

Apomicts in the vegetation of Central Europe

Apomikten in der Vegetation Mitteleuropas

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Abstract

Summed frequency data of apomictic taxa derived from vegetation relevées from Central Europe were correlated with ecological traits – water content of soil, calcium and magnesium content of soil or water, nutrient content of soil or water, environmental dynamics, hemeroby, frequency of stress-tolerant species, salt tolerance, altitude, height, and frequency of annual taxa – of alliances of the Central European vegetation. The partly problematic identification of taxa where apomixis is important for seed production was based on a literature review. In Central Europe, high altitudes favour apomictic taxa. Otherwise, no correlations between ecological factors attributed to the alliances of the European phytosociological system and frequencies of apomictic taxa in the alliances of the European phytosociological system were found. Analyses could not confirm theories on ecological preferences of apomictic taxa; e.g., that competition penalizes apomicts, apomicts have better colonizing abilities than sexual plants, or apomicts have larger ranges than their sexual relatives could not be confirmed.

Keywords: apomixis, apomict traits, apomict distribution, syntaxa, ecological traits, environmental conditions

Erweiterte deutsche Zusammenfassung am Ende des Textes

1. Introduction

Clonal reproduction through seeds, apomixis, occurs in at least 35 plant families, predominantly in Asteraceae, Poaceae, and Rosaceae (RICHARDS 1997). Generally, it is a rare phenomenon occurring in less than 1% of plant species (MOGIE 1992), which arose several times independently in angiosperms (VAN DIJK & VIJVERBERG 2005). However, apomictic taxa are common in Central Europe. They are an important part of the Central European flora and dominant in some vegetation types, e.g. *Poa pratensis* s.l. ranks as 2nd in the phytosociological database of the Czech Republic (CHYTRÝ & RAFAJOVÁ 2003), *Taraxacum* sect. *Ruderalia* as 4th, *Poa nemoralis* as 23rd, and *Hypericum perforatum* as 34th.

Reviews of apomixis in higher plants include WINKLER (1908), STEBBINS (1941), GUSTAFSSON (1946, 1947a, 1947b), NYGREN (1954, 1967), RUTISHAUSER (1967), CHOCHLOV (1967), CHOCHLOV et al. (1978), NOGLER (1984), ASKER & JERLING (1992), MOGIE (1992), KOLTUNOW (1993), and KOLTUNOW & GROSSNIKLAUS (2003). A meta-review of apomixis in

Asteraceae was published by NOYES (2007). Three types of apomixis occur: (1) In diplospory, the megaspore mother cell does not undergo meiosis, which is either completely inhibited (mitotic diplospory, *Antennaria* type) or inhibited at an early stage (meiotic diplospory, *Taraxacum* type) and develops directly into an embryo sac, whose egg cell develops into an embryo. Diplospory is mostly obligatory. In Central Europe it is confined to Asteraceae and Poaceae and frequently paired with autonomous apomixis. (2) In apospory, the unreduced embryo sac, whose egg cell develops into an embryo, has its origin in a somatic cell either from the nucellus or the integument. At an early stage of development ovules may contain competing reduced and aposporous embryo sacs. The former normally do not develop. Apospory is closely associated with pseudogamy, although exceptions exist, e.g. *Hieracium* subgenus *Pilosella* combines apospory with autonomous endosperm formation. Apomixis is nearly always facultative in aposporous apomicts. This combines benefits from both reproductive pathways. Apospory and diplospory are collectively known as generative apomixis. (3) In nucellar or adventitious embryony, the embryo develops directly, without formation of an embryo sac, from a cell of the nucellus or the integument. Endosperm formation may or may not depend on the fertilization of the polar nuclei, termed pseudogamous or autonomous endosperm formation, respectively. Pseudogamous endosperm formation after self-pollination was observed in the *Ranunculus auricomus* complex (HÖRANDL 2006, 2008) and in many Rosaceae (DICKINSON et al. 2007). This information is missing for pseudogamous Poaceae and *Hypericum*. NOIROT et al. (1997) argued that pseudogamous apomixis should be always connected with the ability for self-fertilization. Triploid *Rubus* and pentaploid or heptaploid *Potentilla* taxa might be dependent on pollination by other sources, a problem which deserves further study. Pseudogamy is a confounding fact whose evolutionary significance is not understood.

The potential advantages and disadvantages of apomixis compared to sexual reproduction in plants have been reviewed, among others, by ASKER & JERLING (1992) and RICHARDS (1997). Advantages of apomixis include: (1) persistence of successful gene combinations, (2) rapid dispersal of successful genotypes, (3) continuous availability of seeds for propagation, (4) identical fitness in parent and offspring, (5) no production of unfit zygotes, (6) escape from sterility when non-functional gametes are produced, (7) no need for cross-pollination, (8) no production of pollen in autonomous apomicts, (9) production of new genotypes by residual sexuality in facultative apomicts. The disadvantages of apomixis include: (1) no shedding of deleterious or disadvantageous mutants during meiosis, (2) no repairing of gene defects during meiosis, (3) low degree of genetic variability and hence a reduced evolutionary potential.

ASKER (1979), ASKER & JERLING (1992), MARSHALL & BROWN (1981), RICHARDS (1997), and HÖRANDL (2006) reviewed theories concerning the ecology of apomicts. Apomixis occurs under variable ecological conditions. Several theories developed aiming for an explanation why apomixis has become a successful breeding system in the Central European flora: (1) Apomicts are favoured by disturbed, unproductive habitats; (2) apomicts have a higher colonizing ability than sexual plants; (3) apomicts range into higher elevations than sexual plants; (4) apomicts settle in hybrid habitats in relation to sexual progenitors and (5) tend to have larger ranges than sexual relatives.

Central Europe has a worldwide outstanding coverage of its vegetation with vegetation relevées and taxa differentiation in these relevées generally conforms to high standards. The analysis of vegetation relevées gives excellent information about the ecological requirements of the covered taxa. In this work, the framework of Central Europe's vegetation relevées is

used to reveal ecological preferences of apomictic taxa and to test theories concerning their ecological preferences. But expectations must be cautioned. Apomixis is not randomly distributed among plants. Results might partly reflect traits of families rich in apomicts like Rosaceae, Asteraceae or Poaceae, or results might depend on a trait that is merely connected with apomixis.

2. Material and methods

The geographical focus is Central Europe: Austria, Belgium, Czech Republic, Denmark, France (Alsace), Germany, Holland, Luxembourg, Poland, and Switzerland. In a literature review 54 taxa and taxa groups (Appendix S1) were identified for this geographical background where seeds are to a large part produced by one of the three apomictic pathways. *Rosaceae* have a multicellular archespore. This causes difficulties in the recognition of the origin of the initial cell of the apomeiotic embryo sac and the distinction between apospory and diplospory is vague in many cases. Therefore, apospory and diplospory are not differentiated in *Rosaceae* in Appendix S1. In many other taxa (Appendix S2), apomixis is of minor importance for the production of seeds, e.g. in *Rosa* sect. *Caninae*, apomixis accounts for about 10% of the progeny (NYBOM 2007). In many groups the assessment of the importance of apomictic seed production is based on few investigations. Decisions are often debatable and misjudgements are possible like in *Bidens frondosa* (apomixis claimed for plants from Canada; not included), *Cotoneaster integerrimus* (no cytoembryological prove of apomixis; included), *Euphorbia esula* (apomixis claimed for plants from North America; not included), *Festuca gigantea* (apomixis proved by auxin treatment; included), *Hieracium pilosella* (contains apomictic and sexual strains; included), or *Potentilla crantzii* (apomixis proved for hexaploid plants from Scandinavia, in Central Europe predominantly sexual tetraploid plants; not included). In some taxa apomictic and sexual types have different distributions in Central Europe. In *Taraxacum* sect. *Ruderalia* sexual diploids are about as common as apomictic triploids in two parts of Central Europe: (1) West and Southwest Germany (west of a line Aachen – Würzburg – Munich – Kufstein), Switzerland, and western Austria (Tyrole) and (2) Southeast Germany, eastern Austria, and the southern and eastern parts of the Czech Republic (mainly southern Moravia). Outside these two regions apomictic triploids prevail (DEN NIJS & STERK 1980; JENNISKENS et al. 1984; DEN NIJS et al. 1990; DEN NIJS 1997; UHLEMANN 2001). In *Hieracium pilosella* four ploidy types with different modes of seed production are known from Central Europe. Sexual tetraploids are widespread in lowland areas of Central Europe. Pentaploids and hexaploids prevail in mountainous areas and reproduce only (pentaploids) or mostly (hexaploids) by apomixis. (GADELLA 1984, 1987, 1991; KRAHULCOVÁ & KRAHULEC 1999; KRAHULCOVÁ et al. 2000; KRAHULEC et al. 2004; MRÁZ et al. 2008; POGAN & WCISLO 1989, 1995). Also in *Hieracium cymosum* sexual diploids and apomictic polyploids occur, but the later prevail in Central Europe (ROTREKLOVÁ et al. 2005).

