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Schoenus nigricans (Cyperaceae) xerophytic grasslands on the NE Adriatic islands Cres and Krk (Croatia)

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Several xerophytic grasslands on the NE Adriatic islands Cres and Krk (Croatia) are dominated by tussock-forming *Schoenus nigricans* (Cyperaceae). All vegetation types reported are characterised by the degradation of the vegetation cover due to grazing. Phytosociologically, the vegetation is classified as the *Danthonio-Scorzoneretum villosae* subass. *schoenetosum nigricantis* H-ić 57 of the *Scorzonerion villosae* H-ić 49 alliance within the order *Scorzonero-Chrysopogonetalia*, but partly shows transitions to the *Bromo-Chrysopogonetum grylli* H-ić 60. We differentiated three variants: more xerophytic sites (on Cres), sites characterised by alternating soil humidity (mainly on Krk), and advanced succession stages. Physiognomically all variants are dominated by *Schoenus nigricans* tussocks, which are fostered by sheep grazing and the summer-dry conditions on the compacted soils. Comparison with Central European more humid habitats suggests the hypothesis of an ecotypic differentiation of *Schoenus nigricans* within its European distribution area.

Keywords: *Schoenus nigricans*, Cyperaceae, xerophyte, vegetation, succession, Adriatic, island, Cres, Krk, Croatia

Introduction

Xerophytic grasslands are common on the Kvarner Islands Cres and Krk (Fig. 1). These grasslands form part of the submediterranean and the east-continental grassland vegetation of Croatia (ILIJANIĆ et al. 1972, ŠKORNIK 2003). In general, different types of xerophytic grasslands within the order *Scorzonero-Chrysopogonetalia* frequently containing *Chrysopogon gryllus* (Poaceae) are widespread in this region (HORVATIĆ 1958, HORVATIĆ 1963, HORVAT et al. 1974).

Schoenus nigricans L. is a taxon from the Cyperaceae family, known as a characteristic species of wet mires in Central Europe (e.g., ZOBRIST 1935, OBERDORFER 1977, MARTINČIČ 1991, GRABHERR and MUCINA 1993, POTT 1995). However, *Schoenus nigricans* also tolerates the summer-dry conditions in more continental and (sub)mediterranean parts of Europe, and additionally, is reported from salt marshes, as well as halophilous rocks and

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dunes along the shore (e.g., HORVATIĆ 1963, HORVAT et al. 1974, ERNST 1991). Most sprouts of this tussock-forming species will be dried up during summer. These older sprouts conserve younger sprouts and new inflorescences in the centre of the plant. As it has been demonstrated that sprouts of *Schoenus nigricans* are basically larger in (sub)mediterranean areas than in Central Europe (ERNST 1991), they have the abilityphysiognomically to dominate (sub)mediterranean grasslands. In addition, the tussock-forming growth might be fostered by the use of the grasslands as pastures.

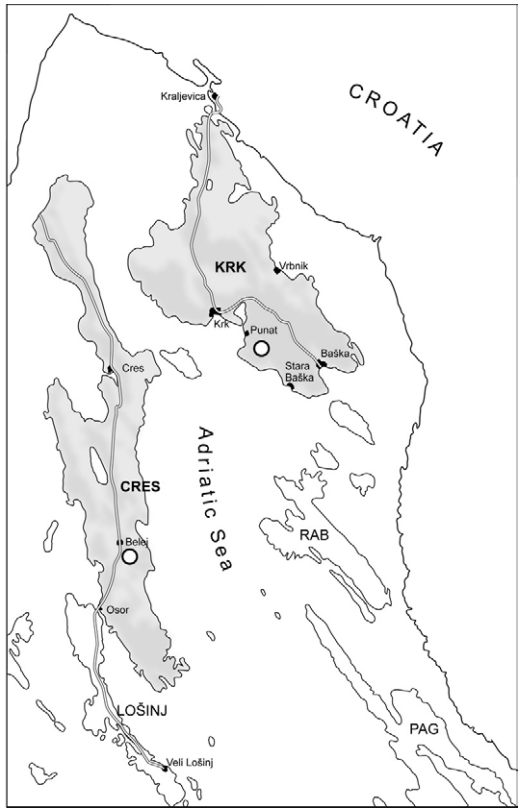

Fig. 1. *Schoenus nigricans* locations (open circles) on the Kvarner islands Cres and Krk represented in this study.

