Phytocoenologia Vol. 43 (2013), Issue 3-4, 183–191
Published online June 2013

Article

Plant communities partially reflect environmental gradients in humanized landscapes: a case study in the Llobregat delta marshes

by Efrem Batriu, Josep M. Ninot, Barcelona, Spain, Pere Rovira, Solsona, Spain & Joan Pino, Bellaterra, Spain

with 4 figures, 3 tables and 1 electronic appendix

Abstract: This study took place in a vegetation mosaic of the Llobregat delta (near Barcelona, Spain), which includes both natural and spontaneously restored coastal marshes. We used a dataset comprising vegetation relevés, soil parameters and water table conditions, and explored their correlation. More precisely, we classified the relevés into three phytosociological alliances (namely Phragmition communis, Salicornion fruticosae and Juncion maritimi) combining the previous information available and the use of PCA ordinations. We studied whether these alliances reflect the main operating environmental gradients (conductivity, sodium absorption rate and water table dynamics) using a GLMM (generalized linear mixed model). The PCA reflected a fair distinctiveness of Salicornion and Phragmition, whereas Juncion was a more heterogeneous unit, related to the varying dominance of different plant species. The three alliances exhibited significant differences in environmental variables and therefore the phytosociological ordination reflected at least partially the main operating environmental gradients. However the assemblage of alliances over the gradients varied between locations, suggesting that the initial species pool or plant dispersal capacity to some extent shapes the dynamics of spontaneous restoration in these marshlands.

Keywords: Alliances, environmental gradients, Juncion maritimi, Mediterranean coastal marsh, Salicornion, salinity, Phragmition, water table

Abbreviations: GLMM = Generalized Linear Mixed Model; SAR = Sodium Adsorption Rate; PCA = Principal Component Analyses

Introduction

The vegetation growing at a particular site reflects how selection from the available flora, by the action of abiotic and biotic factors, gives a species assemblage capable of co-existing under the prevailing conditions (Adam 1993). In traditional ecological interpretations the outcome of these environmental conditions is reflected by the spatial variation in the vegetation in terms of species composition. At the same time, variation in species composition can be classified into a hierarchical system (e.g., through the phytosociological method) that reflects floristic similarities and dissimilarities (Braun-Blanquet 1979). Phytosociological syntaxa have been shown to reflect variation in environmental conditions in different habitat types such as meadows (Hájek & Hájkova 2004; Rodríguez-Rojo & Sánchez-Mata 2006), forests (Bergmeier 2002; Tsiripidis et al. 2007), wetlands (Hajkova et al. 2006) and mires (Casanovas Poch 1996; Hrivnak et al. 2008). Thus, beyond their major objective of classifying plant communities (Willner 2006), phytosociological units can provide a sound basis for understanding the relationships between vegetation variation and environmental gradients.

Classical views in community ecology focused on the importance of competition for resources, and assumed that populations and communities typically exist under equilibrium conditions in habitats saturated with both individuals and species (Rohde 2005). However, much evidence contradicts these assumptions and it is likely that non-equilibrium situations are much more widespread than formerly perceived. Indeed, there is increasing evidence of the influence of the founder effect (the initial pool of species) and stochastic factors on the composition of plant communities (Körner et al. 2008; Poschlod & Biewer 2005).

In coastal marshes, the main gradients determining species occurrence and frequency are soil salinity and moisture (Adam 1993; Ranwell 1972; Batriu et al. 2011). Waterlogging is a limiting factor for root respiration and causes a decrease in redox soil conditions, which in turn may promote the production of particular toxic substances (Pezeshki 2001). Salinity has three types of adverse effects on plants: (i) lowered external water potential, (ii) direct toxic effect of chloride and sodium, and (iii) interference with the uptake of nutrients (Adam 1993). The last two effects depend on the relative proportions of Ca^{2+}, K^{+}, Mg^{2+} and Na^{+} in the soil (Grattan & Grieve 1992). Significant differences in soil salinity or moisture have been found between phytosociological alliances (Alvarez Rogel et al. 2001; Molina et al. 2003) and associations (Bouzille et al. 2001; Sánchez et al.

DOI: 10.1127/0340-269X/2013/0043-0550

www.borntraeger-cramer.de
0340-269X/2013/0043-0550 $ 4.50

1998). Other authors showed the importance of biotic factors such as facilitation (Callaway & Pennings 2000; Pennings et al. 2005; Rubio-Casal et al. 2001) and competition (Pennings et al. 2005) in the distribution of coastal marsh vegetation. These studies indicate that marshland communities are in equilibrium with their environment. In contrast, other studies highlight the importance of historic factors for coastal marsh vegetation assemblages (Bertness & Ellison 1987; Costa et al. 2003). Mediterranean coastal marshes are characterized by a long history of human activity, which in the past has led to a large reduction in their extent (Curcó et al. 2002). However, there are also recent examples of spontaneous restoration after agricultural abandonment (Pino et al. 2009), although restored wetlands typically exhibit differences in their environmental conditions compared with longstanding natural sites (Bruland & Richardson 2005; Lu et al. 2007). This may condition their suitability for some species included in the original vegetation. Moreover, some studies emphasize the importance of the initial pool of species in restoration processes (Poschlod & Biewer 2005). These initial assemblages may lead to unexpected stable vegetation formations that can persist over time (Klötzli & Grootjans 2001). According to Pino et al. (2009), the land-use legacy in our study area might affect the species composition of marshland communities, though the reasons for different species assemblages within similar habitats are not always clear.

The study of vegetation dynamics in disturbed environments offers an exceptional opportunity to clarify ecological processes, according to Margalef (in Terradas 2001). We focused our study on the Llobregat delta, where a long history of human colonization has led to a mosaic of coastal marsh communities that include both natural and restored stands (Pino et al. 2006). Using a set of vegetation relevés with ancillary information on soil and water table conditions monitored for at least one year, we use a phytosociological approach to answer the following questions: i) to what extent do the phytosociological units reflect the main operating environmental gradients? and ii) what is the weight of particular site conditions such as land-use legacy or location?