Data from 82 literature sources and the database of the Czech vegetation, altogether approximately 200,000 relevées (Appendix S3), were used to calculate the frequencies of apomictic taxa in alliances. Apomictic taxa are mostly given as species groups like “*Taraxacum* sect. *Ruderalia*” or “*Rubus fruticosus* agg.”. Taxa of these groups have often very different ecological requirements. The differentiation of the phytosociological unit alliance was based on POTT (1995). For deviations, see Appendix S4. As the mean number of plant species – excluding ferns, mosses, and lichens – per relevée differs widely, nearly by factor 10, among alliances and classes, simple relations of frequencies of apomictic taxa between alliances would be misleading. Therefore, correction factors (CF) were used for calculating the frequencies. It was not possible simply to use proportion of apomictic taxa in a relevée as a measure of the abundance of apomicts. Many relevées were only available as aggregated and shortened tables.

- CF = 2 alliances with an average of < 15 taxa (excluding ferns, mosses, and lichens) per relevée.
- CF = 1 alliances with an average of 15–24 taxa (excluding ferns, mosses, and lichens) per relevée.

CF = 0.67 alliances with an average of 25–34 taxa (excluding ferns, mosses, and lichens) per relevée.

CF = 0.5 alliances with an average of > 34 taxa (excluding ferns, mosses, and lichens) per relevée.

Alliances were used as the basic unit as they are still specific enough to characterize them with ecological traits (see below) and a minimum number of 50 relevées is available for most of them. Associations would be more specific and would allow for a finer ranking with ecological traits but for many the minimum number of relevées would not be available. On the opposite, orders would be too unspecific ecologically but would always allow for a minimum number of 50 relevées.

Alliances with high frequencies of non-angiosperms (ferns, bryophytes, algae) – all alliances of the *Charetea fragilis* Fukarek ex Krausch 1964, *Ruppietea* J. Tx. 1960, and *Zosteretea* Pignatti 1953 – and alliances with fewer than 50 located relevées from Central Europe – *Agrostion alpinae* Jeník et al. 1980, *Deschampsion littoralis* Oberd. et Dierßen in Dierßen 1975, *Galeopsision segetum* Oberd. 1957, *Cypero-Spergularion salinae* Slavnić 1948, *Puccinellion limosae* Soó 1933, *Scorzonero-Juncion gerardii* (Wendelberger 1943) Vicherek 1973, *Crithmo-Limonion* Molinier 1934, *Festucion vaginatae* Soó 1938, *Pruno-Rubion ulmifoliae* O. Bolòs 1954, *Ononido-Pinion* Br.-Bl. 1950 – were not considered for evaluation.

Ecological traits for alliances were rated according to a five rank scale (Appendix S4) for the following factors: (1) Water content of soil, (2) Calcium and Magnesium content of soil or water, (3) Nutrient content of soil or water, (4) Environmental dynamics, (5) Hemeroby, (6) Frequency of stress-tolerant species, (7) Salt tolerance, (8) Altitude, (9) Height of vegetation, (10) Frequency of annual taxa. Information for ratings was derived from synopses of Central European vegetation: Austria: GRABHERR & MUCINA 1993, MUCINA et al. 1993a, b; Czech Republic: CHYTRÝ 2007, 2009, CHYTRÝ et al. 2001; Germany: OBERDORFER 1977, 1978, 1983, 1992, POTT 1995; The Netherlands: SCHAMINÉE et al. 1995, 1996 & 1998, STORTELDER et al. 1999 and personal experience. Alliances like *Arrhenatherion* W. Koch 1926, which span several grades for some factors were rated according to their optimum.

The traits life cycle, life form, and ploidy level for apomictic species have been extracted from literature, mostly from KLOTZ et al. (2002), supplemented by DOBEŠ & VITEK (2000), KIRSCHNER & ŠTĚPÁNEK (1998), MĚSÍČEK & JAVŮRKOVÁ-JAROLÍMOVÁ (1992), POGAN & WCISLO (1990), and STERK (1987).

Mere species numbers of apomicts in geographical regions or ecological units are an inappropriate measure to characterize the importance of apomixis. Apomixis leads in many cases to a very complex sympatric pattern of taxa. In Central European taxonomic tradition every morphologically discernable taxon, partly with regard to range size, is granted species rank. As an exception *Hieracium* species are treated each as broader units encompassing many subordinate taxa, which receive species rank in Scandinavia (for a discussion see SCHUHWERK 2004). In relevées apomictic taxa are often not differentiated at the level of species but as species aggregates like *Taraxacum officinale* or *Rubus fruticosus*. To homogenize vegetation data certain adjustments have been made: (1) only taxa with a frequency of at least five percent are used for evaluations; (2) *Rubus* and *Alchemilla* are treated as one taxon respectively; (3) in *Taraxacum* the sections are used as basic taxa; (4) *Poa pratensis*, *Poa angustifolia*, and *Poa humilis* are treated as one taxon. In *Alchemilla*, *Poa pratensis* s.l., *Rubus*, and the *Taraxacum* sections the total frequency is limited to 100% respectively.

Several problems emerged during the evaluation: (1) Relevées could not be attributed to an alliance. This affected mainly relevées from urban and industrial areas, roadsides, and railway lines (e.g. KOPECKÝ 1978). (2) Atypical, transitional, or heterogeneous stands, which do not fit into the Central European classification system, were underrepresented (CHYTRÝ 2001). (3) Often, only shortened relevées, which omit all taxa with low frequencies, could be analyzed. In some cases, relevées are too shortened to be used for this study, e.g. the study on Danish salt marsh communities by NYGAARD & LAWESSON (1998). (4) Varying approaches to taxon differentiation in *Alchemilla*, *Hieracium*, *Rubus*, or *Taraxacum*. Often it is possible to differentiate half a dozen *Rubus* taxa in a relevée of a forest margin or a dozen *Taraxacum* taxa in a grassland relevée (e.g. RICHARDS 1997). But this is only rarely done.

(5) Apomictic and sexual taxa of *Crataegus*, *Hypericum*, and *Sorbus* were rarely differentiated in the relevées. *Crataegus macrocarpa*, which is probably predominantly apomictic, is common in Central Europe, but was rarely given in the relevées. The apomictic *Hypericum dubium* was widely absent in the relevées, but in many parts of Germany it is more common than the similar sexual *Hieracium maculatum*. (6) Articles about apomixis appeared in many different magazines, some of them difficult to locate. In particular, magazines from the former Soviet Union are often not available in German libraries and some articles have probably been overlooked. (7) For many taxa the data on reproductive mode are unsatisfactory. Often apomixis has only been assessed for few individuals. The amount of facultative sexuality among apomictic individuals and the frequencies and spatial distributions of sexual and apomictic individuals remain unknown. In *Hieracium* subgen. *Hieracium*, *Rubus*, and *Taraxacum* apomixis was proven only for few of the relevant taxa. In many taxa the central question, if seeds are produced to a large part by apomixis, cannot be answered with certainty. Appendix S2 contains about 50 taxa which have been excluded, for various reasons, from this study.

Statistical analyses were conducted with functions provided by the programs Excel and SPSS. Spearman's rank correlation coefficient was used to test for relationships between ecological traits and the frequency of apomicts in alliances.

Plant nomenclature follows BUTTLER & HAND (2008) for indigenous and naturalized vascular plants in Germany and TUTIN et al. (1968–1993) for other Central European vascular plants. Syntaxonomic names follow RENNWALD (2000) and CHYTRÝ et al. (2001).

3. Results

The frequencies of apomicts in alliances of the phytosociological system are shown in Appendix 1, those in classes and in vegetation types in Appendix 2 and Table 1. In Appendix 1 the 21 alliances occurring predominantly at high altitudes are marked with an asterisk. They have a corrected mean of 1.03 (\pm 0.27) apomictic taxa per relevée. The mean of the other alliances is 0.53 (\pm 0.43) apomictic taxa per relevée. The difference is highly significant (Student's t-test: margin of error < 0.001). Using Spearman's rank correlation coefficient only three traits had statistically significant correlations with the frequency of apomictic taxa in alliances (Fig. 1). The trait altitude (correlation coefficient 0.49) was positively correlated, the traits water (correlation coefficient -0.25) and salt (correlation coefficient -0.55) were negatively correlated. No significant correlations exist between traits linked to competition, such as availability of nutrients, environmental dynamics, stress-tolerance, ave-

Table 1. Apomictic taxa in vegetation types.

Tabelle 1. Häufigkeit apomiktischer Taxa in Vegetationstypen.

