The influence of habitat quality on populations: a plea for an amended approach in the conservation of *Agonum ericeti*

Claudia Drees, Andrea Matern, Rikjan Vermeulen, Thorsten Assmann

Drees C., Matern A., Vermeulen R., Assmann Th. 2007. The influence of habitat quality on populations: a plea for an amended approach in the conservation of *Agonum ericeti*. *Baltic J. Coleopterol.*, 7 (1): 1 - 8.

We investigate the catching rate of the stenotopic peat bog ground beetle *Agonum ericeti* by reanalysing seven earlier studies from peat bogs in north-west Germany in order to investigate the relationship of the abundance of the species and parameters of habitat quality. The multiple regression analysis revealed that the cover of peat moss species of hummocks and the cover of other moss species was positively related with the trapping numbers of *A. ericeti* whilst an increasing cover of grass led to a decrease in beetle numbers. The relationships found show the preference of *A. ericeti* for natural or near-natural peat bogs, as an increasing amount of grass in peat bogs is seen to be linked with a deterioration of these habitat types. Our results underline the importance not only of the size and isolation of habitats harbouring endangered species but also of improving the habitat quality which turns out to be a crucial factor for the long-term-persistence of populations. The potential of *A. ericeti* as a target species for monitoring in peat bogs is discussed.

Key words: Agonum ericeti, Carabidae, habitat quality, populations, conservation.

Claudia Drees, Andrea Matern, Thorsten Assmann. Institute of Ecology and Environmental Chemistry, University of Lueneburg, D-21314 Lueneburg, Germany

Rikjan Vermeulen. Willem Beijerinck Biologisch Station, Kanaaldijk 36, 9409 TV Loon, The Netherlands

E-mail of corresponding author: cdrees@uni-lueneburg.de

Introduction

Peat bogs or raised bogs, which covered large parts of the north-western Central European lowlands, have been subject to massive anthropogenic change until only few decades ago. The formerly extensive bogs were cultivated by peat cutting, drainage, ploughing and fertilization with the aim of agricultural and silvicultural use (e.g. Dierssen & Dierssen 2001; Succow & Joosten 2001). Only few remnants of near-natural peat bogs remained in this geographical region. In Lower Saxony, the most bog-rich state in Germany with formerly 6,500 km² of mainly peat bogs, only 260 km² of peat bogs with a reasonable quality (undisturbed peat profiles, moderately drained, few shrubs etc.) still exist (Niedersächsisches Umweltministerium 1997). A

similar situation can be found in Denmark, Belgium or the Netherlands (Gore 1983). Furthermore, the bog remnants are strongly fragmented and isolated. The severe situation of natural or near-natural bogs nowadays is reflected by their consideration as a habitat type which is of "community interest and whose conservation requires the designation of special areas of conservation" (priority habitat type, listed in Annex I of the European Habitats Directive, The Council of the European Communities 2004).

Ombrotrophy resulting in very poor nutrient supply and water saturated conditions together with low temperatures inhibits mineralisation and leads to the formation of peat are the most striking features of peat bogs (Ellenberg 1996). The vegetation of living peat bogs is characterised by Sphagnum-species covering large parts of the bog and by a small-scaled mosaic of wet, sometimes inundated hollows and drier protruding hummocks covered not only by peat moss but also by other moss species, ericoid plants or lichens (e.g. Dierssen & Dierssen 2001; Ellenberg 1996; Göttlich 1990). Abiotic factors that influence the life of animals close to the ground in a peat bog are, amongst others, a pronounced amplitude of daily temperatures because of direct insolations and very low pH values as a result of the cation exchange capacity of the peat moss. Owing to these conditions peat bogs are inhabited by a specialised fauna, called tyrphobionts (review by Spitzer & Danks 2006).

Agonum ericeti is one of these tyrphobiontic species (Lindroth 1945), seen as characteristic species for peat bogs (Krogerus 1960) which shows several adaptations to the special microclimatic conditions of a peat bog such as preference for low pH-values (Krogerus 1960; Mossakowski 1970a, b; Paje & Mossakowski 1984). Agonum ericeti is among only a few species of ground beetles that are able to permanently inhabit treeless centres of bogs (Bezdek et al. 2006). A. ericeti is flightless (Lindroth 1945) and because of its strong stenotopy strictly bound (and only found) in bogs, wet heathlands or bog remnants that are situated, island-like, in the hostile matrix of woodland, agricultural fields or other habitat types.