In our study area, the Kvarner islands of Cres and Krk, we observed xerophytic grasslands frequently characterised by *Chrysopogon gryllus* in combination with more dominant *Schoenus nigricans* tussocks under summer-dry conditions. We assumed that the wide ecological amplitude of *Schoenus nigricans* related to summer dryness might explain this unexpected plant species composition. Here, we describe these vegetation types on the Kvarner Islands Cres and Krk as a first part of our ongoing work on the ecology of *Schoenus nigricans*.

Investigation area and vegetation cover

The compiled relevés (Fig. 1, Tab. 1) represent vegetation types located on Cres (near Belej; relevé numbers 1–6) and Krk (between Punat and Stara Baska; relevé numbers 7–17). Both Kvarner Islands form part of the borderland of the Cretaceous Karst region. However, only at some study sites (relevé numbers 2–6, 8–10; Tab. 1) do rocks stick out of the ground surface of the more or less deep soils developed on the calcareous substratum. Climatically, the (sub)mediterranean investigation area is characterised by rainfall restricted to winter and spring months (cf. JOVANOVIĆ et al. 1986, TOPIĆ and ŠEGULJA 2005).

In general, the strict Mediterranean vegetation area is divided into three sub-areas (HORVATIĆ 1957) with the northernmost district (the »submediterranean vegetational zone of hop and oriental hornbeam forest« [alliance *Ostryo-Carpinion orientalis* p.p.]; TRINAJSTIĆ 1995) including the southern coastal regions of the Istria Peninsula, most of the southern parts of the Cres Island, and only small areas in the southwest of Krk Island (WRABER 1967, TRINAJSTIĆ 1976, YOSHINO 1976). In the strict Mediterranean vegetation region (in particular the southernmost parts of the Cres Island; cf. HORVATIĆ 1957) the primary climax forests are characterised by a *Quercus ilex* canopy layer. But as a result of the long-term destruction of natural vegetation by man the forests have been changed to degraded vegetation types like maquis, garrigue and grasslands (e.g., BRAUN-BLANQUET et al. 1952, HORVAT et al. 1974, TOPIĆ and NIKOLIĆ 2005). Therefore, the Mediterranean climate climax is only rarely existent today. Nevertheless, the portion of evergreen Mediterranean shrubs and trees might amount to nearly 50% of the overall vegetation cover (cf. WRABER 1967 for Slovenia).

The climax plant community of the Mediterranean zone predominant on Cres and Krk is the *Ostryo carpinifoliae-Quercetum ilicis* (H-ić 58) Trinajstić (65) 74 [syn. *Orno-Quercetum ilicis* H-ić (56) 58] characterised by species like *Quercus ilex, Pistacia terebinthus, Phillyrea ilicifolia, Rosa sempervirens, Lonicera etrusca, Ruscus aculeatus, Asparagus acutifolius, Cotinus coggyria*, and *Viola scotophylla* (see also BIONDI et al. 2003). Our investigation sites are mainly located within this Mediterranean area, but on Krk Island locations are closer to the border of the submediterranean eastern Adriatic district, covered by the climax plant community of the *Carpinetum orientalis* H-ič 39 em. Poldini 88 (POLDINI 1988). Characteristic species for this association and the whole alliance (*Ostryo-Carpinion orientalis* Ht 58), respectively, are in particular *Carpinus orientalis, Paliurus spina-christi, Clematis flammula*, and *Helleborus multifidus* ssp. *istriacus.*

The traditional sheep grazing reduces vegetation cover in height and density. Especially the latter fact fosters the occurrences of heliophytes and pioneer species. The degradation stage characterised by *Chrysopogon gryllus* is that of the dry and stony grassland vegetation of the *Bromo-Chrysopogonetum grylli* Ht 60 on neutral to alkaline soils, and the *Danthonio-Scorzoneretum villosae* Ht et H-ič 58 at more humid sites (POLDINI 1989, KALIGARIČ 1997). Concerning the latter association HORVATIĆ (1957) already mentioned the subassociation *Danthonio-Scorzoneretum villosae* subass. *schoenetosum nigricantis* H-ić 57 characterised by the appearance and dominance of *Schoenus nigricans*.