Vegetation type	No. of relevées	No. of apomictic taxa per relevée (standard deviation)
Aquatic communities	9972	0.00
Swamps, tall herb fens, mires	20846	0.11 (0.03)
Maritime communities	9407	0.12 (0.09)
Cliff communities	3953	0.69 (0.21)
Vegetation of open habitats	33962	0.72 (0.26)
Woodlands and scrub	60503	0.78 (0.14)
Heath	8057	0.92 (0.12)
Grassland	52566	0.95 (0.25)

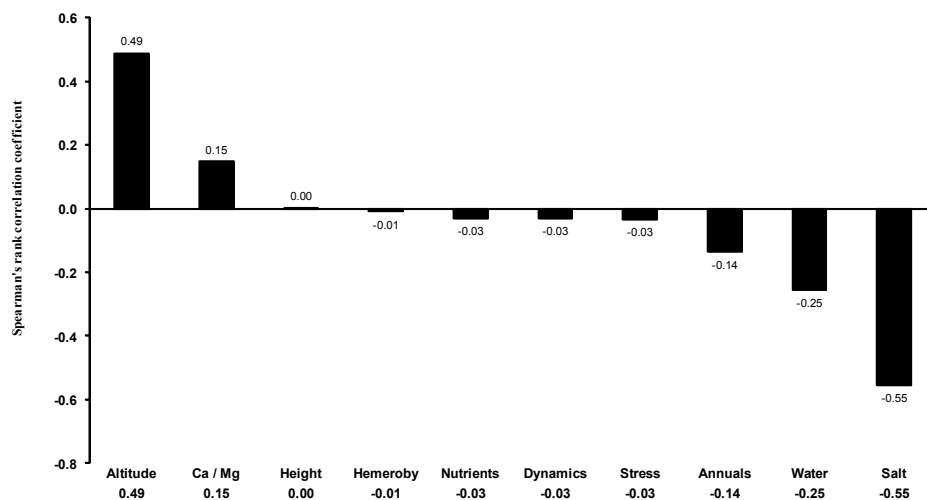


Fig. 1. Spearman's rank correlation coefficients between ecological traits and the occurrence of apomictic taxa in alliances of Central European flora; significance margin ± 0.16 for two-sided test, error margin 0.05; $n = 141$.

Abb. 1. Spearmans Rangkorrelationskoeffizienten zwischen Zeigerwerten und dem Vorkommen von apomiktischen Taxa in den Verbänden der mitteleuropäischen Flora; Signifikanzgrenze $\pm 0,16$ für zweiseitigen Test, Fehlerschwelle 0,05; $n = 141$.

rage height and frequency of apomictic taxa. Higher frequencies of apomicts in long-term stable habitats (grasslands, heaths, woodlands) compared to open habitats (cliff habitats, open or ruderal habitats) were statistically non significant (Student's t-test: 0.35, margin of error: 0.05, significance threshold: 1.7; variance test: 1.6, margin of error: 0.05, significance threshold: 2.96) if vegetation types "aquatic habitats", "maritime habitats", and "swamps, tall herb fens, mires" with very low frequencies of apomicts are excluded. Furthermore, there is no significant negative correlation between the frequency of annuals and apomictic taxa in alliances (spearman's rank correlation -0.14).

A factor analysis revealed no outstanding importance of the variable apomixis. Using all 141 alliances with all ecological factors (including apomixis) as variables, we receive a correlation matrix with many low coefficients between 0.2 and -0.2 (Table 2). The variable "Apomicts" has remarkably low correlations with most other variables. This confirms the results of spearman's rank correlation. Only the variable "Hemeroby" has a distinctly higher coefficient of 0.209 compared to spearman's rank correlation of -0.01.

Table 3 compares ranges of apomictic and sexual taxa pairs. Information for this comparison has been derived from HULTÉN & FRIES (1986), MEUSEL et al. (1965, 1978), MEUSEL & JÄGER (1992), and for *Hypericum* from ROBSON (2002).

4. Discussion

Certain general features, which have been attributed to apomictic taxa, are discussed below. For each of these features a very brief summary of previous discussions is given and it is stated if this survey could find evidence for the statement.

Table 2. Correlation matrix for factor analysis.
Table 2. Korrelationsmatrix für die Faktorenanalyse.

Variable	Apomicts	Water	Ca/Mg	Nutrients	Dynamics	Hemeroby	Stress	Salt	Altitude	Height	Annuals
Apomicts	1	-0.429	0.027	-0.053	-0.086	0.209	0.095	-0.231	0.382	0.063	0.068
Water		1	-0.222	0.282	0.052	-0.130	-0.293	0.103	-0.118	-0.092	-0.467
Ca/Mg			1	0.127	0.062	0.012	-0.037	0.073	0.142	0.005	0.113
Nutrients				1	0.585	0.513	-0.763	0.231	-0.216	0.217	0.197
Dynamics					1	0.561	-0.603	0.340	-0.382	-0.231	0.591
Hemeroby						1	-0.421	0.028	-0.191	0.013	0.359
Stress							1	-0.159	0.317	-0.232	-0.203
Salt								1	-0.438	-0.155	0.189
Altitude									1	-0.067	-0.247
Height										1	-0.210
Annuals											1

Table 3. Ranges of apomictic and sexual taxa pairs. S: the apomictic taxon has a much smaller range than the sexual relative(s). s: the apomictic taxon has a smaller range than the sexual relative(s). e: apomictic and sexual taxa have ranges of about the same size.

Tabelle 3. Verbreitungsgebiete apomiktischer und sexueller Taxapaare. S: Das apomiktische Taxon hat ein deutlich kleineres Verbreitungsgebiet als die sexuellen Taxa. s: Das apomiktische Taxon hat ein kleineres Verbreitungsgebiet als das sexuelle Taxon. e: Apomiktische und sexuelle Taxa haben in etwa gleich große Verbreitungsgebiete.

Apomictic taxon/taxa	Sexual taxon/taxa	Distribution
<i>Sorbus latifolia</i> s.l.	<i>S. aria</i> , <i>S. torminalis</i>	S
<i>Sorbus sudetica</i> , <i>S. algoviensis</i>	<i>S. aria</i> , <i>S. chamaemespilus</i>	S
<i>Sorbus mougeotii</i>	<i>S. aria</i> , <i>S. aucuparia</i>	S
<i>Sorbus intermedia</i>	<i>S. aucuparia</i> , <i>S. aria</i> , <i>S. torminalis</i>	S
<i>Calamagrostis purpurea</i>	<i>C. canescens</i>	s
<i>Crataegus macrocarpa</i>	<i>C. laevigata</i> , <i>C. monogyna</i>	s
<i>Hypericum dubium</i>	<i>Hypericum maculatum</i>	s
<i>Potentilla argentea</i> p.p.	<i>Potentilla argentea</i> p.p.	s
<i>Rubus</i> subgenus <i>Rubus</i> sect. <i>Rubus</i>	<i>R. canescens</i> , <i>R. incanescens</i> , <i>R. ulmifolius</i>	s
<i>Potentilla pusilla</i>	<i>Potentilla cinerea</i>	s
<i>Taraxacum</i> sect. <i>Erythrosperma</i>	<i>Taraxacum erythrospermum</i>	e
<i>Ranunculus auricomus</i> s.l.	<i>Ranunculus cassubicifolius</i> , <i>R. notabilis</i>	e
<i>Hieracium pilosella</i> p.p.	<i>H. pilosella</i> p.p.	e (?)
<i>Potentilla neumanniana</i> p.p.	<i>Potentilla neumanniana</i> p.p.	e (?)

4.1 Disturbance and competition favour apomicts

The opinion has often been expressed that apomixis is favoured in disturbed and unproductive habitats (e.g. STEBBINS 1950). This notion is based upon the “tangled bank hypothesis”, which suggests that in productive, undisturbed environments, with a high degree of competition between siblings, it is favourable to have variable offspring. Uniform offspring should be favoured in disturbed, unproductive habitats (see RICHARDS 1996, 1997). HÖRANDL & PAUN (2007) regard clonal diversity as important for the understanding of distributional success and niche differentiation in apomicts. In moderately disturbed, unstable, and patchy environments such as meadows and pastures, the stabilized genotype diversity shall provide apomicts with an advantage over sexual taxa.

In Central European vegetation, no significant correlations were found between traits linked to competition and disturbance and the occurrence of apomicts (Fig. 1). Furthermore, frequencies of apomicts in long-term stable habitats with above average competition were not significantly higher than in open habitats. This agrees with BIERZYCHUDEK (1985). She could not confirm the hypothesis that apomictic taxa occupy more disturbed habitats than their sexual relatives. Also, DEN NIJS & STERK (1980, 1984) and ROETMAN et al. (1988) found no correlation between management intensity and the occurrence of sexual or apomictic populations in *Taraxacum* sect. *Ruderalia* in the Netherlands and France. On the contrary, JERLING (1986) found in the Swedish flora an overrepresentation of apomictic taxa in habitats with above-average competition, including pastures, meadows, and forests, and an

underrepresentation of these taxa in ruderal habitats, wetlands, and shores. Sexual populations of *Ranunculus auricomus* prefer forests while apomictic populations show a preference for manmade meadows (HÖRANDL & PAUN 2007).

