Ant communities in recently restored dune grassland ecosystems in Belgium (Hymenoptera: Formicidae)

Wouter DEKONINCK¹, Léon BAERT¹, Marc VANKERKVOORDE², Lut VAN NIEUWENHUYSE³ & Frederik HENDRICKX¹

¹ Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1000 Brussels, Belgium (e-mail: wouter.dekoninck@naturalsciences.be)

² Vennestraat 6, B-9051 Sint-Denijs-Westrem, Belgium

³ Monterreystraat 43, B-9000 Gent, Belgium

Abstract

In the period 2000-2001 nature restoration projects drastically reshaped the Nature Reserve in Lombardsijde near the Ijzer Estuary in Flanders, Belgium. Dikes were constructed and new dune grasslands were installed. Seven years after the restoration the ant fauna of these newly created sites was compared with reference sites from foredunes, dune grasslands and grey dunes. Ants were collected with pitfall traps in 10 sample sites during 4 years. Our results showed that after 7 even 10 years of nature restoration, the ant fauna in the newly created sites still differs substantially from those of the reference sites. However, typical dune grassland ant species like *Myrmica specioides, Myrmica sabuleti* and *Lasius psammophilus* were already present at the newly created sites. Our data also suggests that it takes a longer period for characteristic dune grassland ants species to colonize and settle in these new environments than for other invertebrate groups like spiders and carabid beetles that were also collected and studied during the same project and reported before.

Keywords: nature restoration, Formicidae, community analysis, foredunes, grey dunes

Samenvatting

Tijdens de periode 2000-2001 hervormden natuurherinrichtingswerken het natuurreservaat naast het ijzerestuarium te Lombardsijde (Vlaanderen, België) drastisch en dijken en nieuwe duingraslanden werden aangelegd. Zeven jaar na deze restoratie werd de mierenfauna van deze nieuw gecreëerde gebieden vergeleken met referentiesites in helmduinen, duingraslanden en gefixeerde kustduinen met kruidvegetatie. In 10 verschillende sites werden mieren met bodemvallen ingezameld gedurende vier jaar. Onze resultaten tonen aan dat na 7 en 10 jaar natuurherstel, de mierenfauna in deze nieuwe gebieden nog steeds verschilt van deze in de referentiesites. Toch waren typische duingraslandsoorten zoals *Myrmica specioides, Myrmica sabuleti* en *Lasius psammophilus* reeds aanwezig in de nieuwe sites. Onze data suggereren ook dat er een relatief langere periode nodig is alvorens karakteristieke duingrasland mierensoorten zich vestigen in deze nieuwe omgeving in vergelijking met andere invertebraten groepen zoals spinnen en loopkevers die eerder reeds werden besproken.

Résumé

Au cours de la période 2000-2001, des projets de restauration de la nature ont réformé radicalement la réserve naturelle de Lombardsijde située près de l'estuaire de l'Yser dans la Province de Flandre-Occidentale (Belgique). Des digues ont été construites et de nouvelles dunes de différents types telles des dunes grises, des dunes de sable, des dunes mobiles à oyat et des dunes blanches ont été installées. Sept ans après ces aménagements, la faune des fourmis de la réserve a été comparée à celle de sites constitués de dunes similaires mais plus anciennes. Les fourmis ont été collectées à l'aide de pièges à fosse dans 10 sites pendant 4 ans. Nos résultats montrent qu'après 7 ans, voire même 10 ans de

restauration, la faune des fourmis dans ces sites nouvellement créés diffère encore sensiblement de celle des sites de référence. Cependant, des espèces typiques de dunes comme *Myrmica specioides*, *Myrmica sabuleti* et *Lasius psammophilus* sont présentes. Nos données suggèrent en outre que la colonisation et l'installation de fourmis inféodées aux dunes prend plus de temps que celle d'autres espèces telles des scarabées, des carabes ou des araignées, groupes également étudiés dans ce projet.