Material and methods

Study sites and dataset

The Llobregat delta is a microtidal wetland area currently included in the Barcelona conurbation. Climate data obtained from the International Airport of Barcelona (located in the middle of the delta) give an average annual precipitation of 640 mm for the period 1971–2000, with a mean minimum rainfall in July (20 mm) and a mean maximum rainfall in October (91 mm). The mean annual temperature is 15.5 °C, with a highest mean maximum in August (28 °C) and a lowest mean minimum in January (4.4 °C). The area is thus under a Mediterranean pluviseasonal-oceanic bioclimate. Coastal marshes in the Llobregat delta belong to the dry coastal type (Adam 1993).

The study was conducted in the southern hemi-delta of the Llobregat river (Llobregat delta hereafter), south of the city of Barcelona (Catalonia, NE Spain; Fig. 1). This area (7,000 ha) has undergone major land transformations during the last 50 years, including both ecosystem degradation and natural restoration. Marshlands and fixed dunes account for only 13% of the total land cover.

We created a sampling network comprising 43 sampling points distributed across four sites in the Llobregat delta marshes: Magarola, Ricarda, Can Sabadell and Reguerons (Fig. 1). According to Pino et al. (2006) Magarola and Ricarda are stable sites (longstanding natural areas) and Can Sabadell and Reguerons are semi-stable sites (abandoned and spontaneously restored since 1956). Ricarda and Magarola also share a similar position, since both are located close to the shoreline, although the former has important freshwater inputs whereas the latter is more heavily influenced by seawater. Can Sabadell and Reguerons are located 2 km away from the shoreline; the former includes some patches of saline soil, while the latter may be considered mesohaline.

In each site we set up 6–18 sampling points randomly distributed among the three main vegetation types (reedbeds, rushbeeds and halophytic shrubs). Distance between points was at least 20 m. At each sampling point we recorded the species composition and abundance in one circular area of 2 m radius (12.56 m^2), using the Braun-Blanquet method (Braun-Blanquet 1979). Species were identified according to Bolòs et al. (2005). Each sampling point was equipped with a vertically sunk PVC pipe, of 1.5 m in length (reaching 1.3 m in depth) and 32 mm in diameter. In order to monitor the hydrologic conditions, the level and the conductivity of the water table were measured monthly at each point from December 2004 to December 2006. During 2005, samples were also taken every 3 months from the top 20 cm of soil, in order to monitor soil variables.

This gave a dataset of 45 relevés, each with precise information on hydrological and edaphic conditions and their yearly dynamics. In order to obtain a balanced design suitable for the statistic analyses detailed below, 8 of these sampling points where discarded using a random selection process within the overrepresented communities. For more details on sampling and analytical methods see Batriu et al. (2011).

Phytosociological and statistical analyses

The relevés were classified to alliance level according to previously published information from vegetation studies dealing with the Llobregat delta (Bech & Hernández

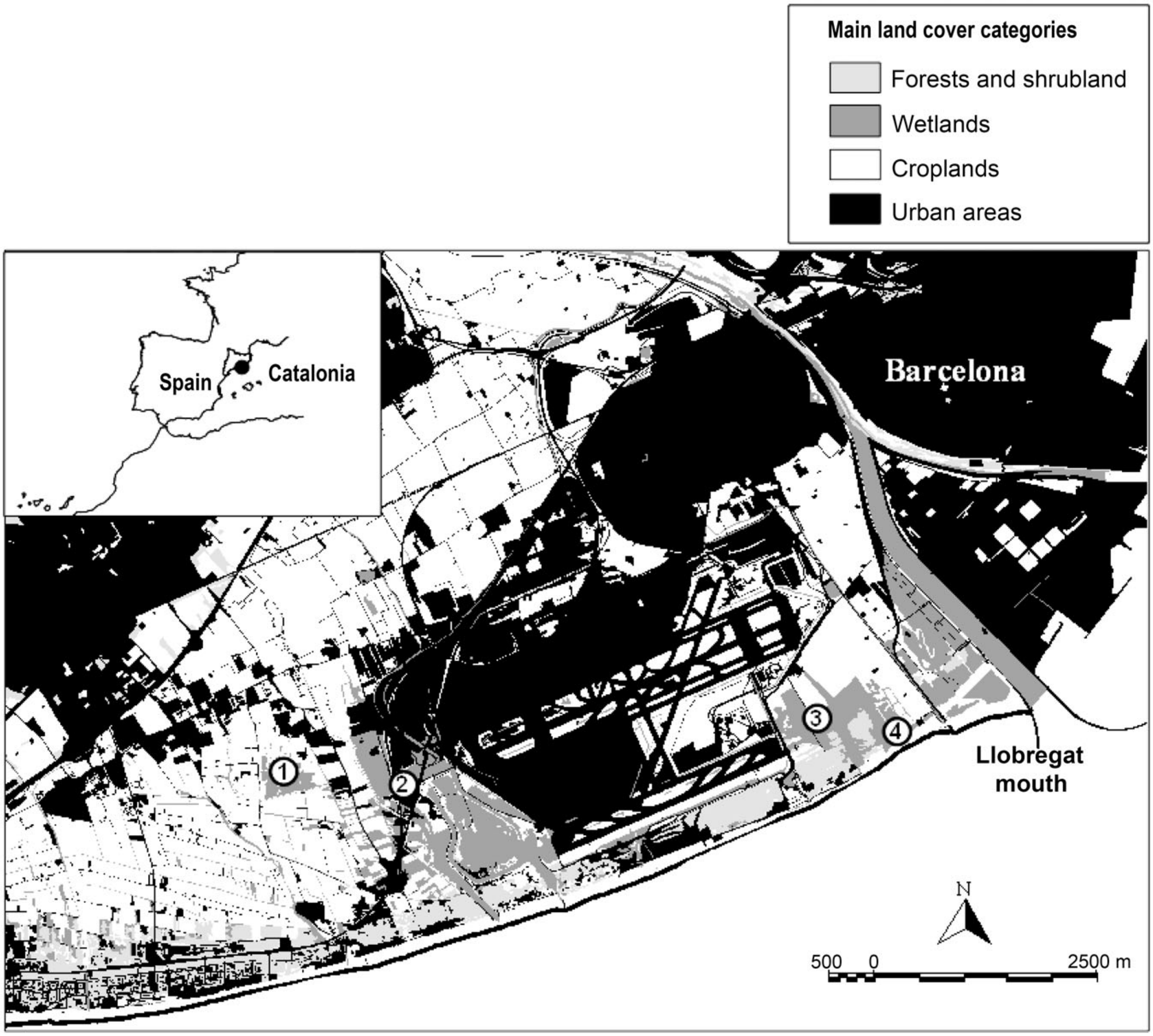

Fig. 1. Map of the study area showing the main land cover categories and the four study sites (circles): 1, Reguerons; 2, Can Sabadell; 3, Ricarda; 4, Magarola.