SUKOPP (1976) defined hemeroby as “an integrative measure for the impacts of all human interventions of ecosystems, whether they are intended or not” (see KOWARIK 1988 for a detailed discussion of the concept). Apomictic taxa span the entire range of hemeroby: *Erigeron annuus* and *Rubus* sect. *Corylifolii* occur mainly in polyhemerobic habitats, *Rubus* sect. *Rubus* is a typical component of mesohemerobic habitats, and many *Alchemilla* and *Hieracium* taxa are associated with oligohemerobic, some even with ahemerobic habitats. No correlation between the number of apomictic taxa in an alliance and its hemeroby value was found (see Fig. 1).

4.2 The colonizing ability of apomicts exceeds that of sexual taxa

Statements such as “apomixis confers advantages to colonizers” are common (e.g. CAMPBELL et al. 1991). This is explained by the ability of apomicts to form a population from one plant and to build up their populations faster than sexual taxa, avoiding the “cost of males” (see BIERZYCHUDEK 1985). STEBBINS (1950) assumed that in apomictic taxa, which are generally polyploid, the genetic resources of several species are pooled and that apomictic taxa are better equipped than their diploid relatives to colonize newly available habitats. GADELLA (1987) found a higher seed production and a greater colonizing ability in apomictic compared to sexual *Hieracium pilosella*. VAN DIJK (2007) found in coexisting apomictic and sexual populations of *Taraxacum* sect. *Ruderalia* a much higher seed set in apomictic plants in years with strongly pollination-limited seed set.

According to vegetation data, no significant correlation exists between the trait “environmental dynamics” and the number of apomictic taxa in an alliance (see Fig. 1). This trait is correlated with unstable habitats that favour annuals and colonizers. It is reasonable to suppose that apomixis is an advantage for colonizers. However apomicts, which are nearly always polyploid in Central Europe, have the disadvantage that their relatively large genome prevents them from living as annuals. Facultative selfers, 20–40% of angiosperms (RICHARDS 1997), like *Erophila verna* share with apomicts the ability to form a population from a single plant. But they do not have a general tendency towards polyploidy. They are well-represented among weeds and ruderal plants.

BIERZYCHUDEK (1985) stated that apomicts are better able to colonize areas opened by glacial retreat. This is difficult to verify with data from Central Europe as all of Central Europe was glaciated or under a strong glacial influence. But, the class *Thlaspietea* Br.-Bl. 1948, which encompasses alpine pioneer vegetation near retreating glaciers, is rather rich in apomicts. It has 0.98 apomicts per relevée, which makes it number 41 of 47 classes (see Appendix 2).

4.3 Apomicts are more common at higher altitudes

Apomixis is associated with arctic and boreal conditions and high altitudes (BIERZYCHUDEK 1985, MOGIE 1992, HÖRANDL 2006, 2010). VANDEL (1928, 1940) termed his finding that parthenogenetic animals often inhabit more northern areas than their sexual relatives “parthénogenèse géographique“. This is often extended to apomictic plants as geographical parthenogenesis (HÖRANDL 2010, HÖRANDL et al. 2008) with a widened definition: Apomictic plants have larger distribution areas, tend to range to higher latitudes and altitudes

than their sexual relatives and tend to colonize previously glaciated areas. Explanations are (1) the fast seed development in a short vegetation period, (2) reproductive success despite the rarity of pollinators, and (3) a low degree of competition. HAAG & EBERT (2004) suggested that marginal habitats, such as high altitudes, have a higher frequency of extinction and recolonization events. This results in genetic bottlenecks, which affect sexual taxa more than asexual taxa. According to HÖRANDL (2006, 2010) the higher abundance of apomictic taxa in higher altitudes may relate to comparatively favourable conditions for their formation, hindrance of sexual reproduction and the superior colonizing abilities of apomicts. Apomictic taxa are largely missing from the nival zone of the Alps (HÖRANDL et al. 2011).

In Central Europe apomicts are clearly more common at higher altitudes (see Fig. 1). Alliances occurring predominantly at higher altitudes have significantly more apomictic species than other alliances (see results). Among the alliances richest in apomictic taxa we find *Poion alpinae* Oberd. 1950 (high altitude grasslands on nutrient rich soils), *Arabidion caeruleae* Br.-Bl. in Br.-Bl. et Jenny 1926 (snow-beds of calcareous soils), *Epilobion fleischeri* Moor 1958 (pioneer vegetation in river valleys of high altitudes), and *Sedo-Scleranthion biennis* Br.-Bl. 1955 (rocky vegetation on base-poor soils of high altitudes).

4.4 Apomicts are perennial hemicryptophytic polyploids

Apomixis is predominantly found among perennial hemicryptophytic polyploids (ASKER & JERLING 1992). BIERZYCHUDEK (1985) claims the rarity of apomictic annuals to be caused by the origin of gametophytic apomicts in allopolyploids. Annuals self-fertilize to a large extent. An involvement in hybridization is less probable than in taxa with cross-fertilization. Gametophytic apomixis is with few exceptions only known in polyploids, tetraploidy is most common. Triploids are rare in pseudogamous taxa, as they require functional pollen. Adventitious embryony is known from diploids and polyploids (ASKER & JERLING 1992).

According to BIERZYCHUDEK (1985) high ploidy levels endow plants, independent of the breeding system, with the ability to tolerate extreme environmental conditions. Already, HAGERUP (1932) and TISCHLER (1935) formulated the hypotheses that extreme environment conditions increase the percentage of polyploid plants as polyploidy bestows plants with the ability to settle in these environments. Therefore, the correlations found between apomicts and certain traits might be valid for polyploids in general. But only a small fraction of the polyploid plants, which comprises about 70% of flowering plants (MASTERSON 1994; for a review see OTTO & WHITTON 2000), are apomictic. KNAPP (1953) argued that the Hagerup-Tischler rule does not apply to plants with similar life forms and that the higher proportion of polyploids in higher altitudes and latitudes is a result of the scarcity of annuals. Also, STEBBINS & DAWE (1987), HÖRANDL (2006), and MARTIN & HUSBAND (2009) did not find larger distribution areas or broader ecological tolerances in polyploids than in diploids. STEBBINS (1984) found a positive correlation between the degree of glaciations during the Pleistocene and the percentage of polyploid taxa.

Why diploidy and gametophytic apomixis are mutually nearly exclusive is not altogether clear. In the pseudogamous *Ranunculus auricomus* s.l. apomixis cannot be transferred by haploid gametes (e.g. NOGLER 1982). However, it is possible in *Hieracium* subgen. *Pilosella* (BICKNELL et al. 2000, using *Hieracium aurantiacum* and *Hieracium piloselloides*). RICHARDS (1996) discussed the linkage of lethal mutation with apomixis genes. This would prevent the formation of haploid pollen tubes in pseudogamous apomicts. CARMAN (1997) argued that gametophytic apomixis is realized by a disturbance of gene expression of different genomes.

The statement of ASKER & JERLING (1992) is confirmed for the Central European flora (Appendix S5). *Erigeron annuus* is the sole annual. There are few apomictic taxa, which are not hemicryptophytes. *Cotoneaster* taxa are nanophanerophytes, *Euphorbia dulcis* and the *Nigritella* taxa are geophytes. *Rubus* subgen. *Rubus* has a special life form (“pseudophanerophyt”) with biennial above ground organs, which are vegetative in their first year and produce flowers in their second, and perennial underground organs. *Nardus stricta* seems to be Central Europe’s only widespread diploid apomict. But its chromosome number of $2n = 26$ is atypically high for a diploid taxon and already TISCHLER (1935) hesitated to classify it as a diploid. Diploids of facultative apomictic *Poa* taxa are probably sexual. In *Potentilla argentea* diploids, long thought to be apomictic, are now known to be sexual (HOLM 1995; HOLM & GHATNEKAR 1996; HOLM et al. 1997).

4.5 Apomictic species have greater ranges than their sexual relatives

BIERZYCHUDEK (1985) and HÖRANDL et al. (2008) listed several examples of apomicts with greater ranges than their sexual relatives. Often, the sexual taxa have ranges centred within much larger ranges of their apomictic relatives (e.g. *Crepis occidentalis*-complex in North America, see GRANT 1981).

In Central Europe we find several cases of apomictic taxa with smaller ranges than their sexual relatives (Table 3). This is especially conspicuous in *Rubus* with a huge number of mostly unnamed taxa of very local distribution (“Lokalsippen” according to Weber 1995). Data from BROCHMANN et al. (2003) compiled by HÖRANDL (2006) for the North Atlantic region confirm this. For Europe as a whole some examples exist. In *Taraxacum* sect. *Palustria* (KIRSCHNER & ŠTĚPÁNEK 1998) there are two sexual taxa of very limited distribution – *T. raii* (GOUAN) GRAY in southern France, *T. tenuifolium* near the northern Adriatic Sea – and several apomictic taxa with large ranges like *T. hollandicum*, which occurs from Belgium to the Eastern Baltic. In *Hieracium alpinum* diploid sexual strains are confined to the Eastern and Southern Carpathians, while triploid apomictic strains occur in the Western Carpathians, the Alps, Scotland, Iceland, Greenland, Scandinavia and Northern Russia (MRÁZ et al. 2009). In *Taraxacum* sect. *Alpestris* one sexual species (*T. carpaticum*) with limited distribution in the southern Carpathians is known besides many apomictic taxa (ŠTĚPÁNEK et al. 2011).