De Vries & Den Boer (1990) used this situation to investigate the relationship between habitat size and long-term-survival of 20 A. ericetipopulations in the Dutch province of Drenthe, formerly also a very bog-rich area that shares the same history of landscape changes as the adjacent Lower Saxony in Germany (De Vries 1996; De Vries & Den Boer 1990). Their results reveal A. ericeti to be present mostly in bog remnants larger than 50 to 70 ha indicating that long-term survival needs a certain habitat size. Another study could show a positive relationship between stenotopic heathland species and habitat size indicating that the extinction probability in small habitat islands is enhanced (De Vries et al. 1996). The relationship was most pronounced for species with a low ability of dispersal, i.e. flightless species.

One key factor for the enhanced extinction probability of a population is their small population size (Purvis et al. 2000; Shaffer 1981) which may drive a population into the downward spiral towards extinction (extinction vortex, Allendorf & Luikard 2007; Gilpin & Soulé 1986). Another factor, which has already been discussed for A. ericeti by De Vries & Den Boer (1990) but not yet investigated, however, might be the quality of the habitat. In suboptimal habitats should low densities more likely be found than in optimal habitats. In this paper we investigate this hypothesis by reanalysing a couple of studies on A. ericeti from north-western German peat bogs. If a relationship between habitat quality and population size can be found it is not only habitat size that has to be preserved but it is also the habitat quality of the site that becomes important to nature conservation issues.

MATERIAL AND METHODS

Data from Assmann (1981; 1982; 1983) and Mossakowski (1977) as well as unpublished data from Assmann and from Falke et al. from seven different peat bog areas in northwest Germany were taken for our analysis (Table 1). In order to compare the trapping numbers of *Agonum ericeti* from different studies, abundance values were calculated as year catch per trap. Trapping periods covered the months from March or April to September or October in all cases, thus the whole period of locomotory activity of the species (according to Lindroth 1945) was studied.

Moreover, for our analyses we took data from relevées from the surrounding of the traps which are included in the analysed studies. We considered the following parameters: (1) cover of peat moss species of hummocks (mainly *Sphagnum magellanicum* and *S. rubellum*; *Sphagnum magellanicum* community, Sphagnetum magellanici), (2) cover of other *Sphagnum* species, (3) cover of moss species other than *Sphagnum*, (4) cover of grass, (5) cover of cyperacean grass, (6) cover of *Erica tetralix*, (7) cover of *Calluna vulgaris*, (8) cover of bare soil and (9) cover of trees and shrubs (all estimates in %) (cf. Table A1, Appendix). Data on vegetation cover were arcsin-transformed.

Variables were tested for correlation (Spearman Rank correlation) using Statistica (ver. 7.1). From pairs of significantly correlated predictor variables only one variable was taken for subsequent multiple regression analysis (with the animal number of A. ericeti as response variable), whilst the other was omitted from the respective analysis but taken for calculating a different multiple regression without considering the first variable in this analysis. Multiple linear regression analyses were calculated using R 2.3.0 (R Development Core Team 2006). First models considered all predictor variables, the least significant predictor variable was omitted and a new model was calculated and compared to the first model. This (stepwise backward) procedure was repeated until only predictor variables with significant influence on the response variable remained (cf. Sokal & Rohlf 1995).

Additionally, we calculated our regression models (1 and 2, cf. Table 2) with the 1981-data only (n=11, cf. Table 1) in order to assess a possible influence of different weather conditions in the different study years.