YOSHINO (1976) pointed out the effect of the bora wind which seems to be responsible for a less dense vegetation cover at exposed sites. He categorised the degree of the vegetation cover into three grades: i) rough, ii) middle, and iii) dense. These vegetation cover degrees of a given climax community qualitatively represent the percentage of the overall plant cover in a certain area. In this sense, a rough degree sensu YOSHINO (1976) appears to

be predominant in the northern and southern regions of Krk, and at higher elevations of Cres, while the main part of the latter island shows a middle degree. Our vegetation relevés represent areas on both islands characterised by a middle degree.

Grazing by goats and sheep, the predominant factor forming vegetation in the study area, has been continued until recent times. The effects of the bora winds might compound results of grazing especially at exposed sites (i.e. fostering sparse vegetation cover). But more obviously, abandonment of pasture use has a strong effect in the opposite direction.

Materials and methods

The phytosociological work was performed in 2004 at two study sites on the islands of Cres and Krk (Fig. 1, Tab.1), according to the BRAUN-BLANQUET approach (BRAUN-BLANQUET 1964). Plant names are mainly based on the Flora Europaea (TUTIN et al. 1964, TUTIN et al. 1968–1980), but with the addition of PIGNATTI (1982) in some cases.

Results

The floristic composition of our study sites is compiled in an association table containing 17 vegetation relevés (Tab. 1). Generally, the habitus of all vegetation types listed is characterised by open skeletal and compacted soils in combination with *Schoenus nigricans* tussocks (Fig. 2). Furthermore, almost all meadows and pastures of the investigated areas frequently contain *Chrysopogon gryllus*, *Bromus condensatus*, and *Bromus erectus* (Poaceae). In the system of the Croatian submediterranean and Mediterranean plant communities (HORVATIĆ 1963) these vegetation types form part of the alliance *Scorzonerion villosae* within the order *Scorzonero-Chrysopogonetalia* within the class *Festuco-Brometea* Br.-Bl. et Tx. 43 (cf. ROYER 1991). Our relevés show a high degree of resemblance to the *Danthonio-Scorzoneretum villosae* and *Danthonio-Scorzoneretum villosae*

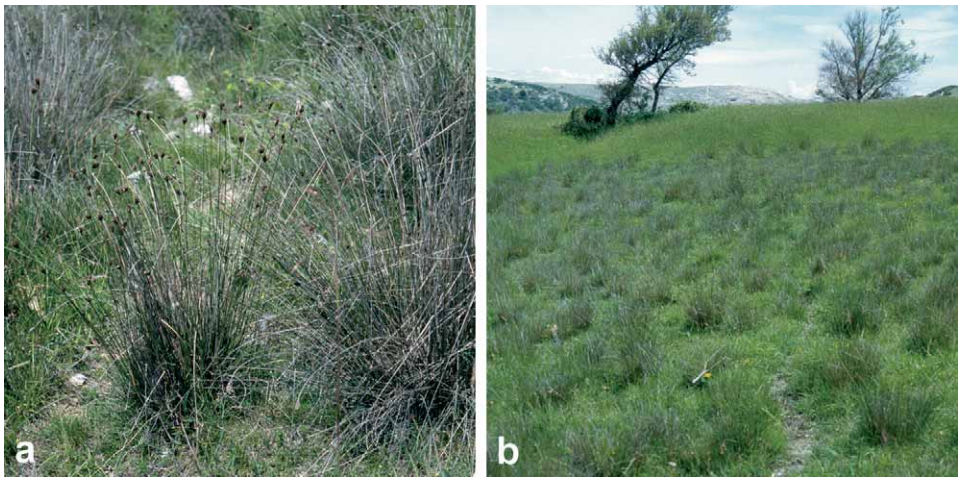

Fig. 2. *Schoenus nigricans* on the Kvarner islands Cres and Krk: a – *Schoenus nigricans* tussocks; b – The *Danthonio-Scorzoneretum villosae* subass. *schoenetosum nigricantis* showing an advanced succession stage (photo credits: K.-G. Bernhardt).

subass. *schoenetosum nigricantis*, respectively, reported by HORVATIĆ (1963) from Pag Island, which is close to our investigation areas on Cres and Krk (cf. KOJIĆ 1957). Overall, the vegetation is characterised by a relatively large number of plant species representing higher syntaxa (VC, OC, KC; see Tab.1).