4.6 Miscellaneous

Vegetation data show a significant negative correlation between the frequency of apomicts and the availability of water or salt in an alliance (see Fig. 1). These correlations seem as yet unreported. However, it would be incorrect to generalize these findings. All alliances in these habitats are very poor in species and many of their taxa tend to vegetative propagation, e.g. *Elodea*, Lemnaceae, or *Ranunculus* subgenus *Batrachium*. And apomicts are not generally missing. Several apomictic species of *Limonium* (BAKER 1966) grow on maritime cliffs and salt marshes in Western Europe and the Mediterranean. Likewise, *Taraxacum* sect. *Palustris* is often associated with (sub)saline habitats (KIRSCHNER & ŠTĚPÁNEK 1998). *Callitriche palustris*, which reproduces probably predominantly by apomixis, is rarely distinguished in relevées from other species of *Callitriche*.

BAYER et al. (1991) found in western North America for the apomictic complex *Antennaria rosea* Greene s.l. habitats to be either intermediate (“hybrid habitats”) or similar to those of their sexual progenitors. In Central Europe, we find predominantly examples of

similar habitat requirements of apomictic taxa and at least one of the presumed progenitors. The *Sorbus latifolia*-group has *Sorbus aria* and *Sorbus torminalis* as sexual progenitors. All taxa settle in dry, open woodland. *Hypericum desetangsii* and *Hypericum perforatum* have similar habitat requirements and prefer xerophytic grassland and ruderal sites. The other progenitor *Hypericum maculatum* prefers grassland with more humid conditions. In other examples the apomictic taxon settles into a habitat which is a part of the habitat diversity of one of its parent: *Calamagrostis rivalis* occurs on river shoreline. One progenitor *Calamagrostis canescens* is a moorland species while *Calamagrostis epigejos* has a very wide ecological range including river shorelines. Taxa of the *Potentilla collina*-group prefer slightly trampled sites in nutrition poor grassland. The progenitor *Potentilla argentea* settles many habitats in base poor open sites and co-occurs with the *Potentilla collina*-taxa. The other progenitors *Potentilla neumanniana* and *Potentilla cinerea* are found in nutrition poor, xerophytic grassland.

5. Conclusions and open questions

Connecting frequency of apomictic taxa in alliances of the Central European vegetation system with ecological traits of alliances theories concerning ecological preferences of apomictic taxa could largely not be confirmed for Central Europe. Maybe the occurrence of apomictic taxa depends primarily on factors which facilitate their origin. Similar ideas have already been formulated by HÖRANDL (2006, 2009). Apomictic taxa in Central Europe are nearly always polyploid and might arise from hybridization (CARMAN 1997). So, the spatial occurrence of apomictic taxa might represent the probability of hybridizations in the recent geological past. Hybridizations occur probably more frequently in areas with large-scale disturbance than in long-time stable habitats. In Central Europe, severe climate changes in the Pleistocene facilitated hybridization. This is in accordance with the observation that in Crete and Cyprus, despite the fact that habitat diversity is similar to Central Europe, apomicts are nearly missing. Man's influence could not be detected in my survey. But it seems probable that we are involved in the origin of, at least, apomictic *Crataegus*, *Rubus*, and *Taraxacum* taxa. Hopefully, the now available simplified methods for the detection of apomixis like flow cytometry (KRAHULCOVÁ & ROTREKLOVÁ 2010) will enlarge the database of sexual or apomictic seed production. Generally, more care should be taken in vegetation science to differentiate between taxa in difficult groups. In *Rubus* it is possible to differentiate the few obligate sexual taxa. *Crataegus*-taxa can be identified while fruiting. But, in other cases it is impossible to differentiate between morphologically similar apomictic and sexual plants. E.g. sexual diploid *Potentilla argentea* is under field conditions indistinguishable from apomictic hexaploid *Potentilla argentea*, even as there are strong indications that the later is allopolyploid (PAULE 2010). Also, it is impossible under field conditions to differentiate sexual and apomictic strains of *Hieracium pilosella* or *Potentilla neumanniana*.

Theories concerning ecological preferences of apomictic taxa could probably be tested with more success using datasets from large areas of similar climate like from Europe, East Asia, Western North America, and Eastern North America. A prerequisite for this are relevés with rigorous taxa differentiation and a thorough knowledge about the occurrence of apomixis in higher plants.

Erweiterte deutsche Zusammenfassung

Einleitung – Apomikten, Pflanzen die genetisch zur Mutterpflanze identische Samen bilden, stellen einen bedeutenden Anteil an der Vegetation Mitteleuropas. In der pflanzensoziologischen Datenbank Tschechiens (CHYTRÝ & RAFAJOVÁ 2003) stehen *Poa pratensis* s.l. auf dem 2., *Taraxacum* sect. *Ruderalia* auf dem 4., *Poa nemoralis* auf dem 23. und *Hypericum perforatum* auf dem 34. Häufigkeitsrang. Übersichten über apomiktische Pflanze haben u. a. GUSTAFSSON (1946, 1947a, b), NYGREN 1954a, 1967), RUTISHAUSER (1967) sowie ASKER & JERLING (1992) publiziert. Es werden drei Typen von Apomixis unterschieden: (1) Diplosporie beinhaltet die Ausbildung eines unreduzierten Embryosacks aus der Embryosackmutterzelle. Aus der Eizelle des Embryosacks entwickelt sich ohne Befruchtung der Embryo. (2) Aposporie ist die Bildung des unreduzierten Embryosacks aus einer somatischen Zelle. Aus der Eizelle des Embryosacks entwickelt sich wiederum ohne Befruchtung der Embryo, wobei oft eine Befruchtung des Embryosackkerns zur Endosperm Bildung notwendig ist. (3) Bei der Nucellar- oder Adventivembryonie entwickelt sich der Embryo direkt aus Zellen des Nucellus oder des Integuments.

ASKER (1979), ASKER & JERLING (1992), MARSHALL & BROWN (1981), RICHARDS (1997) sowie HÖRANDL (2006) haben Theorien zusammengefasst, die sich mit der Ökologie apomiktischer Sippen beschäftigen. Danach sollen (1) apomiktische gegenüber sexuellen Sippen in gestörten, unproduktiven Ökosystemen Konkurrenzvorteile haben, (2) apomiktische Sippen eine höhere Ausbreitungsfähigkeit besitzen; (3) apomiktische Sippen eher Hochlagen besiedeln, (4) apomiktische Sippen Übergangshabitat im Vergleich mit ihren sexuellen Ausgangsarten besiedeln und (5) apomiktische Sippen zumeist über größere Areale als ihre sexuellen Verwandten verfügen.

Mitteleuropa hat eine weltweit einmalige Abdeckung mit Vegetationsaufnahmen. In dieser Arbeit wird versucht, auf breiter Grundlage von in Mitteleuropa verfügbaren Vegetationsaufnahmen Theorien zur ökologischen Präferenz von Apomikten zu überprüfen.

Material und Methoden – Der geographische Hintergrund der Arbeit ist Mitteleuropa [Österreich, Belgien, Tschechien, Dänemark, Frankreich (nur Elsass), Deutschland, die Niederlande, Luxemburg, Polen, Schweiz]. In einer Literaturstudie wurden 54 Sippen und Artengruppen (Anhang S1) identifiziert, bei denen Samen zu einem großen Teil über Apomixis gebildet werden. Etwa 50 Taxa, für die Apomixis angegeben wird, bleiben aus verschiedenen Gründen unberücksichtigt (Anhang S2).

Daten aus 82 Literaturquellen und die Datenbank zur tschechischen Vegetation, zusammen etwa 200 000 Vegetationsaufnahmen, wurden für die Untersuchung herangezogen (Anhang S3). Als Basis für Auswertungen wurde der Verband verwendet. Da die durchschnittliche Zahl der Pflanzenarten pro Vegetationsaufnahme in den Verbänden sehr unterschiedlich ist, wurden Korrekturfaktoren verwendet (s. Kapitel 2). Es wurden nur Verbände berücksichtigt, für die mindestens 50 Vegetationsaufnahmen ermittelt werden konnten, ebenso blieben von Farnen, Moosen oder Algen dominierte Verbände unberücksichtigt.

Zeigerwerte für die Verbände wurden in einer 5teiligen Skala für (1) Wasserverfügbarkeit, (2) Calcium- und Magnesiumverfügbarkeit, (3) Nährstoffverfügbarkeit, (4) Umweltdynamik, (5) Hemerobie, (6) Häufigkeit stressresistenter Arten, (7) Salz-Toleranz, (8) Höhenlage, (9) Höhe der Vegetation sowie (10) Häufigkeit annualer Arten abgeschätzt (Anhang S4).