RESULTS

The data taken for this analysis are shown in Table A1 (Appendix). Correlation analyses revealed a significant positive relationship of the

 No. of site.
 Sample site
 Geographical position
 Year of Sampling
 No. of traps
 Plot
 Reference

 1-7
 Hahnenmoor
 N 52.65300° E 007.65870°
 1981
 3-8
 1, 3-7, 9
 Assmann 1982

 8-10
 Lengener Meer
 N 53.37320°
 1981
 5
 1-3
 Assmann 1983

Table 1: Set of studies taken for the meta-analysis. Sample site, geographical position (World Geodetic System, 1984 (WGS 84)) year of sampling, number of traps, name/number of plots chosen for

site	e. Sumple site	position	Sampling	110. 01 11405	1100	Reference
1-7	7 Hahnenmoor	N 52.65300° E 007.65870°	1981	3-8	1, 3-7, 9	Assmann 1982
8-1	0 Lengener Meer	N 53.37320° E 007.87030°	1981	5	1-3	Assmann 1983
11	Venner Moor	N 52.43260° E 008.18310°	1981	3	1	Assmann unpubl.
12-1	14 Esterweger Dose	N 53.02500° E 007.62890°	1969-1970	4	I-III	Mossakowski 1977
15	NSG Im Teichbruch	N 52.41005° E 007.87671°	1984	4	4	Assmann unpubl.
16-1	19 Oppenweher Moor	N 52.51090° E 008.50430°	1980	4-8	1, 3-5	Assmann 1981
20-2	21 Tinner Dose	N 52.78400° E 007.37300°	2000-2001	5	H, I	Falke et al. unpubl.

3

Table 2: Regression models describing the catching rates of *Agonum ericeti* by up to four significant predictor variables. Predictor variables of the first model are given by their variable number (cf. text). For every model adjusted r^2 and p are given, for the predictor variables the regression coefficient and p. For both models n=21. Asterisks indicate the level of significance: ***: p<0.001; **: p<0.01; *: p<0.05; n.s.: not significant.

			Predictor variables in final model					
Predictor variables in first model	Model	Adjusted r ²	р	(1) <i>Sphagnum</i> species of hummocks	(3) other mosses	(4) grass	(8) bare soil	Inter- cept
1 2 3 4 5 6 9	- 1	0 7602	4.17 * 10 ⁻⁶	+0.160	+2.225	-1.692	ns	0.62
1345679	-	0.7002		***	**	*	11.0.	0.02
1234589	2	0 8080	$222 * 10^{-6}$	+1.303	+1.995	-1,628	-1,301	26.70
1345689	- 2	0.0089	2.32 10	***	**	**	*	30.70

response variable (number of *A. ericeti* in one trap opened for one activity season) to the cover of *Sphagnum* species of hummocks (variable no. 1) and a significant negative correlation to the cover of other *Sphagnum* species (2). Other predictor variables were – in the univariate analysis – not correlated significantly with the number of *A. ericeti*.

Correlation analyses of the predictor variables showed that the cover of *Sphagnum* species other than hummock *Sphagnum* species (2) and the cover of *Calluna vulgaris* (7) were correlated and that the amount of *Erica tetralix* (6) was significantly related to the cover of bare soil (8). From these pairs of variables only one predictor each was used in the same multiple regression analysis (cf. Table 2).

Multiple regression analyses showed two final regression models that explain between 76 and 80% of the variance of the number of *A. ericeti* by considering three and four predictor variables, respectively (Table 2). Both models show coinciding results: Whilst the cover of hummock *Sphagnum* species (1) and the cover of other moss species (3) had a positive influence on the catching rate of *A. ericeti*, an increasing cover of grass (4) led to a decrease of *A. ericeti* numbers, for both models.

Our comparative analysis with 11 sites only which had been investigated in 1981 (cf. Table 1) revealed both models, model 1 and model 2, still significantly describing the trapping numbers of *A. ericeti* (Model 1: adjusted $r^2 = 0.9603$, p< 0.001; Model 2: adjusted $r^2 = 0.9698$, p < 0.001).

DISCUSSION

The results of this meta-analysis show that trapping numbers of *Agonum ericeti* depend on certain vegetational factors, such as the cover of *Sphagnum* species of hummocks and the cover of other moss species. Although we used the results of pitfall traps and therefore only obtained information about the activity density instead of the real density (e.g. Thiele 1977), we did obtain certain information about the relative density of *A. ericeti* in the investigated sites, which was sufficient for our analysis. Moreover, the mean density of ground beetles was shown to be linearly related to the numbers of individuals captured in pitfall traps (Baars 1979).