Introduction

Despite the global decline of natural habitats, substantial efforts are made to preserve, restore or even to re-create threatened ecosystems. In order to evaluate the development of restored habitats or areas, it is important to focus not only on the vegetation and usually studied animal groups like birds, as other less studied taxonomic groups like several invertebrate groups may provide additional information on ecosystem restoration. Invertebrates like carabid beetles (KOTZE et al., 2011) and spiders (PEARCE & VENIER, 2006) offer good possibilities in this context as they are highly speciose and occupy a wide range of different habitats, moreover they are easy to collect in a standardized way. Coastal terrestrial ecosystems like estuaries, dunes and dune grasslands are declining and threatened habitats in Western Europe and in particular in Flanders because of growing tourism and construction of harbours. In 2001, the Flemish Government started a large scaled nature development project along the river Ijzer estuary (Belgium) (HOFFMANN et al., 2005). This project mainly focussed on the expansion of the pre-existing limited surface of old salt marsh, as well as towards increasing contact zones between mud flats, salt marsh and coastal dune habitats (Fig. 1). The first two phases of the restoration project consisted of the demolition of the buildings and roads of the former naval basis and the removal of the jetties and quays of the former military harbour and slipway. The excavated sandy soil from the guays was used to build dune-like hills above the pits left by the removal of the buildings as well as a dune-like dike along the tidal mud flat created after the removal of the harbour and the slipway. Parts of these dikes were planted with marram grass tussocks (Ammophila arenaria). Other lower parts were quickly colonised by the typical vegetation of grey dunes and dune grassland.



Fig. 1. The River Ijzer Estuary before (left, 1999) restoration works and after (right, 2004). Black arrows mark some of the places were restoration works were done.

In order to evaluate the development of the natural ecosystem on these artificial habitats several groups of invertebrates (firstly ground beetles and spiders, later also ants) were studied during a long term continuous sampling (complete year cycles) along several transects from seaside marram dunes to inland dune grassland and moss dunes as well as on the margins of a newly created dune pond. Assemblages, derived from these sampling campaigns in dune grasslands habitats, were compared between old and new sites and revealed strong responses in the spider and ground beetle assemblages during the first years after the nature restoration measures (DESENDER *et al.*, 2006). Several beetles and spiders new to the study area as well as a marked increase within the area of several target species with high conservation interest (Red data book species) were observed (DESENDER, 2005; MAELFAIT *et al.*, 2007). However, results from carabid beetles and spiders also suggest that additional management measures will probably be necessary for a further successful development of the nature restoration area.

Since 2008, we monitored ant assemblages in the newly created dune grasslands ecosystems and on the newly created dikes. Ants were only included in the monitoring scheme later as previous research revealed that ant assemblages respond slowly to newly created habitats in western-European habitats (DEKONINCK *et al.*, 2001a). In newly created forests for instance in Flanders, a time span of 20-25 years appeared insufficient to establish an ant community comparable to the reference old forests (DEKONINCK *et al.*, 2008). Also on some newly created heathlands on former arable fields in Flanders it was obvious that it takes a fairly long time before ants settle (DEKONINCK *et al.*, 2001b).

The aims of this study are: i) to give an overview of ant species collected at Lombardsijde Nature Reserve near the Ijzer Estuary during the period 2008-2011 in old dune grasslands sites and newly created dune habitats after 7-10 years of restoration; ii) to evaluate the difference in species composition of artificially created sand dunes and the typical fauna of undisturbed dune grassland after a period of 7-10 years.

Material and methods

Study area

All 10 sampling sites were situated in the dune area of the River Ijzer in Lombardsijde (Fig. 2). The classification and sample codes of the sampled sites are presented in Table 1 together with their habitat type. We sampled four reference fore-dunes. Two of them are situated on the seaward side (site A and AB). These sites belonged to the association Ammophiletum arenarii with a groundcover of marram grass tussocks of about 50% in the year 2001-2002. The two other reference sites of fore-dunes were situated on the landward site (sites C and CM). On these latter two sites about 5 to 10% is covered with low growing grasses, herbs, and Euphorbia paralias. These four sites were used here as targets to assess the quality of the three newly created dune sands on the new dikes: sites, DY, F and G. Sites F and G are situated 50 m apart on a newly built dike about 500 m inland from the fore-dunes (Fig. 1). Site DY was situated on another dyke more closely to the reference sites but facing the River Ijzer estuarium. All new dikes were built with excavated sand with a content of finer soil particles (clay, organic matter) of about 10 %. At site G and DY about 0.5 m of mineral sand with a 5 to 10% content of shell fragments was added on top and planted with marram grass tussocks. By 2004, G showed a ground cover of about 50% of marram tussocks with in between some 5% grasses and herbs. From only about 10% ground cover during the growing season in 2001, site F (not planted with marram grass tussocks) evolved in 2004 to a cover of about 95% of sod forming grasses, mosses and herbs, kept short by sheep grazing.