Ergebnisse – Anhang 1 zeigt die Häufigkeiten apomiktischer Sippen in Verbänden, Anhang 2 deren Häufigkeit in Klassen und Tabelle 1 in Vegetationstypen. Die 21 Verbände, die vornehmlich in Hochlagen vorkommen, haben eine durchschnittliche Häufigkeit von 1,03 (\pm 0,27 SA) apomiktischen Sippen pro Vegetationsaufnahme, der Durchschnitt der anderen Verbände ist 0,53 (\pm 0,43 SA). Der Unterschied ist hoch signifikant. Nur drei Zeigerwerte zeigen eine signifikante Korrelation mit dem Vorkommen apomiktischer Sippen (Abb. 1): Salzgehalt (Spearman's Rangkorrelation – 0,55), Höhenlage (Spearman's Rangkorrelation 0,49) und Wasserverfügbarkeit (Spearman's Rangkorrelation – 0,25). Größere Häufigkeiten apomiktischer Sippen in langfristigen stabilen Habitaten (Grünland, Heide, Wald)

gegenüber offenen, eher dynamischen Habitaten (Felsspalten, Ruderalflächen) waren statistisch nicht signifikant. In einer Faktorenanalyse (Tab. 3) zeigt die Variable Apomixis nur geringe Korrelation mit den meisten anderen Variablen.

Diskussion – *Apomikten kommen in Mitteleuropa nicht häufiger in durch Störung geprägter Vegetation vor* – Die Meinung, dass Apomixis in gestörten Habitaten begünstigt ist, wurde vielfach geäußert (z. B. STEBBINS 1950). In der mitteleuropäischen Vegetation ließ sich dies Annahme nicht bestätigen. Ähnliche Ergebnisse erzielten auch DEN NIJS & STERK (1980, 1984), BIERZYCHUDEK (1985) sowie ROETMAN et al. (1988). Vor dem Hintergrund der eingangs genannten These wäre auch ein Zusammenhang zwischen Hemerobie (SUKOPP 1976, KOWARIK 1988) und dem Vorkommen apomiktischer Sippen zu erwarten, der jedoch nicht gefunden wurde (Abb. 1). Apomiktische Sippen kommen regelmäßig in allen Hemerobiestufen vor: *Erigeron annuus* und *Rubus* sect. *Corylifolii* besiedeln vornehmlich polyhemerobe Habitats. *Rubus*-Arten sind typische Vertreter mesohemerober Lebensräume; viele *Alchemilla*- und *Hieracium*-Arten besiedeln oligo-, teilweise auch ahemerobe Habitats.

Ist die Ausbreitungsfähigkeit von Apomikten größer als die sexueller Sippen? – Da Apomikten bei der Samenproduktion nicht auf Fremdbestäubung angewiesen sind, wird häufig angenommen, dass Apomikten bei der Neubesiedlung von Lebensräumen begünstigt sind (z. B. CAMPBELL et al. 1991). Nach BIERZYCHUDEK (1985) hatten Apomikten Vorteile bei der Besiedlung der nacheiszeitlichen Landschaft. Die Vegetationsdaten zeigen keine positive Korrelation zwischen Verbänden mit hohen Zeigerwerten für Umweltdynamik, die viele Arten mit guten Ausbreitungsfähigkeiten besitzen, und der Häufigkeit von Apomikten. Die Annahme Bierzychudeks müsste durch den Vergleich standörtlich ähnlicher Gebiete mit und ohne starken eiszeitlichen Einfluss geprüft werden. Mitteleuropa stand aber generell unter starkem eiszeitlichem Einfluss. Ein Hinweis auf diesen Zusammenhang ist aber die überdurchschnittliche Häufigkeit von Apomikten in der Klasse *Thlaspietea* (0,98 Apomikten pro Aufnahme, 41. von 47 Klassen in der Häufigkeit von Apomikten, Anhang S2), die häufig im Umfeld von Gletschern vorkommt.

Apomikten sind in Hochlagen relativ häufig – Eine größere Häufigkeit apomiktischer Sippen wird häufig mit den arktischen und borealen Vegetationszonen sowie Hochlagen in Verbindung gebracht (BIERZYCHUDEK 1985, MOGIE 1992, HÖRANDL 2006, 2010). VANDEL (1928, 1940) prägte für die Beobachtung, dass parthenogenetische Tiere häufiger nördliche Gebiete besiedeln als ihre sexuellen Verwandten den Begriff "parthénogenèse géographique". Dieser Begriff wird oft auch für Pflanzen verwendet (HÖRANDL et al. 2008, 2010), allerdings mit erweiterter Definition: Apomiktische Arten haben größere Verbreitungsgebiete und neigen dazu, Hochlagen und nördlichere Gebiete zu besiedeln als ihre sexuellen Verwandten, und sie haben zudem eine Tendenz ehemals stärker vergletscherte Gebiete eher zu besiedeln. Für Mitteleuropa kann bestätigt werden, dass Apomikten in Hochlagen deutlich häufiger sind in tieferen Lagen (Abb. 1). Unter den Verbänden mit dem höchsten Anteil an Apomikten finden sich *Poion alpinae* Oberd. 1950, *Arabidion caeruleae* Br.-Bl. in Br.-Bl. et Jenny 1926, *Epilobion fleischeri* Moor 1958 und *Sedo-Scleranthion biennis* Br.-Bl. 1955.

Durch Hybridisierung entstandene Apomikten besiedeln nicht überwiegend Übergangshabitats – BAYER et al. (1991) fand im westlichen Nordamerika für den apomiktischen Komplex *Antennaria rosea* Greene s.l., dass die Habitats der Apomikten oft im Übergangsbereich zwischen denen der Elternarten liegen. In Mitteleuropa finden wir dagegen eher Beispiele dafür, dass die Habitats von durch Hybridisierung entstandenen apomiktischen Sippen eher denen einer der Ausgangsarten entsprechen. So besiedeln die Arten der *Sorbus latifolia*-Gruppe Habitats, in denen auch die beiden sexuellen Ausgangsarten *Sorbus aria* und *Sorbus torminalis* vorkommen. In anderen Fällen besiedelt eine apomiktische Sippe einen Teil des Habitatspektrums einer Ausgangsart: *Calamagrostis rivalis* besiedelt den Uferbereich von Flüssen. Hier kommt auch *Calamagrostis epigejos* vor, eine Sippe mit weiter Habitatsamplitude. Viele Sippen der *Potentilla collina*-Gruppe besiedeln betretene Bereiche in Magerrasen, einen Biotoptyp, in dem auch eine der Elternarten, *Potentilla argentea*, vorkommt.

Apomiktische Arten haben in Mitteleuropa nicht größere Areale als ihre sexuellen Verwandten – BIERZYCHUDEK (1985) und HÖRANDL et al. (2008) listen diverse Beispiele dafür auf, dass apomiktische Sippen ein größeres Areal als ihre sexuellen Verwandten besitzen. Im Idealfall, wie bei dem *Crepis-occidentalis-Komplex* in Nordamerika, liegen die Areale der sexuellen Arten etwa im Zentrum der viel größeren Areale ihrer apomiktischen Verwandten (GRANT 1981). In Mitteleuropa finden wir dagegen neben Gruppen mit etwa gleichen Arealgrößen Fälle, in denen apomiktische Arten deutlich kleinere Areale als ihre sexuellen Verwandten aufweisen (Tab. 3). Dies ist besonders auffällig in der Gattung *Sorbus*. Aber auch in der Gattung *Rubus* existiert eine große Zahl meist unbeschriebener, sehr kleinflächig verbreiteter Sippen (Weber 1995). Betrachtet man ganz Europa, finden sich allerdings verschiedene Gruppen, für die die o. g. Hypothese zutrifft: *Hieracium alpinum*, *Taraxacum* sect. *Alpestris* und *Taraxacum* sect. *Palustria*.

Apomikten sind mehrjährige, polyploide Hemikryptophyten – Nach ASKER & JERLING (1992) sind apomiktische Sippen hauptsächlich mehrjährige Hemikryptophyten. Dies kann für die mitteleuropäische Flora bestätigt werden (Anhang S5). Nur wenige Arten weichen ab: *Erigeron annuus* s.l. ist annuell, *Cotoneaster*-Taxa sind Nanophanerophyten, *Euphorbia dulcis* und die *Nigritella*-Arten sind Geophyten. *Rubus* subgen. *Rubus* hat eine spezielle Lebensform als "Pseudophanerophyt". *Nardus stricta* gilt als einzige diploide apomiktische Sippe in Mitteleuropa, aber die Chromosomenzahl ist mit $2n = 26$ für eine diploide Sippe untypisch hoch.

