1985.

Geranio purpurei-Cardaminetalia hirsutae Brullo in Brullo and Marceno 1985

Parietarium lusitanico-mauritanicae Rivas-Martínez and Cantó 2002

Geranio purpurei-Galietum minutuli Rivas Martínez, Costa, Castroviejo and E. Valdés 1980 *omphalodetosum kuzinskyanae* Neto, J.P. Fonseca and J.C. Costa subass. nova hoc loco

Discussion

Germination

The results obtained in seed viability suggest that all viable seeds germinate in the first year. No seeds germinated in the second year (Table 1). These results suggest that seeds of *O. kuzinskyanae* have a short period of dormancy, germinating just after the first rains of autumn, and that, probably, the seed bank is scarce or even absent. Similarly, high germination rates, between 70 and 90%, in the first year were reported for *O. littoralis* subsp. *gallaecica*, and also in other *ex situ* assays (Serrano and Carbajal 2004).

Habitat requirements

Several soil characteristics are easily explained: (1) the content of organic matter is high, probably because the communities with *O. kuzinskyanae* are located in proximity to or under the shrub canopy; (2) the adsorbent complex is saturated mostly by calcium ions, because there is a high proportion of shells in sandy sediments and/or due to the presence of small limestone pebbles originating from limestone substrata; (3) the values of sodium are high, probably due to the proximity to the sea and are the consequence of salt spray; (4) the pH is alkaline due to the high values of Ca^{2+} and Na^+ . These findings explain the contribution of the limestone substrata in the distribution area of *O. kuzinskyanae*. However, they do not mean that this species requires calcium-rich soils, as illustrated in Table 3; (v) the concentration of iron is high, due to the abundance of this metal in the clay/ferric iron complex “terra rossa”, which results from the chemical erosion of the limestone substrata. Similarly *O. littoralis* grows on a sandy substrate, enriched in shell debris that provides calcium ions (Bioret 1989).

Both species live in sandy soils and coastal areas. However, as stated above, *O. littoralis* occurs mostly in grey dunes (Géhu 1964; Serrano and Carbajal 2004; Servane 2005). Thin sandy soils covering rocky substratum represent a rare habitat for this species, having been reported solely for Galicia in exceptional situations (Serrano and Carbajal 2004).

On the contrary, *O. kuzinskyanae* is mostly present in sandy loam or loamy sand soils. In sandy soils, the presence of *O. kuzinskyanae* is restricted to areas where the soil is reduced to a thin layer (never exceeding 70 cm deep). It is important to point out that some large populations of *O. kuzinskyanae* are located near typical dune systems with grey dunes and deep sandy soils (Albuquerque, Bernardes, and Fonseca 2004), but the species does not occur in these soils. This suggests that *O. kuzinskyanae* is unable to colonize deep sandy soils.

We propose that the ecological contrasts depicted above can be easily explained if the populations of *O. littoralis/O. kuzinskyanae* are limited both in ecological niche and geographical distribution by hydric stress. A

complex set of interactions involving water availability, light and temperature may explain why a member of the clade lives on exposed sands, while the other reaches its ecological optimum under the shade of shrubs.

Omphalodes littoralis lives in the coasts of Galicia and western France, where a temperate oceanic climate provides frequent rains (distributed throughout the growing season) and low average temperatures. This prevents water stress and allows the subsistence of *O. littoralis* in full sun, and in deep and well-drained sandy soils, like coastal dunes.

Omphalodes kuzinskyanae lives under Mediterranean climate, near the coastal frontier between the Eurosiberian and Mediterranean regions (Costa et al. 2009), where shade can strongly reduce temperature and limit water loss in soil and plants. This can explain its sciophytic behaviour.

Soils occupied by *O. kuzinskyanae* have an important fraction of clay. The presence of clay allows a higher capacity for water retention than pure sand, and reduces infiltration. It can also increase microporosity, which improves the access of the root system to the water.

Deepness of sandy soil can also be important in water availability. In deep sandy soils, all the rainwater is rapidly filtered through the sand. This produces a very dry superficial horizon. However, in the habitat of *O. kuzinskyanae*, the presence of a horizontal limestone pavement, close to the ground surface can partially delay the percolation. In some places, where the limestone is not fissured, it leads to the formation of shallow water tables. The extensive gap between the geographical ranges of *O. littoralis* and *O. kuzinskyanae* can be partly explained by the inability of *O. kuzinskyanae* to colonize deep sandy soils. As stated above, the shoreline from north of Lisbon to south Galicia is almost continuously sandy. In this stretch of the Portuguese coast, dune systems occur together with climatic conditions that are much dryer than in Galicia with higher temperatures, fewer spring fogs and less frequent rains, especially in the second half of the species life cycle.