1976; Bolòs 1962) or with nearby coastal marshes such as the Ebre delta (Curcó 2003) and Empordà marshes (Gesti 2006). The phytosociological scheme and nomenclature follows Rivas-Martínez et al. (2001).

Once classified, principal component analyses (hereafter PCA) were performed on the relevés to assess the reliability of the classification obtained (Legendre & Gallagher 2001). We transformed the abundance/dominance 6-grade values of the species using the ordinal transformation described by van der Maarel (1979). The resulting matrix was distance-emulating transformed (Legendre & Gallagher 2001) using the Hellinger distance in order to avoid the effect of null abundance in the PCA ordination. All the above analyses were performed using the GINKGO package (De Cáceres et al. 2007).

We performed a generalized linear mixed model (hereafter GLMM) using a gaussian error, taking the alliance type as the fixed factor and site as the random factor. The environmental variables used were those identified as being most important for plant distribution by Batriu et al. (2011) using the same dataset, namely mean level of the water table (hereafter water table), maximum conductivity of the water table (hereafter conductivity), and mean Sodium Adsorption soil Ratio (hereafter SAR). To test the importance of alliance type as predictor of environmental variables that determine plant distribution, we compared the full model with a model without any fixed factor but only site as random effect. These comparisons were done through an ANOVA test using Chi squared distribution as recommended by Crawley (2007). To assess the importance of site factor in environmental variables we calculated the percentage of variance explained for this factor. Finally, to compare alliances between them, these vegetation types were used as *a priori* contrast in the models analyzed thought GLMM. For the effects of *a priori* contrast, |t|>2 was considered significant at any degree of freedom (Crawley 2007). We performed all these statistical analyses using R 2.4.1 (R Development Core Team 2009), and GLMM using the function lmer of the package lme4 version 0.99375-31 (Bates et al. 2008).

Results

According to previously published phytosociological information, the relevés belonged to three different alliances, each included in a distinct vegetation class (Table 1, Appendix). These alliances were: Phragmition communis Koch 1926 (reed beds, hereafter Phragmition) from Phragmito-Magnocaricetea Klika 1941, Salicornion fruticosae Br.-Bl. 1933 (halophytic shrubby formations, hereafter Salicornion) from Salicornietea fruticosae Br.-Bl. et Tüxen ex A. et O. Bolòs 1950 and Juncion maritimi Br.-Bl. ex Horvatic 1934 (rush beds, hereafter Juncion) from Juncetea maritimi Br.-Bl. 1952.

The first three axes of the PCA ordination explained 60.2% of the variance found in the floristic relevés. These three axes were mainly correlated with the abundance of five species: *Arthrocnemum fruticosum*, *Juncus maritimus*, *Phragmites australis*, *Spartina versicolor* and *Juncus acutus* (Fig. 2). Axis 1 was mainly correlated with *A. fruticosum*, *P. australis* and *J. maritimus* and explained 29.2% of variance; axis 2 was mainly correlated with *J. acutus* and *A. fruticosum* and explained 20.2% of variance; and axis 3 was mainly correlated with *S. versicolor* and *P. australis* and explained 10.8% of variance. According to these three axes, the Salicornion and the Phragmition relevés formed two relatively well delimited groups, whereas the Juncion relevés formed a more disperse, apparently heterogeneous group. A further PCA of the Juncion plots showed the main role played in this distribution by three potentially dominant species, namely *Juncus acutus, J. maritimus* and *Spartina versicolor* (Fig. 3).

In the GLMM, the majority of the water table variance was associated with site (Table 2). In contrast, the percentage of explained variance of conductivity and SAR values associated with site were 36% and less than 1% respectively (Table 2). Alliance factor had a significant ($p < 0.05$) effect on the residual variance of all three variables, and significant differences between alliances were also observed (Table 3). Conductivity and mean SAR were significantly higher in the Salicornion stands than in the Phragmition or Juncion ones, and the Phragmition stands had a higher water table than the Juncion and Salicornion stands (Table 3, Fig. 4).

Table 1. Distribution of the points sampled according to sites and vegetation alliances.

		Alliance			
		Salicornion	Phragmition	Juncion	Total
Site	Magarola	4	2	6	12
	Ricarda	2	3	6	11
	Can Sabadell	3	2	3	8
	Reguerons	0	3	3	6
Total		9	10	18	37

Discussion

Vegetation units and environmental gradients

The hierarchy of phytosociological classification allows formal vegetation generalizations and comparisons. However, according to Webb (in Adam 1993) the relationships between communities would be best expressed in a multidimensional classification reflecting a number of floristic (and, by implication, environmental, biotic or historic) gradients. It may be argued that it is not the aim of the phytosociological method to reflect environmental gradients. However, clear differences in environmental conditions between distinct phytosociological units have been noted in many vegetation types, as previously stated.

Previous studies have associated Salicornion with high values of soil conductivity (Alvarez Rogel et al. 2001; Molina et al. 2003), Juncion with intermediate values (Molina et al. 2003) and Phragmition with low ones (Burdick et al. 2001; Molina et al. 2003). Our results partially agree with this pattern, since Salicornion stands had clearly higher values of conductivity and SAR than Juncion and Phragmition stands. However, the range of conductivity and SAR exhibited by Juncion stands overlapped with that occupied by those of Phragmition. Thus only Salicornion can be used as a reliable predictor of high water table conductivity and adverse ionic soil conditions.