The negative population response for *A. ericeti* on short wet winters recently described by Prins et al. (2007) did not influence our analysis significantly as revealed by our regression models calculated with data from 1981 only. Since the sample sites were geographically close it is unlikely that climatic conditions differ highly between the sites

The considered sites were situated within the range of raised bogs in the oceanic influenced climate (Gore 1983; Göttlich 1990) which, unless

influenced by humans, typically showed peat moss layers dominated by Sphagnum magellanicum, S. rubellum and S. papillosum as the predominant species (Dierssen & Dierssen 2001; Ellenberg 1996). This vegetation type characterises oligotrophic, natural or near-natural, living peat bogs with pH-values below 4.8 (Succow & Joosten 2001). Sphagnum magellanicum dominated bogs are listed as "active raised bogs" in the European Natura 2000 list of protected habitat types (code: 7110, The Council of the European Communities 2004). In the whole area they are endangered (Succow & Joosten 2001). The relationship between the trapping numbers of A. ericeti and the cover of certain Sphagnum species confirms the findings by Krogerus (1960) and Mossakowski (1970a; 1970b) that this species is a very typical species for undisturbed or only marginally disturbed raised bogs. Our analysis confirms the earlier findings statistically for the first time.

Our analysis further revealed that the numbers of *A. ericeti* specimens decrease with the cover of grass in the surrounding of the traps. Grassy vegetation (typically *Molinia caerulea*) indicates raised bogs that are degraded to a certain degree by drainage or peat cutting (code: 7120, The Council of the European Communities 2004). The growth of *Molinia* is promoted by enhanced Navailability because of increasing mineralisation after drainage (Limpens et al. 2003) and, to a higher amount, because of rising atmospherical nitrogen input (Tomassen et al. 2003; Tomassen et al. 2004).

A degradation of the habitat led to obviously lower activity density and therefore to a decreased number of individuals per area unit. A decreasing density may result in a decreasing growth rate of the population ('Allee effect'; Stephens et al. 1999) if, at low population densities, mate encounters are rare. Additionally, with low population density the impact of stochasticity (e.g. a by chance unbalanced sex ratio or bad weather conditions not allowing successful reproduction in one year) becomes more important (cf. Pullin 2002). Our results show that the impact of habitat quality should not be neglected when the vulnerability of a population has to be estimated. This result fits well to the assumption of De Vries & Den Boer (1990) that the survival probability of A. ericeti seems to be enhanced in high-quality habitats. Främbs mentions the significance of habitat structure for this species, which might also comprise aspects of habitat quality (Främbs 1988, 1994). Thomas et al. (2001) first found that both habitat quality and isolation of habitat patches influence the persistence of three butterfly species, Krauss et al. (2005) give another example. The first finding for ground beetles being influenced also by habitat quality was published recently by Small et al. (2006). A. ericeti is another ground beetle species whose long-termsurvival is shown to be influenced by both isolation (De Vries & Den Boer 1990) and habitat quality.

This characteristic makes *A. ericeti* a potential target species for monitoring in peat bogs, because of its strong habitat preference for natural or near-natural conditions in contrast to most other species of this habitat type (Spitzer & Danks 2006). Moreover, the persistence of *A. ericeti* in peat bogs indicates not only a high level of habitat quality at present but also in recent years. This capability of the species under study has not yet been used for monitoring measures so far, but becomes especially important in the framework of monitoring in peat bogs which has to be conducted in the habitat types of the Natura 2000 network (The Council of the European Communities 2004) every six years.

ACKNOWLEDGEMENTS

The authors would like to thank Dr. Jens Günther, Dr. Bodo Falke, Benjamin Hölscher, Markus Persigehl, Boris Rosenkranz, and Ursel Wageringel for unpublished data of the Tinner Dose area.