As reference site for grey dunes, site E was selected. At present, this grey dune site has a *Cladonio-Koelerietalia* vegetation (PROVOOST *et al.*, 2004), but was composed of a *Polygalo-Koelerion* closed grassland with a well-developed sod layer in 2001-2004. It was short-grazed by sheep. During the 1990's the site had much more open grey dune vegetation dominated by lichens and mosses and is characterized by a poorly developed organic soil layer. The two new grey dune sites KM and MO are situated only 100 m apart. However, vegetation succession differed strongly after 10 years. Site KM constitutes an open grey dune vegetation dominated by lichens and mosses as a *Tortulo-Koelerion*. Site MO became more dominated by mosses and grasses and had a very dense but low vegetation without almost any bare sand present.

Type of dune grassland ecosystem	Details of habitat	History	Code of the site	Orientation
Ancient foredune	seaward side	REF	А	Parallel
	Souward Side	REI	11	with sea
Ancient foredune	segward side	DEE	٨D	Parallel
Allelent loredulle	seaward side	KEF	AD	with sea
A paient foraduna	landword side	DEE	C	Parallel
Allelent loredulle	landward side	KEF	C	with sea
Ancient foredune	landword side	DEE	CM	Parallel
	landward side	KEF	CIVI	with sea
Now foredure	planted with marrow grass	NEW	DV	Along Ijzer
New Ioredune	planted with marrain grass		DI	estuarium
New foredune	plantad with marrow grass	NEW	G	Along Ijzer
	planted with marrain grass	INLEW	U	estuarium
New foredune	not planted with marram grass	NEW	F	Along Ijzer
	not plained with marrain grass	INLEW	Г	estuarium
Ancient grey dune	Cladonio-Koelerietalia	REF	Е	Inland
New grey dune	lichens, Tortulo-Koelerion	NEW	КМ	Inland
New grey dune	dens grassland with mosses	NEW	МО	Inland

Table 1. Description of the 10 sampled sites in the dune grasslands in the nature reserve and restoration area (REF=a site used as a reference site for newly created dune grasslands; NEW= newly created dune ecosystem).



Fig. 2. Location of all 10 sampled sites in the Nature reserve and restoration area near the Ijzer estuarium in Nieuwpoort, Belgium. All sites are presented by a code and listed in Table 1.

Sampling

Ant sampling was performed from 2008 until 2012 by means of pitfall traps (three glass jars per sampling site; with a diameter of 9,5 cm, filled with a formalin solution as fixative and emptied and refilled at fortnightly intervals). A species was present in a site when during several occasion several ant workers were collected. For some species we only were able to collect aleate gynes and or males. When for a certain species these were the only records on that site, we did not consider this species to be a species contributing to the ant species richness and they were catalogued as accidently collected species. To compare ant communities we did not use abundances but only presence and absence of the species at each site. Specimens were deposited in the ant collection at Royal Belgian Institute for Natural Sciences (RBINS, I.G.: 32.167).

Ecological / functional groups

Each ant species recorded was attributed to one of the following ecological groups based on its habitat preference in Flanders (DEKONINCK *et al.*, 2012) : i) habitat specialist for dune habitats = ant species that is common in dune habitats and which can be abundant in this habitat and is very rare outside dunes; ii) Temporary parasites of grasslands = *Chthonolasius* spp. (yellow parasitic ant species) characteristically found in grassland ecosystems where its host is abundant; iii) eurytopic species = ant species without any habitat preference in Flanders.

Results and discussion

During the four years of sampling, 17 ant species were collected. Some species were only present as alates and considered as 'accidentally collected species' at those sites. These species are indicated with an * in Table 2 and as grey bars in figure 3.

Table 2. Overview of the collected ant species per site. Y is a species which has colonized the site as it was discovered several times or continuously during the sampling, * is for a species of which only alates were collected at that site and colonization was not confirmed as no workers were collected (accidentally collected species).