In terms of the water table, the predictive value of alliances was significant in our case, although we cannot rule out the possibility that most of the variation in this factor was due to the site factor. According to Molina et al. (2003) Phragmition stands are widespread over lagoons and irrigation ditches, where they experience a longer flooding period than Juncion maritimi and Salicornion communities. However, Haslam (1970) reported that *Phragmites* stands (attributed to Phragmition) can also thrive in places where the depth of the water table exceeds 1 m. Our results encompass these two contrasting situations. So, although the mean level of

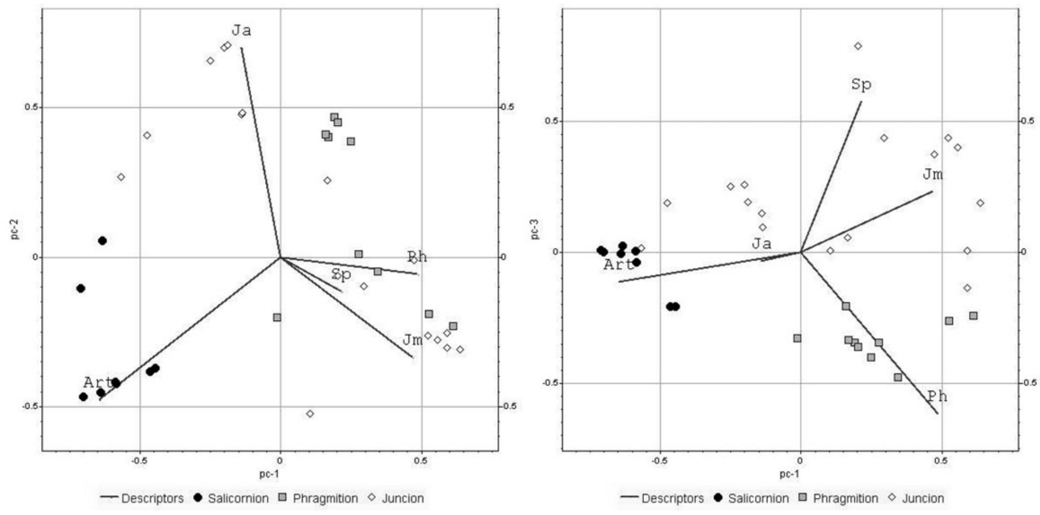

Fig. 2. Position of the relevés on the three first axes of PCA. Grey lines represent the dispersion (line angle) and weight (line length) of species. Emulating distance method using Hellinger distance was applied to the original relevés matrix. Species codes: Art, *Arthrocnemum fruticosum*; Ja, *Juncus acutus*; Jm, *Juncus maritimus*; Ph, *Phragmites australis*; Sp, *Spartina versicolor*.

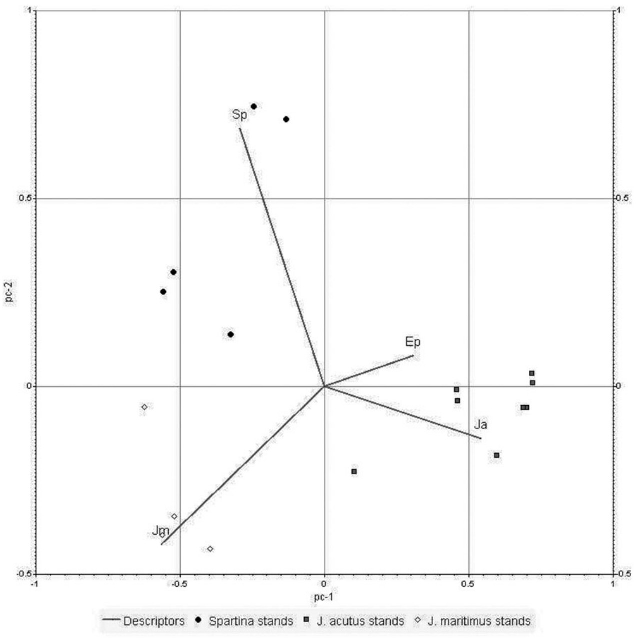

Fig. 3. Position of Juncion maritimi relevés on the two first axes of a PCA. Grey lines represent the dispersion (line angle) and weight (line length) of species Emulating distance method using Hellinger distance was applied to the original relevés matrix. Species codes: Ep, *Elymus pungens* subsp. *campestre*; Ja, *Juncus acutus*; Jm, *Juncus maritimus*; Sp, *Spartina versicolor*.

water table was significantly higher in Phragmition than in the other alliances studied, the site factor had a strong effect upon this parameter in areas in which the Phragmition stands were found. Thus, a given Phragmition stand cannot be used as a good predictor of the water table level.

Table 2. Effect of the factor alliance tested through ANOVA between a GLMM with alliance as the fixed factor and site as the random factor, and a GLMM only with site as the random factor. The two last columns show the percentage of variance of site factor, and the residual percentage of the simplified GLMM ($^{+}$ percentage of variance < 0.001%, * p < 0.05, *** p < 0.001).

	Effect of alliance		Model % of variance	
Variable	Chi Sq	p	Site	Residual
Mean water table	68.999	0.03175*	74%	26%
Max conductivity	35.697	0.00000002***	36%	64%
SAR	21.161	0.00003***	+	100%

Table 3. Results of *a priori* contrast, with alliance as the fixed factor, of those variables with a significant effect on the site factor (* p < 005, at any degree of freedom). Alliance codes: S, Salicornion fruticosae; Ph, Phragmition communis; J, Juncion maritimi.

Variable	Contrast	St error	t Value
Mean water table	Salicornion vs Phragmition	2.738	2.741*
	Salicornion vs Juncion	2.319	–1.067
	Phragmition vs Juncion	2.099	2.377*
Max conductivity	Salicornion vs Phragmition	4,065	–4.063*
	Salicornion vs Juncion	3,462	–4.354*
	Phragmition vs Juncion	3,129	–0.231
SAR	Salicornion vs Phragmition	3.403	–3.093*
	Salicornion vs Juncion	2.976	–2.487*
	Phragmition vs Juncion	2.675	–0.584