APPENDIX

No.	Cover in % Nu									Number
of	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	of
site	Sphagnum	Other	Other	Grass	Cyperacean	Erica	Calluna	bare soil	Trees,	Agonum
	species of	Sphagnum	moss		grass	tetralix	vulgaris		shrubs	ericeti
	hummocks	species	species							
1	0	0	0	5	5	20	40	30	0	6,3
2	0	0	0	0	40	40	20	20	0	6,3
3	5	0	0	0	15	25	10	40	0	3,7
4	5	10	0	0	10	65	5	25	0	3,4
5	15	0	5	5	25	40	20	15	5	23,1
6	45	15	5	5	20	30	10	40	0	25,9
7	0	95	0	0	15	0	0	5	0	3,2
8	20	5	0	5	15	35	10	5	20	4
9	10	60	0	0	5	25	5	5	5	2,8
10	0	90	0	0	5	0	0	10	5	1,2
11	0	55	0	0	45	30	0	10	5	3
12	85	5	5	0	20	5	0	0	0	166,3
13	35	0	50	0	5	0	80	0	0	187,8
14	100	0	0	0	15	0	10	0	0	187,5
15	5	15	0	15	20	55	10	20	5	6
16	0	90	0	5	15	0	0	0	0	0,8
17	0	70	5	25	30	10	15	0	5	0,6
18	0	0	10	10	5	70	5	5	10	4
19	0	0	20	5	5	5	60	15	5	1,9
20	75	0	0	10	5	25	15	2,5	0	10,6
21	0	15	0	15	10	87	0	5	0	0,7

Table A1: Compilation of data on vegetation cover in the plots and the number of *Agonum ericeti* individuals captured (given as catching rate per trap and activity period.

REFERENCES

- Allendorf, F. W., G. Luikard 2007. Conservation and the genetics of populations. Blackwell, Malden, Massachusetts.
- Assmann, T. 1981. Ein Beitrag zur Kenntnis der Carabidenfauna des Oppenweher Moores. Osnabrücker naturwissenschaftliche Mitteilungen **8**:161:171.
- Assmann, T. 1982. Faunistisch-ökologische Untersuchungen an der Carabidenfauna naturnaher Biotope im Hahnenmoor (Coleoptera, Carabidae). Osnabrücker naturwissenschaftliche Mitteilungen 9:105-134.
- Assmann, T. 1983. Über die Bodenkäferfauna des Naturschutzgebietes "Lengener Meer" im Kreis Leer (Ostfriesland) (Coleoptera: Carabidae et Silphidae). Drosera **83**:5-12.
- Baars, M. A. 1979. Catches in pitfall traps in relation to mean densities of Carabid Beetles. Oecologia **41**:25-46.
- Bezdek, A., J. Jaroš, K. Spitzer. 2006. Spatial distribution of ground beetles (Coleoptera: Carabidae) and moths (Lepidoptera) in the Mrtvż luh bog, Šumava Mts (Central Europe): a test of habitat island community. Biodiversity and Conservation 15:395-409.
- De Vries, H. 1996. Viability of ground beetle populations in fragmented heathlands. Landbouwuniversiteit, Wageningen.

The influence of habitat quality on populations: a plea for an amended approach in the conservation...

- De Vries, H. H., P. J. Den Boer. 1990. Survival of populations of *Agonum ericeti* Panz. (Col., Carabidae) in relation to fragmentation of habitats. Netherlands Journal of Zoology **40**:484-498.
- De Vries, H. H., P. J. Den Boer, T. S. Van Dijk. 1996. Ground beetle species in heathland fragments in relation to survival, dispersal, and habitat preference. Oecologia **107**:332-342.
- Dierssen, K., B. Dierssen 2001. Moore. Ulmer, Stuttgart.
- Ellenberg, H. 1996. Vegetation Mitteleuropas mit den Alpen. Ulmer, Stuttgart.
- Främbs, H. 1988. Habitatpräferenz von Carabiden (Coleoptera) auf Palsmooren in Torne-Lappmark, Schweden. Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie **6**:379-390.
- Främbs, H. 1994. The importance of habitat structure and food supply for Carabid beetles (Coleoptera, Carabidae) in peat bogs. Memoirs of the Entomological Society of Canada **169**:145-159.
- Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19-34. In M. E. Soulé, (ed.) Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts.
- Gore, A. J. P. 1983. Introduction. Pages 1-34. In A. J. P. Gore, (ed.). Mires: Swamp, Bog, Fen and Moor General Studies. Elsevier, Amsterdam.
- Göttlich, K., (ed.) 1990. Moor- und Torfkunde. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Krauss, J., I. Steffan-Dewenter, C. B. Muller, T. Tscharntke. 2005. Relative importance of resource quantity, isolation and habitat quality for landscape distribution of a monophagous butterfly. Ecography 28:465-474.
- Krogerus, H. 1960. Ökologische Studien über nordische Moorarthropoden I. Commentationes biologicae **21**:1-238.