	Ancient foredune			New foredunes			Grey dunes			
	REF	REF	REF	REF	NEW	NEW	NEW	REF	NEW	NEW
SPECIES		AB	С	CM	DY	G	F	Е	KM	MO
Habitat specialist for dunes										
Myrmica specioides Bondroit, 1918		Υ	Υ	Υ			Υ	Y	Y	Υ
Myrmica rugulosa Nylander, 1849		Y	Y	Y						
Myrmica sabuleti Meinert, 1861		Y	Y	Υ		Y	Y	Y	Y	Y
Lasius psammophilus Seifert, 1992			Y					Y	Y	Y
Temporary parasites										
Lasius meridionalis (Bondroit, 1920)							*	Y		
Lasius mixtus (Nylander, 1846)		*								
Lasius sabularum (Bondroit, 1918)							*		*	
Lasius umbratus (Nylander, 1846)		Y						Y		
Eurytopic species										
Lasius niger (Linnaeus, 1758)	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Tetramorium caespitum (Linnaeus, 1758)		Y	Y	Υ	Y	Y	Y	Y	Y	Y
Lasius flavus (Fabricius, 1782)			*				Y			
Myrmica rubra (Linnaeus, 1758)		Y					*			
Myrmica scabrinodis Nylander, 1846	Y	Y		Y						Y
Alates of species not characteristic for dunes										
Anergates atratulus (Schenck, 1852)						*				
Hypoponera punctatissima (Roger, 1859)										
Lasius fuliginosus (Latreille, 1798)				*					*	
Stenamma debile (Foerster, 1850)				*						
Species established		8	6	6	2	3	5	7	5	6
Species not established		1	1	2	0	1	3		2	

Four species are listed on the Provisionary Red List of ants for Flanders (DEKONINCK *et al.*, 2005): *Anergates atratulus* (Critically endangered), *Myrmica specioides* (Vulnerable), *Lasius psammophilus* (Vulnerable) and *Lasius meridionalis* (Vulnerable).

We found no difference in ant species richness (excluding alates) between the different dune grassland ecosystems (i.e. ancient foredunes, newfore dunes and grey dunes). However species richness was significantly higher in ancient compared to new habitats for all types of dune grassland ecosystems (exact Man-Withney U test p=0.0095).

Lasius niger and *Tetramorium caespitum* were present in all old as well as all new sites, suggesting that these two species quickly colonized all newly created habitats. With the exception of one single site in new dune habitat, *Myrmica sabuleti* was also present in new as well as old dune habitats.

Myrmica specioides which is a characteristic ant species for xerophyllic dune grasslands (DEKONINCK & BONTE, 2004; DEKONINCK *et al.*, 2012) was found in all reference sites and colonized already all recently established grey dunes and one of the new foredunes (site F).

Another ant species typical for dune grasslands and other sandy habitats like heathlands is *Lasius psammophilus* (DEKONINCK & BONTE, 2004). This species appeared to be restricted to grey dunes only. It also colonized already all the newly created grey dunes. *Myrmica rugulosa* was only collected in all four foredune reference sites, but did not yet colonize the new foredunes.

Some of the species were only collected by alate sexuals (*Stenamma debile*, *Lasius fuliginosus*, *Hypoponera punctatissima* and *Anergates atratulus*). The first two are so called accidently collected species for the nature reserve as their typically habitat is not in dune grassland ecosystems but in forests and forest edges.

For some species, workers were restricted to few sites only. When workers are lacking we might assume that the species did not yet colonized this site, nevertheless new queens do arrive. It seems that in such cases the site is not yet favorable.



Fig. 3. Number of ant species collected at the different sites. Numbers are presented according to the ecological/functional groups we used (temp. parasites = temporary parasites: species that start a new colony by temporary parasiting another ant species).

Conclusion

An uncomplete colonization of the newly created dune sites was observed even after 10 years of dune development. Eurytopic species like *T. caespitum*, *L. niger* and *M. sabuleti* appear to colonize the newly created dune grassland easily. Other species characteristic for grey dunes like *L. psammophilus* and *M. specioides* were also able to colonize the new grey dunes, but were found on a subset of the sites only. Especially the ant fauna of newly created dikes seems to differ from the reference foredunes. Several species characteristic for dune grassland ecosystems are lacking on the new dikes,

but also other ant species that are less characteristic for dune grassland ecosystems are lacking (like *M. scabrinodis and M. rubra* both species are more characteristic for wet habitats and grassland with high moisture).