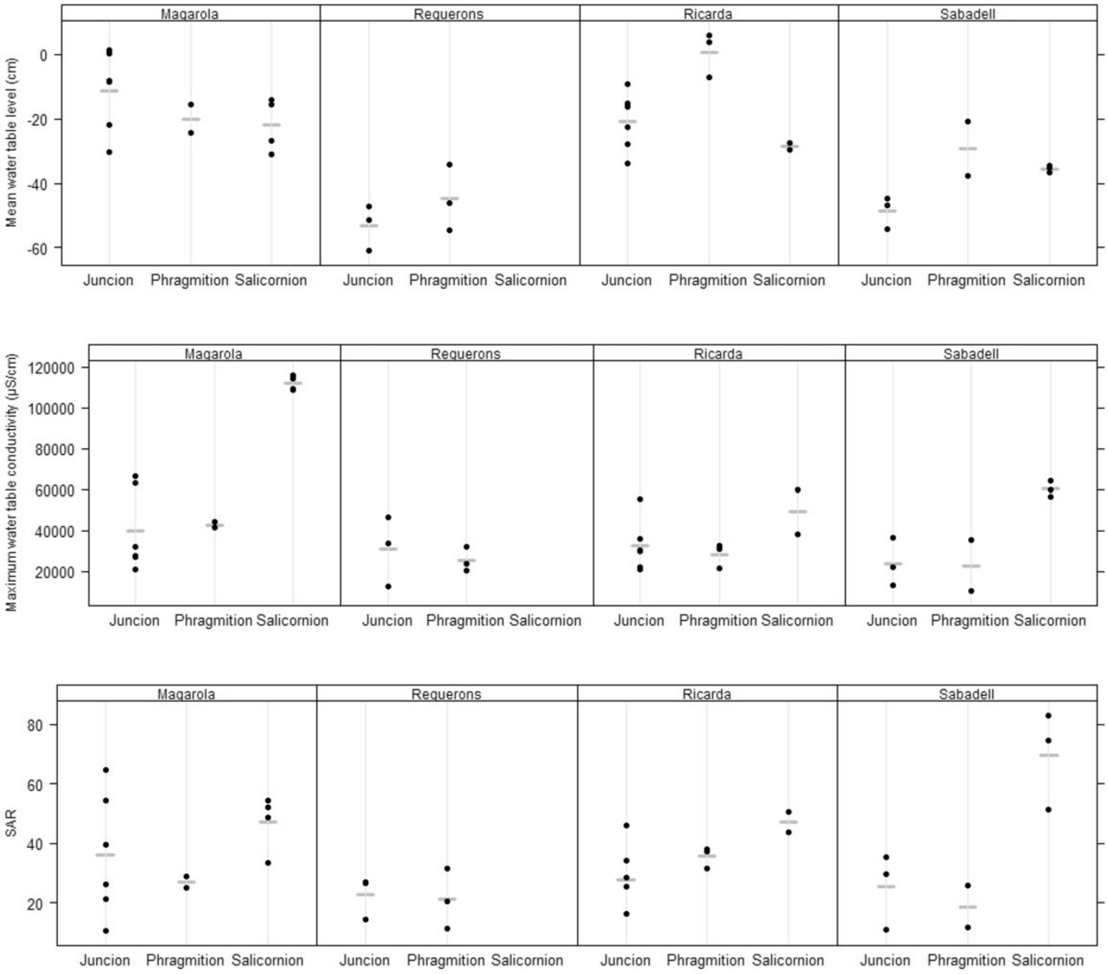

Fig. 4. Plot of the mean water table level (top), maximum water table conductivity (medium) and mean soil SAR ratio (bottom), according to sites and alliances. Black dots indicate sampling points values and grey lines indicate means for each group of sampling points.

Implications for understanding vegetation

The substantial percentage of variance related to site factor in some ecological variables means that the distribution of vegetation units along some ecological gradients may be a consequence of historical factors. Although determining the relationship between these historical aspects and vegetation composition was beyond the capacity of our experimental design, we have a number of related comments, as discussed below.

The importance of the site factor for the saline gradient was negligible, as shown by the clear association between the upper part of this gradient and the Salicornion stands. This may imply that the setting of these stands is not affected by the surrounding Phragmition or Juncion stands, but depends on diaspore availability and the further development of Salicornion species.

Unlike the saline gradient, the response to the water table gradient was greatly affected by the site factor, with Phragmition and Juncion exhibiting the most variation along this gradient. Given the noticeable overlap between these alliances on the water table gradient, one may ask why Phragmition and Juncion stands occupied such different niches at different sites at similar points on this gradient.

P. australis exhibits a low level of floral fertility and seedling establishment (Ishii & Kadono 2002), although this does not seem to restrict its capacity for colonization (Pino et al. 2009). This species is able to re-colonize gaps that arise through disturbance events thanks to its clonal growth. It creates a canopy that shades other marsh plants and also modifies the habitat by increasing the accumulation of plant litter and by altering the physicochemical conditions of the soil (Meyerson et al. 2000; Minchinton et al. 2006; Seliskar et al. 2004). Thus, the common reed is in most cases able to engineer the environment to exclude other species that would otherwise be highly competitive. This phenomenon is considered a positive feedback mechanism, and is common in spontaneous succession and restoration processes (Klötzli &

Grootjans 2001). This mechanism of competitive exclusion may produce almost monospecific stands in distinct environmental conditions (e.g. contrasting ranges of water table level). In these cases phytosociology cannot find distinct units in varying environments because of the lack or scarcity of differential taxa. The same limitation applies in other plant communities dominated by clonal species such as *Juncus subnodulosus, J. effusus, Carex fusca* and *Molinia coerulea* (e.g. Rodwell 1991, Grabherr & Mucina 1993).

As previously stated, Juncion stands exhibit floristic divergence, which makes them a heterogeneous group (Fig. 3). This is primarily due to the varying degrees of dominance of *J. acutus*, *J. maritimus* and *S. versicolor*, which is associated with different levels of water table (Batriu et al. 2011). In fact, some of these differences have been described for different phytosociological ranks. *J. maritimus* and *S. versicolor* stands belong to Spartino-Juncetum maritimi O. Bolòs 1962, an association including two subassociations defined by the dominant species (spartinetosum O. Bolòs 1962, dominated by *Spartina versicolor*; and Juncetosum maritimi O. Bolòs 1962, dominated by *Juncus maritimus*). Stands dominated by *J. acutus* are frequently difficult to attribute to any phytosociological association and even alliance, because this rush is a rather ubiquitous species; they are mostly included in Juncetalia maritimae, but in some cases they have been linked to Holoschoenion. According to Gesti & Vilar (2003) our *J. acutus* stands may belong to the association Spartino-Juncetum maritimi, thus being considered a consequence of disturbance in *J. maritimus* stands, or may belong to the association Elymo curvifolii-Iridetum spuriae (Rivas-Martínez) Cirujano 1981, a rush formation that occupies less waterlogged soils than *J. maritimus* stands. Our *J. acutus* stands certainly appeared to be associated with disturbance because they were found as dominant formations in semi-stable localities, but these localities also had a lower water table. So in this case, as in *P. australis* stands, both environmental and historical factors may be responsible for the presence of *J. acutus* stands. However, in contrast to reed stands, *J. acutus* stands exhibited some species divergence from the other Juncion stands. They can thus be distinguished as a subassociation within Spartino-Juncetum maritime, based on vegetation dynamics.