Fehlen apomiktische Sippen weitgehend in Wasservegetation und in der Vegetation salzreicher Standorte? – Die signifikanten negativen Korrelationen zwischen der Häufigkeit apomiktischer Sippen und der Verfügbarkeit von Wasser sowie Kalium- oder Natrium-Salzen (Abb. 1) werden als Artefakte angesehen. Alle Verbände mit hohen Zeigerwerten für die beiden Faktoren sind artenarm. In Wasservegetation sind Arten mit vegetativer Fortpflanzung auffällig häufig. Zudem fehlen in Europa Apomikten salzreichen Lebensräumen nicht vollständig. Viele apomiktische *Limonium*-Arten wachsen an Felsküsten Westeuropas und des Mittelmeers (BAKER 1966). Viele Arten von *Taraxacum* sect. *Palustria* (KIRSCHNER & ŠTĚPÁNEK 1998) besiedeln salzreiches Grünland.

Acknowledgements

I am indebted to many people for their help. Erwin Bergmeier, Göttingen, enabled me to use the geobotanical library of the Albrecht von Haller Institute of Plant Science of the Georg August University in Göttingen. Milan Chytrý, Brno, prepared an extract of the database of the Czech vegetation. Douglas Fiebig, Schlitz, improved the English. František Krahulec, Průhonice, kindly read an earlier draft of this article. Franz Schuhwerk, Munich, helped at the differentiation of apomictic and sexual *Hieracium* taxa. Franz Speta, Linz, informed me about unpublished results of seed set in *Ornithogalum* taxa with uneven ploidy. Alexander Sennikov, Saint Petersburg, sent me Russian articles not available in Germany, which was translated by Galina Sperling, Osnabrück. Herbert Sukopp, Berlin, pointed out several historical articles about polyploidy. Susanne Renner, Munich, provided information about apomixis in *Bryonia*. The reviewer's comments have been very helpful.

The present study was supported financially by the research funding program "LOEWE – Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz" of Hesse's Ministry of Higher Education, Research, and the Arts.

Supplements and Appendices

Appendix 1. Number of apomictic taxa per relevée in alliances, acronyms of phytosociological classes in parenthesis. Correction factor (CF): 2 for classes with an average of < 15 angiosperm taxa per relevée; 0.67 for alliances with an average of 25–34 angiosperm taxa per relevée; 0.5 for alliances with an average of > 34 angiosperm taxa per relevée. Alliances occurring predominantly at high altitudes are marked with an asterisk.

Anhang 1. Zahl apomiktischer Taxa pro Vegetationsaufnahme in Verbänden, Akronyme der Klassen in Klammern. Korrekturfaktoren (CF): 2 für Klassen mit einer durchschnittlichen Zahl von < 15 Gefäßpflanzenarten pro Aufnahme; 0,67 für Verbände mit einer durchschnittlichen Zahl von 25–34 Gefäßpflanzenarten pro Aufnahme; 0,5 für Verbände mit einer durchschnittlichen Zahl von > 34 Gefäßpflanzenarten pro Aufnahme. Verbände, die vornehmlich in Hochlagen vorkommen, sind mit einer Stern versehen.

Alliance (Class)	Releveés	No. of apomictic taxa per relevé	CF	Corrected No. of apomicts per relevé	Rank for No. of apomicts
Puccinellion maritimae s.l. (AST)	2288	0.00	2	0.00	1
Lemnion minoris s.l. (LEM)	1579	0.00	2	0.00	1
Eleocharition acicularis (LIT)	349	0.00	2	0.00	1
Hydrocotylo-Baldellion s.l. (LIT)	533	0.00	2	0.00	1
Littorellion uniflorae (LIT)	229	0.04	2	0.08	1
Phragmition australis (PHR)	4227	0.00	2	0.00	1
Hydrocharition morsus-ranae (POT)	761	0.00	2	0.00	1
Nymphaeion albae (POT)	1740	0.00	2	0.00	1
Potamogetonion pectinati (POT)	2446	0.00	2	0.00	1
Ranunculion fluitantis s.l. (POT)	1340	0.00	2	0.00	1
Zannichellion pedicellati (POT)	202	0.00	2	0.00	1
Spartinion maritimae (SPA)	479	0.00	2	0.00	1
Thero-Salicornion strictae s.l. (TH-SA)	528	0.00	2	0.00	1
Scorpidio-Utricularion (UTR)	168	0.00	2	0.00	1
Sphagno-Utricularion (UTR)	134	0.00	2	0.00	1
Bolboschoenion maritimi (PHR)	1019	0.00	2	0.00	1
Rhynchosporion albae (SC-CA)	818	0.00	2	0.01	1
Sphagnion magellanici s.l. (OX-SP)	1973	0.00	2	0.01	1
Glycerio-Sparganion (PHR)	834	0.01	2	0.02	1
Thlaspion calaminariae (VIO)	100	0.04	1	0.04	1
Agropyro-Honkenyion peploides (CAK)	345	0.03	2	0.06	1
Caricion atrofusci-saxatilis (SC-CA)	395	0.06	1	0.06	1
Ericion tetralicis (OX-SP)	608	0.04	2	0.09	1
Caricion lasiocarpae (SC-CA)	1250	0.09	1	0.09	1
Caricion remotae (MO-CA)	769	0.05	2	0.09	1
Salicion cinereae (FRA)	2392	0.16	0.67	0.11	1
Corynephorion canescentis (KO-CO)	1929	0.12	1	0.12	1
Salicion albae (SAL P)	952	0.18	0.67	0.12	1
Aperion spicae-venti (STE)	8288	0.13	1	0.13	1
Atriplicion littoralis (CAK)	1043	0.06	2	0.13	2
Betulion pubescentis (VA-PI)	1110	0.17	1	0.17	2
Chenopodion rubri (BID)	465	0.18	1	0.18	2
Oxycocco-Ericion tetralicis (OX-SP)	372	0.09	2	0.18	2
Nanocyperion flavescentis s.l. (IS-NA)	1926	0.03	1	0.03	2
Filipendulion (MO-AR)	1460	0.19	1	0.19	2
Digitario-Setarion (STE)	1939	0.19	1	0.19	2

Alliance (Class)	Relevés	No. of apomictic taxa per relevé	CF	Corrected No. of apomicts per relevé	Rank for No. of apomicts
Ammophilion arenariae (AMM)	1021	0.10	2	0.20	2
Polygono-Chenopodion polyspermi (STE)	871	0.30	0.67	0.20	2
Caricion nigrae (SC-CA)	2412	0.21	1	0.21	2
Caricion firmae (EL-SE)	743	0.32	0.67	0.21	2
Caricion davallianae (SC-CA)	1721	0.22	1	0.22	2
Armerion halleri (VIO)	251	0.23	1	0.23	2
Caucalidion platycarpi (STE)	1721	0.36	0.67	0.24	2
Bidention tripartitae (BID)	1056	0.12	2	0.24	2
Magnocaricion elatae (PHR)	3147	0.12	2	0.24	2
Alnion glutinosae (ALN)	1384	0.37	0.67	0.25	2
Dicrano-Pinion (VA-PI)	2079	0.30	1	0.30	2
Salsolion ruthenicae (STE)	463	0.32	1	0.32	2
Vaccinon myrtilli (CA-UL)	837	0.35	1	0.35	2
Alnion incanae (QU-FA)	5437	0.53	0.67	0.35	2
Senecionion fluviatilis (GA-UR)	2279	0.38	1	0.38	2
Erico-Pinion sylvestris (ER-PI)	1430	0.76	0.5	0.38	2
Armerion maritimae (AST)	3207	0.19	2	0.39	2
Erico-Pinion mugi (ER-PI)	1112	0.67	0.67	0.44	2
Fumario-Euphorbion (STE)	2458	0.45	1	0.45	2
Tilio platyphylli-Acerion pseudoplatani (QU-FA)	2644	0.69	0.67	0.46	2
Empetrium nigri (CA-UL)	501	0.23	2	0.46	2
Petasition paradoxii (THL)	334	0.49	1	0.49	3
Thlaspion rotundifolii (THL)	165	0.49	1	0.49	3
Cratoneurion commutati (MO-CA)	391	0.25	2	0.49	3
Cytiso ruthenici-Pinion (ER-PI)	508	0.75	0.67	0.50	3
Sedo albi-Veronicion dillenii (KO-CO)	236	0.76	0.67	0.51	3
Cardamino-Montion s.l. (MO-CA)	615	0.26	2	0.53	3
Molinion (MO-AR)	2263	1.07	0.5	0.54	3
Asplenion serpentini (ASP)	82	0.28	2	0.56	3
Caricion ferruginea s.l. (EL-SE)	406	1.12	0.5	0.56	3
Piceion excelsae (VA-PI)	3919	0.56	1	0.56	3
Sisymbrium (STE)	1184	0.58	1	0.58	3
Luzulo-Fagion (QU-FA)	4407	0.58	1	0.58	3
Arction lappae (ART)	1581	0.59	1.00	0.59	3
Festucion valesiacae (FE-BR)	977	1.19	0.5	0.60	3
Thero-Airion (KO-CO)	797	0.91	0.67	0.61	3
Seslerion albicantis s.l. (EL-SE)	618	1.22	0.5	0.61	3
Koelerion glaucae (KO-CO)	576	0.62	1	0.62	3
Stipo-Poion carniolicae (FE-BR)	200	1.24	0.5	0.62	3
Aegopodion podagrariae (GA-UR)	1531	0.63	1	0.63	3
Fagion sylvaticae (QU-FA)	13188	0.98	0.67	0.65	3
Seslerio-Festucion pallentis (KO-CO)	764	1.32	0.5	0.66	3
*Loiseleurio-Vaccinon (LO-VA)	201	0.67	1	0.67	3
Agropyro-Rumicion (MO-AR)	3094	0.69	1	0.69	3
Onopordion acanthii s.l. (ART)	341	1.03	0.67	0.69	3
*Calamagrostion villosae (BE-AD)	295	0.70	1	0.70	3