The interpretation of the presence of the temporary parasitic ant species of the genus *Chthonolasius* is less straightforward. Only for *L. meridionalis* and *L. umbratus* workers were found, and this confirms their establishment at these sites. The establishment of *L umbratus* and *L. meridionalis* was confirmed in three and one site respectively (see Table 2). Although aleate gynes of *Chthonolasius* species were collected in newly created sites, the presence of workers and, hence, their nests, could not be confirmed. *Lasius meridionalis*, which in most cases parasites the typical dune ant species *L. psammophilus*, can be considered as a target species for dune restoration. However, pitfall traps might not be the best way to detect this species. Therefore we do recommend supplemental hand sampling in the sites and especially screening for subterranean nest of *Chthonolasius* species.

The presence of the workerless obligate parasitic ant species *Anergates atratulus* is worth mentioning. This is a rare ant species in Belgium that parasites *Tetramorium* spp, mainly in heathlands. It was only recently discovered in the coastal dunes of Belgium (LAMBRECHTS & VANKERKHOVEN, 2007) despite its host *T. caespitum*, is a dominant ant species in these ecosystems.

Our results on ant communities are in line with the conclusions from DESENDER *et al.* (2006; 2007) and MAELFAIT *et al.* (2007) on carabid beetles and spiders respectively. These authors concluded that the newly created dune-like habitat can be considered a valuable enlargement of the natural habitats for several typical dune living insect species amongst carabids and, spiders. However for the latter taxonomic group, more specialised dry dune species did not yet establish populations in the new habitats after 5 years. This trend appears similar for some ant species. This is in particular the case for ant species typical for dunes. These species did not colonized new sites after 10 years of restoration and management. However, the presence of some target species after 10 years of dune development indicates a positive, though still uncomplete, restoration of the dune grassland ecosystems at Nieuwpoort.

Acknowledgements

R. Claus and Viki Vandomme are acknowledged for his continuous help in long-term field sampling of the Ijzer estuary area. Our long-term studies are financially supported by the RBINS (Dept. Entomology and Scientific Service Heritage) and between 2001-2004 by the 'MONAY'-project (financed by the Nature Department of AMINAL, Ministry of the Flemish Community). The nature restoration project was realised by the Flemish Community with financial support of the European Community through LIFE. M. Hoffmann and S. Provoost kindly provided maps and aerial photographs of the Ijzer estuary. Konjev Desender† and Jean-Pierre Maelfait† are acknowledged as inspirers of the long-term invertebrate monitoring at the River Ijzer Estuary.

References

- DEKONINCK W. & BONTE P., 2004. Mieren in de Vlaamse kustduinen: een overzicht van de waargenomen soorten en hun belang voor het duinecosysteem. *In*: PROVOOST S & BONTE D (Eds). Levende duinen: een overzicht van de biodiversiteit aan de Vlaamse kust. *Mededelingen van het Instituut voor Natuurbehoud*, 22, Brussel: pp 194–207.
- DEKONINCK W., VERSTEIRT V. & GROOTAERT P., 2001a. Rediscovery of a colony *Polyergus rufescens* (LATREILLE, 1798) in Belgium: Observations at the "Hageven" Nature reserve (Hymenoptera, Formicidae). *Bulletin S.R.B.E./K.B.V.E.*, 137: 98–101.
- DEKONINCK W., VERSTEIRT V. & GROOTAERT P., 2001b. Praktijkgericht onderzoek naar kansen en belangrijke stuurvariabelen voor natuurontwikkeling op gronden met voormalig intensief landbouwgebruik. Partim Invertebraten VLINA99/02, Rapport ENT.2001.05, KBIN, 262 pp + bijlagen.
- DEKONINCK W., MAELFAIT J.-P., VANKERKHOVEN F. & GROOTAERT P., 2005. Remarks on the distribution and use of a provisional red list of the ants of Flanders (Formicidae, Hymenoptera). *In*: PROCTER D. & P.T. HARDING (Eds). JNCC Report No. 367 Proceedings of *IN* Cardiff 2003, Red Lists for Invertebrates: their application at different spatial scales – practical issues, pragmatic approaches, 74–85.