- Limpens, J., F. Berendse, H. Klees. 2003. N deposition affects N availability in interstitial water, growth of *Sphagnum* and invasion of vascular plants in bog vegetation. New Phytologist **157**:339-347.
- Lindroth, C. H. 1945. Die fennoskandischen Carabidae: I: Spezieller Teil. Goteborgs Kungliga Vetenskaps och Vitter Hets-Samhalles Handlingar Sjatte Foljden. Series B 4:1-709.
- Mossakowski, D. 1970a. Das Hochmoor-Ökoareal von Agonum ericeti (Panz.) (Coleoptera, Carabidae) un die Frage der Hochmoorbindung. Faunistisch-Ökologische Mitteilungen **3**:378-392.
- Mossakowski, D. 1970b. Ökologische Untersuchungen an epigäischen Coleopteren atlantischer Moor- und Heidestandorte. Zeitschrift für wissenschaftliche Zoologie **181**:233-316.
- Mossakowski, D. 1977. Die Käferfauna wachsender Hochmoorflächen in der Esterweger Dose. Drosera **77**:63-72.
- Niedersächsisches Umweltministerium, (ed.) 1997. Umweltmonitoring von Zustand und Nutzung der Hochmoore - Auswertung von Satellitendaten für das Niedersächsische Moorschutzprogramm, Hannover.
- Paje, F., D. Mossakowski. 1984. pH-preferences and habitat selection in carabid beetles. Oecologia 64:41-46.
- Prins, D., A. van Vliet, R. Vermeulen 2007. Fenologie van Loopkevers & Klimaatverandering. Een onderzoek naar de effecten van klimaatverandering op basis van de langstlopende continue ecologische meetreeks ter wereld, Loon, Netherlands.
- Pullin, A. S. 2002. Conservation Biology. Cambridge University Press, Cambridge.
- Purvis, A., L. G. John, C. Guy, M. M. Georgina. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society B: Biological Sciences 267:1947-1952.

- R Development Core Team. 2006. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. Bioscience 31:131-134.
- Small, E., J. P. Sadler, M. G. Telfer. 2006. Do landscape factors affect brownfield carabid assemblages? Science of the Total Environment 360:205-222.
- Sokal, R. R., F. J. Rohlf 1995. Biometry: the principles and practice of statistics in biological research. Freeman, New York.
- Spitzer, K., H. V. Danks. 2006. Insect biodiversity of boreal peat bogs. Annual Review of Entomology 51:137-161.
- Stephens, P. A., W. J. Sutherland, R. P. Freckleton. 1999. What is the Allee effect? Oikos **87**:185-190.
- Succow, M., H. Joosten, (eds). 2001. Landschaftsökologische Moorkunde. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- The Council of the European Communities. 2004. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Page 57. Office for Official Publications of the European Communities.
- Thiele, H. U. 1977. Carabid Beetles in Their Environments. Springer, Berlin.
- Thomas, J. A., N. A. D. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis, B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proceedings of the Royal Society London **B 268**:1791-1796.
- Tomassen, H. B. M., A. J. P. Smolders, L. P. M. Lamers, J. G. M. Roelofs. 2003. Stimulated growth of *Betula pubescens* and *Molinia caerulea* on ombrotrophic bogs: role of

high levels of atmospheric nitrogen deposition. Journal of Ecology **91**:357-370.

Tomassen, H. B. M., A. J. P. Smolders, J. Limpens, L. P. M. Lamers, J. G. M. Roelofs. 2004. Expansion of invasive species on ombrotrophic bogs: desiccation or high N deposition? Journal of Applied Ecology 41:139-150.

> Received: 05.04.2007. Accepted: 31.05.2007.