The three alliances considered herein are relatively similar in various aspects, at least within the study area. All are related to one or another stress factor, are characterized by a few species, and show equivalent distribution patterns in the landscape. For these reasons, and according to the assumption that the alliance level corresponds to a particularly good ecological descriptor (Terradas 2001), these alliances could be expected to reflect the main operating ecological gradients relatively well. However, as in other hierarchical classification methods, the diversity of communities within the units of the same phytosociological level (i.e. alliance) is not always equally balanced. In our case study, the Juncion alliance is floristically more diverse and heterogeneous across sites. Thus, unlike Salicornion and Phragmition, our Juncion stands can be divided into distinct lower vegetation units, which thrive under different abiotic conditions.

Moreover, most phytosociological sampling and the described vegetation units reflect semi-natural, relatively well-preserved habitats (Pino et al. 2009), while strongly altered landscapes are now widespread. The case discussed herein reflects a few of the problems with which phytosociology has to deal when applied to man-altered landscapes. In many cases phytosociology states an eventual monoclimax after facilitation succession models like those of Connell and Slatery (Krebs 2001). However, a polyclimax approach seems more realistic in most altered landscapes, according to the climax pattern hypothesis of Whittaker (Krebs 2001). In this approach communities are viewed as the product of multiple circumstances, including historic factors such as disturbance events, lottery effects in colonization, and inhibitory processes from established dominant species. This is particularly true in coastal marshes where unexpected stable plant formations appear during succession (Adam 1993; Klötzli & Grootjans 2001). In our case study, the alliances overlapping along some segments of the environmental gradients may be understood as polyclimax phenomena in these segments.

Concluding remarks

Within a given landscape, the phytosociological classification at the alliance level partially reflects the most important operating gradients in the area studied, i.e. the salinity gradient and associated effects. However, this hierarchical system cannot reflect other operating gradients, mainly because of (i) the different floristic diversity between different alliances, and (ii) the inability to differentiate distinct vegetation units from near-monospecific stands of the same species, thriving in different environments.

Both problems are intrinsic limitations of the method, but the system could be improved if more attention were paid to dominant vegetation formations in disturbed areas, through accurate sampling of traditional relevés together with ecological data. Although studying the mechanisms operating in vegetation dynamics was beyond the scope of this work, we conclude that these factors cannot be ignored in any vegetation study or restoration planning and monitoring. In our case, the initial species pool or the plant dispersal capacity of some vegetation types (e.g. Phragmition or Salicornion) seem to have driven the vegetation dynamics in the spontaneous restoration of marshlands on the Llobregat delta.

Acknowledgements: We thank J.M. Blanco for statistical assistance and A. Pérez-Haase for discussion of results. The Department of the Environment and Housing of the Catalan government funded this research.

References

Adam, P. (1993): Saltmarsh Ecology. – Cambridge University Press, Cambridge.

Alvarez Rogel, J., Ortiz Silla, R. & Alcaraz Ariza, F. (2001): Edaphic characterization and soil ionic composition influencing plant zonation in a semiarid Mediterranean salt marsh. – Geoderma **99**: 81–98.

Bates, D., Maechler, M. & Bolker, B. (2009): The lmer package for R: linear mixed-effects models using S4 classes, version 099375-31. Available: http://cranrprojectorg/web/packages/lme4/indexhtml via the INTERNET. Accessed 2009 16 April.

Batriu, E., Pino, J., Rovira, P. & Ninot, J.M. (2011): Environmental control of plant species abundance in a macrotidal Mediterranean saltmarsh. – Appl. Veg. Sci. **14**: 358–366.

Bech, J. & Hernandez, A.M. (1976): Estudio sobre suelos y vegetación del delta del Llobregat. – Collect Bot. (Barcelona) **10**: 31–107.

Bergmeier, E. (2002): Plant communities and habitat differentiation in the Mediterranean coniferous woodlands of Mt Parnon (Greece). – Folia Geobot. **37**: 309–331.

Bertness, M.D. & Ellison, A.M. (1987): Determinants of pattern in a New-England salt-marsh plant community. – Ecol. Monogr. **57**: 129–147.

Bolòs, O. de (1962): El paisaje vegetal barcelonés. – Catedra Ciudad de Barcelona, Barcelona.

Bolòs, O. de, Vigo, J., Masalles, R.M. & Ninot, J.M. (2005): Flora Manual dels Països Catalans. –Editorial Pòrtic, Barcelona.

Bouzille, J.B., Kerneis, E., Bonis, A. & Touzard, B. (2001): Vegetation and ecological gradients in abandoned salt pans in western France. – J. Veg. Sci. **12**: 269–278.

Braun-Blanquet, J. (1979): Fitosociología. Bases para el estudio de las comunidades vegetales. – JH Blume, Madrid.

Bruland, G.L. & Richardson, C.J. (2005): Spatial variability of soil properties in created, restored, and paired natural wetlands. – Soil. Sci. Soc. Am. J. **69**: 273–284.

Burdick, D.M., Buchsbaum, R. & Holt, E. (2001): Variation in soil salinity associated with expansion of Phragmites australis in salt marshes. – Environ. Exp. Bot. **46**: 247–261.

Callaway, R.M. & Pennings, S.C. (2000): Facilitation may buffer competitive effects: Indirect and diffuse interactions among salt marsh plants. – Am. Nat. **156**: 416–424.

Casanovas Poch, L. (1996): Contribution to the knowledge of the Pyrenean mires. – Folia Botanica Miscellanea **10**: 175–201.