DEKONINCK W., DESENDER K. & GROOTAERT P., 2008. - Establishment of ant communities in forests established on former agricultural fields: colonisation and 25 years of management are not enough (Formicidae: Hymenoptera). *European Journal of Entomology*, 105(4): 681–689.

DEKONINCK W., IGNACE D., VANKERKHOVEN F. & WEGNEZ F., 2012. - Verspreidingsatlas van de mieren van België - Atlas des fourmis de Belgique. *Bulletin S.R.B.E./K.B.V.E.*, 148: 95–186.

- DESENDER K., 2005. Ground beetle diversity monitoring and the evaluation of a recent nature restoration project: A long-term case study in dune and salt marsh habitats along the Belgian coast. *In*: SERRANO J.J. & GOMEZ-ZURITA C.R. (Eds). XII European Carabidologists Meeting, 'Ground beetles as a key group for biodiversity conservation studies in Europe'. Nausicaa Edicion Electronica, Murcia, Spain, pp. 29–38.
- DESENDER K., BAERT L. & MAELFAIT J.-P., 2006. Evaluation of recent nature development measures in the river Ijzer estuary and long-term ground beetle and spider monitoring (Coleoptera, Carabidae; Araneida). *Bulletin Institut royal Sciences naturelles Belgique, Entomologie*, 76: 103–123.
- DESENDER K., MAELFAIT J.-P. & BAERT L., 2007. Ground beetles as 'early warning-indicators' in restored salt marshes and dune slacks. *In*: ISERMANN M & KIEHL K (Eds.) Restoration of coastal Ecosystems Coastline Reports 7, pp 25–29.
- HOFFMANN M., ADAM S., BAERT L., BONTE D., CHAVATTE N., CLAUS R., DE BELDER W., DE FRÉ B., DEGRAER S., DE GROOTE D., DEKONINCK W., DESENDER K., DEVOS K., ENGLEDOW H., GROOTAERT P., HARDIES N., LELIAERT F., MAELFAIT J.-P., MONBALIU J., POLLET M., PROVOOST S., STICHELMANS E., TOORMAN E., VAN NIEUWENHUYSE H., VERCRUYSSE E., VINCX M. & WITTOECK J., 2005. Integrated monitoring of nature restoration along ecotones, the example of the Yser Estuary. *In*: HERRIER J.-L., MEES J., SALMAN A., SEYS J., VAN NIEUWENHUYSE H. & DOBBELAERE I. (Eds). Proceedings 'Dunes and Estuaries 2005' International Conference on Nature Restoration Practices in European Coastal Habitats, Koksijde, Belgium, 19-23 September 2005. VLIZ Special Publication 19, xiv + 685pp. pp. 191–208.
- KOTZE D.J., BRANDMAYR P., CASALE A., DAUFF Y-RICHARD E., DEKONINCK W., KOIVULA M., LÖVEI G.L., MOSSAKOWSKI D., NOORDIJK J., PAARMANN W., PIZZOLOTTO R., SASKA P., SCHWERK A., SERRANO J., SZYSZKO J., TABOADA A., TURIN H., VENN S., VERMEULEN R., ZETTO T., 2011. - Forty years of carabid beetle research in Europe – from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. *In*: KOTZE D.J., ASSMANN T., NOORDIJK J., TURIN H., VERMEULEN R. (Eds.) Carabid Beetles as Bioindicators - biogeographical, ecological and environmental studies. *ZooKeys*, 100: 55–148.
- LAMBRECHTS J. & VANKERKHOVEN F., 2007. Unieke mierenfauna in de fossiele duinen van Adinkerke. *Natuur.focus*, 6 (4): 130–131.
- MAELFAIT J.-P., DESENDER K. & BAERT L., 2007. Colonisation and source-sink dynamics in spiders and ground beetles after dry dune habitat restoration along the Belgian coast. *In*: M. ISERMANN & K. KIEHL (Eds): Restoration of Coastal Ecosystems. *Coastline Reports*, 7: 4152.
- PEARCE J.L. &VENIER L.A., 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. *Ecological Indicators*, 6(4): 780–793.
- PROVOOST S., AMPE C., BONTE D., COSYNS E. & HOFFMANN M., 2004. Ecology, management and monitoring of grey dunes in Flanders. *Journal of Coastal Conservation*, 10: 33–42.