Concerning the evolutionary history of this group (*O. kuzinskyanae/O. littoralis*), two alternative hypotheses are plausible: (1) the ancestor of both species evolved in a dry climate and, when it colonized sandy soils, it found its ecological optimum in shady habitats. Then, during the first humid phase of the current interglacial, it migrated north to Galicia and France, where it became heliophytic in the presence of a wetter climate (well distributed rainfall throughout the year almost without dry periods and with moderate temperatures); or (2) the ancestor of this group was probably able to live on sands, under full sun, in cool wet environments. Upon the establishment of drier conditions, in the second half of the present interglacial, it would have become extinct in most of its former range. It would have survived in the extreme northwest of its distribution area, where wet and cool conditions persisted. It would have also survived near Lisbon, mostly under shade, in sandy soils that have

sufficient clay and are sufficiently thin to ensure access to water, in late spring.

Phytosociological conclusions

Phytosociological analyses show that *O. kuzinskyanae* lives in heliophytic and sciophytic communities although it was shown that *O. kuzinskyanae* is a sciophytic species. Indeed, comparisons of developmental parameters between plants growing under strong shaded and sunny places are statistically significant (Table 3).

Interestingly, *O. littoralis* shows strict heliophytic behaviour. In Galicia, the species inhabits grey dunes usually in communities of *Viola henriquesi-Silenetum littoreae*, a heliophytic community (Serrano and Carbajal 2004). However, within this community, *O. littoralis* only occurs in the wetter sector of its distribution, Galicia, one of the rainiest regions in the Iberian Peninsula. Indeed the southernmost sector of the *Viola henriquesi-Silenetum littoreae* (between south Galicia and Aveiro) is characterized by the absence of *O. littoralis*. Along the French coast, Bensettiti et al. (2002), summarizing previous studies, considered *O. littoralis* as heliophytic and thermophytic. According to these authors, the occurrences in shaded habitats, like pine woods, are restricted to edges and clearings. Furthermore, Dupont and Lahondère (1995), describing the ecology of *O. littoralis*, stressed its heliophytic character and its preferential occurrence in heliophytic fixed dunes communities, like *Thymo-Helichrysetum* Géhu and Sissingh in Sissingh 1974, *Roso-Ephedretum* Kuhnholz-Lordat (1927) 1931 and *Artemisio-Ephedretum* Géhu and Sissingh in Sissingh 1974. Only in the Mediterranean region (south of Aveiro), due to the rainfall and temperature conditions, *Omphalodes* psammophilous species (*O. kuzinskyanae*) prefer the shadow areas of *Juniperus turbinata* and *Cistus ladanifer* Mediterranean maquis. In the Sintra region (Sintrano district; Costa et al. 1999), *O. kuzinskyanae* clearly shows its optimum in shaded areas, which led us to put the new syntaxa *omphalodetosum kuzinskyanae* in a phytosociological alliance that comprises ephemeral annual semi-shaded psammophilous plants *Parietario lusitanico-mauritanicae*.

Some propositions for *Omphalodes kuzinskyanae* protection and conservation

As *O. kuzinskyanae* is a threatened taxon, our results raise serious concerns regarding its conservation. Juniper and other coastal maquis are becoming rare on the Portuguese coast, due to the pressures of tourism. Their increasing rarity pushes *O. kuzinskyanae* to heliophytic communities, which are suboptimal, or even unsuitable. In a context of global warming, a small increase in average temperature or drier springs, together with the absence of a seed bank, may lead this species to a very high risk of extinction. For an annual plant that does not

have a seed bank, a single dry season after germination can have a drastic impact. Hence, protection and restoration of coastal maquis (mainly Juniper maquis) is of prime importance to its long-term conservation. This proposal would increase the area of psammophilous *Juniperus turbinata* maquis (a priority habitat of Nature 2000 Network – 2250 * Coastal dunes with *Juniperus* spp.), which has been reduced in recent decades. Moreover, it would permit the expansion of the endangered taxa *O. kuzinskyanae*.

Acknowledgement

This work was supported by the Portuguese Foundation for Science and Technology (FCT) through the project FCT – PTDC/AAC-AMB/111349/2009.

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