Costa, C.S.B., Marangoni, J.C. & Azevedo, A.M.G. (2003): Plant zonation in irregularly flooded salt marshes: relative importance of stress tolerance and biological interactions. – J. Ecol. **91**: 951–965.

Crawley, M.J. (2007): The R book. John Wiley & Sons Ltd, West Sussex, England

Curcó, A. (2003): Estudis sobre el poblament vegetal del delta de l'Ebre: flora, vegetació i ecologia de comunitats vegetals [thesis]. – Barcelona: Universitat de Barcelona, Departament de Biolgia Vegetal. Available from: Universitat de Barcelona.

Curcó, A., Ibánez, C., Day, J.W. & Prat, N. (2002): Net primary production and decomposition of salt marshes of the Ebre delta (Catalonia, Spain). – Estuaries **25**: 309–324.

De Cáceres, M., Oliva, F., Font, X. & Vives, S. (2007): Ginkgo, a program for non-standard multivariate fuzzy analysis. – Adv. Fuzzy Sets Syst. **2**: 41–56.

Gesti, J. (2006): El poblament vegetal dels aiguamolls de l'Empordà. – Institut d'Estudis Catalans, Barcelona.

Gesti, J. & Vilar, L. (2003): Vegetation changes from Les Llaunes natural reserve (NE Iberian Peninsula) after seventeen years of management: Evaluation by means of GIS. – Vie Milieu **53**: 15–25.

Grabherr, G. & Mucina, L. (1993): Die Pflanzengesellschaften Österreichs, Teil II, Natürliche waldfreie Vegetation. – Gustav Fischer Verlag, Jena.

Grattan, S.R. & Grieve, C.M. (1992): Mineral Element acquisition and growth-response of plants grown in saline environments. – Agr. Ecosys. Environ. **38**: 275–300.

Hajek, M. & Hajkova, P. (2004). Environmental determinants of variation in Czech Calthion wet meadows: a synthesis of phytosociological data. – Phytocoenologia **34**: 33–54.

Hajkova, P., Hajek, M. & Apostolova, I. (2006): Diversity of wetland vegetation in the Bulgarian high mountains, main gradients and context-dependence of the pH role. – Plant Ecol. **184**: 111–130.

Haslam, S.M. (1970): The Performance of Phragmitescommunis Trin in Relation to Water-Supply. – Ann. Bot. **34**: 867–877.

Hrivnak, R., Hajek, M., Blanar, D., Kochjarova, J. & Hajkova, P. (2008): Mire vegetation of the Muranska Planina Mts – formalised classification, ecology, main environmental gradient and influence of geographical position. – Biologia **63**: 368–377.

Ishii, J. & Kadono, Y. (2002): Factors influencing seed production of Phragmites australis. – Aqua Bot. **72**: 129–141.

Klötzli, F. & Grootjans, A.P. (2001): Restoration of natural and semi-natural wetland systems in Central Europe: Progress and predictability of developments. – Restoration Ecol. **9**: 209–219.

Körner, C., Stöcklin, J., Reuther-Thiebaud, L. & Pelaez-Riedl, S. (2008): Small differences in arrival time influence composition and productivity of plant communities. – New Phytol. **177**: 698–705.

Krebs, C.J. (2001): Ecology: the experimental analysis of distribution and abundance. – Benjamin Cummings, St Francisco.

Legendre, P. & Gallagher, E.D. (2001): Ecologically meaningful transformations for ordination of species data. – Oecologia **129**: 271–280.

Lu, J.W., Wang, H.J., Wang, W.D. & Yin, C.Q. (2007): Vegetation and soil properties in restored wetlands near Lake Taihu, China. – Hydrobiologia **581**: 151–159.

Meyerson, L.A., Saltonstall, K., Windham, L., Kiviat, E. & Findlay, S. (2000): A comparison of Phragmites australis in freshwater and brackish marsh environments in North America. – Wetlands Ecol. Manage. **8**: 89–103.

Minchinton, T.E., Simpson, J.C. & Bertness, M.D. (2006): Mechanisms of exclusion of native coastal marsh plants by an invasive grass. – J. Ecol. **94**: 342–354.

Molina, J.A., Casermeiro, M.A. & Moreno, P.S. (2003): Vegetation composition and soil salinity in a Spanish Mediterranean coastal ecosystem. – Phytocoenologia **33**: 475–494

Pearcy, R.W., Ehleringer, J., Mooney, H.A. & Rundel, P.W. (1991): Plant Physiological Ecology. –Chapman and Hall, London.

Pennings, S.C., Grant, M.B. & Bertness, M.D. (2005): Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. – J. Ecol. **93**: 159–167.

Pezeshki, S.R. (2001): Wetland plant responses to soil flooding. – Environ. Exp. Bot. **46**: 299–312.

Pino, J., Segui, J.M. & Alvarez, N. (2006): Invasibility of four plant communities in the Llobregat delta (Catalonia, NE of Spain) in relation to their historical stability. –Hydrobiologia **570**: 257–263.

Pino, J., Vila, M., Alvarez, N., Segui, J.M. & Guerrero, C. (2009): Niche breadth rather than reproductive traits explains the response of wetland monocotyledons to land-cover change. – Appl. Veg. Sci. **12**: 119–130.

Poschlod, P. & Biewer, H. (2005): Diaspore and gap availability are limiting species richness in wet meadows. – Folia Geobot. **40**: 13–34.

R Development Core Team (2009): R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.Availabel: http://wwwR-projectorg.

Ranwell, D.S. (1972): Ecology of saltmarshes and sand dunes. – Chapman and Hall, London.

Rivas-Martínez, S., Fernández-González, F., Loidi, J., Lousã, M. & Penas, A. (2001): Syntaxonomical checklist of vascular plant communities of Spain and Portugal to association level. – Itinera Geobotanica **14**: 5–341.

Rodriguez-Rojo, M.P. & Sanchez-Mata, D. (2006): Hay meadow communities (Arrhenatherion Koch 1926) throughout the Iberian Central Range (Spain). – Phytocoenologia **36**: 231–246.

Rodwell, J.S. (1991): British plant communities, Volume 2, Mires and heaths. – Cambridge University Press, Cambridge.