Tab. 1. List of 17 phytosociological relevés from Cres and Krk representing xerophytic *Schoenus nigricans* grasslands. VC, character of the alliance; OC, character of the order; KC, character of the class. Species with low frequencies (Relevé numbers in parentheses): *Carex distans* (14) 1, *Ranunculus* cf. *muricatus* (13) 1, *Festuca rupicola* (12) +, *Taraxacum* spec. (11) +, *Rosa* spec. juv. (11) r, *Polygala vulgaris* (15) 1, *Plantago argentea* (15) 1, *Euphorbia exigua* (5) +, *Cerastium* cf. *glutinosum* (4) +, cf. *Bellevalia* spec. (3) 1, *Fumana* spec. (3) 1, *Centaurium erythraea* (3) +, *Euphorbia fragifera* (17) +.

Serial number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Cres (C), Krk (K)	C	C	C	C	C	C	K	K	K	K	K	K	K	K	K	K	K
Relevé area size (m²)	30	30	30	30	30	30	20	30	30	30	30	30	30	30	30	30	30
Vegetation cover (%)	80	75	75	70	70	70	85	80	80	80	80	85	85	60	90	90	95
Exposition	W	SW	SE	SE	SE	SE	–	–	–	–	–	–	–	–	–	E	E
Inclination (%)	10	8	10	10	10	10	–	–	–	–	–	–	–	–	–	5	5
Species number	16	14	13	20	16	14	11	17	18	20	16	21	15	12	21	24	25
Schoenus nigricans	4	4	4	4	4	4	5	4	4	4	4	3	4	4	4	4	3
D1: rock vegetation species																	
Stipa eriocaulis ssp. *eriocaulis*	+	+	1	1	+	1	.	.	.	.	.	.	.	.	.	.	.
Anthericum ramosum	1	1	+	+	1	+	.	.	.	.	.	.	.	.	.	.	.
Edraianthus tenuifolium	+	+	.	+	+	+	1	.	.	.	.	.	.	.	.	.	.
Onosma dalmaticum	.	.	+	1	+	1	.	.	.	.	.	.	.	.	.	.	.
Euphorbia nicaeensis	+	+	.	+	.	.	1	.	.	.	.	.	.	.	.	.	.
D2: alternate wet/dry land species																	
Carex flacca ssp. *flacca*	.	.	.	.	.	.	2	+	1	1	+	1	1	1	.	2	1
Genista tinctoria	.	.	.	.	.	.	.	+	+	2	2	2	1	1	2	2	2
Orchis laxiflora	.	.	.	.	.	.	.	.	1	+	+	.	.	+	.	.	.
Taraxacum Sect. *Palustria*	.	.	.	.	.	.	.	2	1	.	.	.	.	.	.	.	.
Juncus bufonius	.	.	.	.	.	.	.	.	.	.	2	+	1	+	.	.	.
D3: advanced succession stage																	
Galium album ssp. *album*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	2
Salvia pratensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2
Clematis flammula juv.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	2
Acer monspessulanum juv.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	2
Colchicum spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	1
Quercus pubescens juv.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2
Juniperus oxycedrus juv.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
VC: *Scorzonerion villosae* H-ić 49																	
Danthonia alpina	.	.	.	.	.	.	.	2	1	1	2	+	1	1	1	.	.
Scorzonera villosa ssp. *villosa*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	1
Prunella laciniata	.	.	.	.	.	.	.	.	.	.	.	+	1	+	.	.	+
Inula salicina	.	.	.	.	.	.	.	.	.	2	+	.	.	.	.	1	1
Dorycnium pentaphyllum	.	.	.	+	+	.	2	.	.	.	+	.	.	.	.	.	.