Rubio-Casal, A.E., Castillo, J.M., Luque, C.J. & Figueroa, M.E. (2001): Nucleation and facilitation in salt pans in Mediterranean salt marshes. – J. Veg. Sci. **12**: 761–770.

Sanchez J.M., Otero X.L. & Izco J. (1998): Relationships between vegetation and environmental characteristics in a salt-marsh system on the coast of Northwest Spain. – Plant Ecol. **136**: 1–8.

Seliskar, D.M., Smart, K.E., Higashikubo, B.T. & Gallagher, J.L. (2004): Seedling sulfide sensitivity among plant species colonizing Phragmites-infested wetlands. – Wetlands **24**: 426–433.

Terradas, J. (2001): Ecología de la Vegetación. – Ediciones Omega, Barcelona.

Tsiripidis, I., Karagiannakidou, V., Alifragis, D. & Athanasiadjs, N. (2007): Classification and gradient analysis of the beech forest vegetation of the southern Rodopi (northeast Greece). – Folia Geobot. **42**: 249–270.

Van der Maarel, E. (1979): Transformation of cover-abundance values in phytosociology and its effects on community similarity. – Plant Ecol. **39**: 97–114.

Willner, W. (2006): The association concept revisited. – Phytocoenologia **36**: 67–76.

Addresses of the authors

Efrem Batriu, Josep M. Ninot, Group of Geobotany and Vegetation Mapping, Department of Plant Biology, University of Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain.
Pere Rovira, Centre Tecnològic Forestal de Catalunya (CTFC), Crta. de Sant Llorenç de Morunys km 2, 25280 Solsona, Spain.
Joan Pino, Centre for Ecological Research and Forestry Applications (CREAF), Autonomous University of Barcelona, 08193 Bellaterra, Spain.
Corresponding author: efrembatriu@hotmail.com

Electronic appendix

Appendix. Alliance tables with the relevés taken from the four sites.

Appendix data associated with this article can be found in the online version at
www.schweizerbart.de/journals/phyto

Appendix. Alliance tables with the relevés taken from the four sites (Ma, Magarola; Ri, Ricarda; Sa, Can Sabadell; Re, Reguerons; see Figure 1 for location).

Juncion maritimi Br-Bl ex Horvatic 1934

	Ma2	Ma5	Ma6	Ma13	Ma15	Ri4	Ri6	Ri10	Ma3	Ma7	Ma14	Ma17	Ri2	Ri7	Ri11	Ma16	Ma18	Sa2	Sa7	Sa8	Re1	Re3	Re4
Juncus acutus	1			2	1			1								4	4	4	4	4	5	4	4
Spartina versicolor	5	5	5	5	5	5	5	5	2	2	1												
Phragmites australis subsp. *australis*	2	1	1	2	2		1	1	+	+	2	+	1	1	3	+							
Juncus maritimus		2			1	+	2	3	4	5	5	5	5	5	5		2						
Elymus pungens subsp. *campestre*						+												3	5	4	+		
Agrostis stolonifera						+												+				1	
Arthrocnemum fruticosum												2				2				1			
Aster squamatus																	1				1	+	

Taxa with less than 3 occurrences:

Phragmites australis subsp. *chrysanthus* in Ma2 (+)
Sonchus maritimus in Ma6 (1) Ri4 (1)
Brachypodium phoenicoides in Ma6 (1) Ri4 (2)
Dorycnium pentaphyllum subsp. *gracile* in Ri4 (1) Ri6 (1)
Schoenus nigricans in Ri4 (1)
Calystegia sepium in Ma2, Ma15 (+)
Oenanthe lachenalii in Ma18 (1)
Carex extensa in Ma18 (1)
Inula crithmoides in Ma18 (1)
Paspalum vaginatum in Ma18 (5)
Suaeda vera in Sa2 (1) Sa8 (3)
Atriplex prostrata in Re1 (1) Re4 (2)
Plantago crassifolia in Re3 (2)
Bromus racemosus in Re3 (+)
Dipsacus fullonum subsp. *fullonum* in Re3 (+)
Festuca arundinacea in Re3 (2)
Galium aparine in Re3 (+) Re4 (1)
Asparagus officinalis in Re3 (+)
Beta vulgaris in Re4 (1)
Cirsium vulgare in Re4 (+)
Bromus madritensis in Re4 (+)
Hordeum marinum in Re4 (+)
Sonchus asper in Re4 (1)
Torilis arvensis in Re4 (+)

Salicornion fruticosae Br-Bl 1933

	Ma1	Ma8	Ma10	Ma11	Ri1	Ri5	Sa1	Sa4	Sa5
Arthrocnemum fruticosum	4	5	5	4	5	5	5	5	5
Juncus subulatus	2	1	1						
Atriplex portulacoides		1	1						
Suaeda vera					1	1	+	+	
Phragmites australis subsp. *australis*					+	+			
Juncus acutus							+	2	

Taxa with less than 2 occurrences:

Scirpus maritimus in Ma1 (1)
Scirpus cernuus in Ma8 (1)
Aster tripolium in Ri1 (+)
Inula crithmoides in Sa4 (1)

Phragmition australis Koch 1926

	Ma9	Ma12	Ri3	Ri8	Ri12	Sa3	Sa6	Re2	Re5	Re6
Phragmites australis subsp. *australis*	4	4	5	5	4	5	5	5	4	5
Juncus acutus	4	3					2		3	2
Phragmites australis subsp.*chrysanthus*		1	1		3					
Agrostis stolonifera						+	1			
Calystegia sepium						1	3			

Taxa with less than 2 occurrences:
Atriplex prostrata in Ma12 (+)
Cynanchum acutum in Ma12 (2)
Scirpus maritimus in Ri3 (1)
Juncus maritimus in Ri8 (1)
Aeluropus littoralis in Sa3 (+)
Arthrocnemum fruticosum in Sa3 (+)
Aster tripolium in Sa3 (+)
Juncus subulatus in Sa3 (3)
Oenanthe lachenalii in Sa3 (+)
Elymus pungens subsp. *campestre* in Sa6 (1)
Avena barbata in Re2 (1)
Bromus madritensis in Re2 (+)
Galium aparine in Re2 (2)
Lepidium draba in Re2 (+)