Tab. 1. – continued

Serial number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Cres (C), Krk (K)	C	C	C	C	C	C	K	K	K	K	K	K	K	K	K	K	K
Relevé area size (m²)	30	30	30	30	30	30	20	30	30	30	30	30	30	30	30	30	30
Vegetation cover (%)	80	75	75	70	70	70	85	80	80	80	80	85	85	60	90	90	95
Exposition	W	SW	SE	SE	SE	SE	–	–	–	–	–	–	–	–	–	E	E
Inclination (%)	10	8	10	10	10	10	–	–	–	–	–	–	–	–	–	5	5
Species number	16	14	13	20	16	14	11	17	18	20	16	21	15	12	21	24	25
Plantago holosteum	.	+	.	2	.	+	+	.	.	.	.	.	.	.	.	.	.
OC, KC Festuco-Brometea Br.-Bl. et Tx. 43																	
Chrysopogon gryllus	2	2	2	2	1	3	1	1	2	2	1	2	2	1	.	+	.
Brachypodium pinnatum ssp. *rupestre*	+	.	.	1	.	.		.	1	1	1	.	+	+	.	.	.
Bromus erectus / condensatus	2	1	2	2	1	.	1	2	3	3	3	3	3	2	2	3	3
Festuca rubra ssp. *juncea*	2	1	1	2	+	1	.	.	.	1	+	1	1	.	.	.	.
Koeleria macrantha	.	1	.	+	+	1	+	.	.	.	.	.	.	.	1	1	+
Lotus corniculatus agg.	.	.	.	.	.	.	.	+	1	+	1	1	1	.	1	1	1
Sanguisorba minor ssp. *polygama*	.	.	.	.	.	.	.	1	2	2	2	1	1	2	.	.	.
Orchis coriophora ssp. *fragans*	+	1	.	1	.	+	+	+	+	+	.	+	+	.	.	.	.
Thymus longicaulis	1	1	2	.	+	.	+	.	.	1	.	.	.	.	.	.	.
Eryngium amethystinum	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	+	+
Brachypodium distachyon	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthyllis vulneraria ssp. *rubriflora*	.	.	.	+	.	2	.	.	.	.	.	.	.	.	.	.	.
Accompanying species																	
Leucanthemum heterophyllum	.	.	.	+	+	.	+	.	.	.	.	+	+	.	1	1	1
Centaurea deusta ssp. *concolor*	.	.	.	.	.	.		+	2	2	.	1	.	.	1	1	2
Orchis morio ssp. *picta*	.	.	.	.	.	.	.	.	.	.	+	+	+	.	+	+	+
Brachypodium sylvaticum	.	.	.	.	.	.	.	.	1	1	+	.	.	.	2	1	2
Ornithogalum refractum	.	.	.	.	.	.	+	1	2	1	.	+	.	.	.	1	.
Polygala comosa	.	.	.	.	.	.	.	+	+	1	.	.	.	.	1	.	1
Carex caryophyllea	.	.	.	.	.	.	.	.	.	.	2	1	.	1	.	.	.
Betonica officinalis	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	2	2
Dactylis glomerata	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	1	2
Ophrys holoserica	.	.	.	+	+	.	.	.	.	.	.	.	.	.	+	.	+
Orchis morio ssp. *morio*	+	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.
Orchis tridentata	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.
Blackstonia perfoliata ssp. *serotina*	.	.	.	+	.	+	.	.	.	.	.	.	.	.	+	.	.
Scorzonera austriaca	+	+	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.
Genista sylvestris ssp. *dalmatica*	+	.	1	.	+	.	.	.	.	.	.	.	.	.	.	+	+
Teucrium montanum	2	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.
Anacamptis pyramidalis	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.
Cynosurus cristatus	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.
Anthoxanthum odoratum	.	.	.	.	.	.	.	+	.	.	.	+	1	.	.	.	.

Schoenus nigricans as stress-tolerant species predominates on the summer-dry soils in all vegetation types compiled (Fig. 2). Nevertheless, we differentiate three variants (D1–D3; see Tab.1) defined as floristic groups following the methodology of BRAUN-BLANQUET (1964):

1. Predominant occurrences of characteristic rocky steppe (grassland) species like *Stipa eriocaulis* ssp. *eriocaulis* and *Onosma dalmaticum*, which we found exclusively on Cres. The soils of these sites have a distinctive xerophytic character (D1).
2. Species dominate that are indicative of soils changing permanently from wet (winter) to dry (summer) conditions. Therefore, we assume a higher degree of humidity compared with the previous variant. Obviously, this mesophilous situation is more characteristic of the sites on Krk (D2; cf. KALIGARIČ 1997).
3. The species composition includes taxa of advanced succession stages (*Quercetalia pubescentis*), which are indicative of the (recent) abandonment of (sheep) grazing (D3).

Discussion

The investigated vegetation communities dominated by tussock-forming *Schoenus nigricans* plants might be the result mainly of two factors:

1. Degradation of vegetation in consequence of sheep grazing.
2. Pre-adaptation (in growth form and physiological properties; e.g. stress-tolerance) to compacted soils under summer-dry conditions.

The first factor can be indirectly deduced by the advanced succession stages observed (D3) leading to *Quercetalia pubescentis* bush stages, especially on Krk Island. Within these stages, *Schoenus nigricans* tussocks start to recede physiognomically due to abandonment of grazing and the increasing dominance of woody plants. In consequence of their transitional status these vegetation types are comparatively species-rich (D3 in Tab. 1). The areas on Cres Island, which seems to be drier, probably need longer time periods to develop into these later stages. Predominantly flat areas in the vicinity of the reported vegetation types show a less dense *Schoenus nigricans* cover and even more plant species of advanced succession stages probably indicating the recent reduction of grazing intensity. But generally, it might be difficult to deduce recent use (i.e. grazing) directly from the current appearance of *Schoenus nigricans* tussocks, as it is known that this species builds up vegetation types composed of 30 year old individuals (SPARLING 1968, ERNST and van der HAM 1988).

As a second factor, the compacted soils, which retain water from the winter rain season to the summer-dry period, are important for species composition as well as dominance and growth form of *Schoenus nigricans* plants. The frequently observed ponds and wet depressions in the pastures of Krk may serve as further indications for the local but common occurrences of compacted soils and the possibility of water storage during summer. The ability of *Schoenus nigricans* to develop a root system up to 1.20 m in depth as reported from dune habitats (ERNST and van der HAM 1988) might be an additional factor for the species' success in the summer-dry study region. One last aspect enhancing the dominance of *Schoenus nigricans* under the described conditions might be the species' higher salt tolerance as indicated by its coastal habitats (e.g., also known from *Juncus acutus*), enabling the species to tolerate dry periods because of its own high osmotic pressure.

As the dominance of *Schoenus nigricans* on compacted soils in the (sub-)mediterranean study area is most striking, and in contrast to the Central European preferences of the

species (cf. ZOBRIST 1935, OBERDORFER 1977, MARTINČIČ 1991, GRABHERR and MUCINA 1993, POTT 1995), further ecological investigations are encouraged. These analyses might cover the quantitative ecological characterisation of different *Schoenus nigricans* habitats (e.g., soil, humidity parameters, microclimate) as well as an ecophysiological and/or molecular characterisation of the species at population level. The latter population genetic studies (including population samples from Central Europe for comparison) might help to answer the question whether genetically differentiated ecotypes exist within the species. And if confirmed, this intraspecific differentiation has to be correlated with vegetation and ecological parameters as well as tested in greenhouse experiments to uncover its evolutionary relevance.

Cultivation experiments carried out by ERNST (1991) representing different European *Schoenus nigricans* localities also point to an ecotypic differentiation within the species. Although only plants from coastal habitats (dunes) were analysed, this author found differences in fruit and seed weight, sprout height, as well as time until flowering (start of the reproductive phase) among Mediterranean and Central European (North Sea) coastal *Schoenus nigricans* individuals. *Schoenus nigricans* plants from the here described vegetation types might represent another discrete ecotype.

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