Alliance (Class)	Relevés	No. of apomictic taxa per relevé	CF	Corrected No. of apomicts per relevé	Rank for No. of apomicts
*Rhododendro-Vaccinon (LO-VA)	445	0.71	1	0.71	3
Lolio-Plantaginon (MO-AR)	1427	1.07	0.67	0.71	3
Phalaridion arundinaceae (PHR)	295	0.36	2	0.72	3
Koelerio-Phleion phleoides (FE-BR)	1734	1.49	0.5	0.74	4
Xerobromion (FE-BR)	451	1.50	0.5	0.75	4
Cirsio-Brachypodion (FE-BR)	594	1.51	0.5	0.76	4
Genistion pilosae (CA-UL)	1586	0.38	2	0.76	4
*Adenostylion alliariae (BE-AD)	203	0.76	1	0.76	4
Saginon procumbentis s.l. (PO-PO)	896	0.38	2	0.77	4
Geranion sanguinei (TR-GE)	909	1.17	0.67	0.78	4
Galio-Alliarion s.l. (GA-UR)	1492	0.80	1	0.80	4
Calthion (MO-AR)	5209	1.20	0.67	0.80	4
*Elynion myosuroides (CA-KO)	65	0.81	1	0.81	4
Koelerion arenariae (KO-CO)	1570	1.21	0.67	0.81	4
*Salicion eleagni (SAL P)	85	0.81	1	0.81	4
*Juncion trifidi (CAR)	73	0.85	1	0.85	4
Quercion pubescentis s.l. (QU-FA)	1548	1.70	0.5	0.85	4
*Androsacion vandellii s.l. (ASP)	136	0.43	2	0.85	4
Bromion erecti s.l. (FE-BR)	3016	1.72	0.5	0.86	4
Carpino-Prunion (RH-PR)	683	0.87	1	0.87	4
*Androsacion alpinae (THL)	212	0.88	1	0.88	4
Sambuco-Salicion capreae (RH-PR)	801	0.90	1	0.90	4
*Drabion hoppeanae (THL)	136	0.90	1	0.90	4
Alysso-Sedion (KO-CO)	434	0.91	1	0.91	4
Dauco-Melilotion (ART)	1171	1.37	0.67	0.92	4
*Cystopteridion fragilis (ASP)	137	0.46	2	0.92	4
Quercion roboris (QUE)	4770	0.93	1	0.93	4
*Potentillion caulescentis (ASP)	583	0.48	2	0.96	4
Juncion squarrosi (CA-UL)	722	1.01	1	1.01	4
*Stipion calamagrostis (THL)	255	1.01	1	1.01	4
Polygono-Trisetion (MO-AR)	2811	2.06	0.5	1.03	4
Atropion belladonnae (EPI)	192	1.57	0.67	1.05	5
*Abieto-Piceion (VA-PI)	1973	1.05	1	1.05	5
Carici piluliferae-Epilobion angustifolii (EPI)	563	1.05	1	1.05	5
Saginon maritimae (SAG)	466	0.53	2	1.05	5
Convolvulo-Agropyrion repentis (ART)	1355	1.05	1.00	1.05	5
*Rumicion alpini (GA-UR)	143	1.60	0.67	1.07	5
Stipo-Poion xerophilae (FE-BR)	215	2.15	0.5	1.08	5
Berberidion vulgaris s.l. (RH-PR)	1759	0.54	2	1.08	5
Cnidion dubii (MO-AR)	866	1.63	0.67	1.09	5
Plantagini-Festucion ovinae (KO-CO)	2425	1.63	0.67	1.09	5
Violion caninae (CA-UL)	2731	1.65	0.67	1.10	5
*Caricion curvulae (CAR)	176	1.66	0.67	1.10	5
Chelidonio-Robinion (ROB)	356	1.10	1	1.10	5
Festucion variae (CAR)	114	1.66	0.67	1.11	5
Lonicero-Rubion silvatici (FRA)	706	1.11	1	1.11	5

Alliance (Class)	Relevées	No. of apomictic taxa per relevé	CF	Corrected No. of apomicts per relevé	Rank for No. of apomicts
*Salicion herbaceae (SAL H)	103	1.16	1	1.16	5
Trifolion medii (TR-GE)	821	1.76	0.67	1.17	5
Arrhenatherion (MO-AR)	7379	1.78	0.67	1.19	5
*Nardion strictae (CA-UL)	931	1.82	0.67	1.21	5
Cynosurion cristati (MO-AR)	9034	1.83	0.67	1.22	5
Salicion arenariae (RH-PR)	259	0.68	2	1.28	5
Carpinion betuli (QU-FA)	5567	1.96	0.67	1.31	5
*Poion alpinae (MO-AR)	361	2.76	0.5	1.38	5
Melampyrium pratensis (TR-GE)	715	1.40	1	1.40	5
*Arabidion caeruleae (THL)	94	1.40	1	1.40	5
*Epilobion fleischeri (THL)	71	1.43	1	1.43	5
*Sedo-Scleranthion biennis (KO-CO)	99	1.69	1	1.69	5
*Centrantho-Parietion (ASP)	188	0.94	2	1.87	5
Pruno-Rubion radulae (RH-PR)	1209	1.90	1	1.90	5
Number of relevées	197.757			0.6 (\pm 0.44)	

Appendix 2. Frequencies of apomictic taxa in classes of the phytosociological system. Correction factor (CF) as in Appendix 1.

Anhang 2. Zahl apomiktischer Taxa pro Vegetationsaufnahme in Klassen. Korrekturfaktoren wie in Anhang 1.

Class	No. of relevées	Apomictic taxa per relevée	CF	Apomictic taxa per relevée (corrected)
Lemneta (LEM)	1579	0.00	2	0.00
Potamogetoneta (POT)	6489	0.00	2	0.00
Utricularieta (UTR)	302	0.00	2	0.00
Littorelletea (LIT)	1151	0.00	2	0.00
Thero-Salicornieta (TH-SA)	528	0.00	2	0.00
Spartineta (SPA)	479	0.00	2	0.00
Oxycocco-Sphagneta (OX-SP)	2953	0.05	2	0.09
Isoeto-Nanojunceta (IS-NA)	1926	0.03	2	0.06
Astereta (AST)	5495	0.10	1	0.10
Scheuchzerio-Cariceta (SC-CA)	6596	0.12	1	0.12
Cakileta (CAK)	1043	0.06	2	0.13
Violetea (VIO)	351	0.13	1	0.13
Bidenteta (BID)	1521	0.15	1	0.15
Phragmiteta (PHR)	9522	0.10	2	0.20
Ammophileta (AMM)	1366	0.13	2	0.26
Stellarieta (STE)	16924	0.33	1	0.33
Montio-Cardamineta (MO-CA)	1775	0.19	2	0.37
Alneta (ALN)	1384	0.37	1	0.37
Elyno-Seslerieta (EL-SE)	1767	0.88	0.5	0.44
Saliceta purpureae (SAL P)	1037	0.49	1	0.49
Vaccinio-Piceeta (VA-PI)	9081	0.52	1	0.52
Erico-Pineta s.l. (ER-PI)	3079	0.89	0.67	0.60

Class	No. of relevées	Apomictic taxa per relevée	CF	Apomictic taxa per relevée (corrected)
Galio-Urticetea (GA-UR)	5302	0.60	1	0.60
Loiseleurio-Vaccinietea (LO-VA)	646	0.69	1	0.69
Koelerio-Corynepherea (KO-CO)	8033	1.02	0.67	0.68
Quercu-Fagetea (QU-FA)	32791	1.07	0.67	0.72
Betulo-Adenostyletea (BE-AT)	498	0.73	1	0.73
Artemisietea vulgaris (ART)	4591	1.13	0.67	0.76
Polygono-Poetea (PO-PO)	896	0.38	2	0.77
Festuco-Brometea (FE-BR)	7187	1.54	0.5	0.77
Asplenietea (ASP)	2651	0.39	2	0.78
Carici-Kobresietea	65	0.81	1	0.81
Calluno-Ulicetea (CA-UL)	7308	0.91	1	0.91
Caricetea curvulae (CAR)	363	1.39	0.67	0.93
Quercetea (QUE)	4770	0.93	1	0.93
Molinio-Arrhenatheretea (MO-AR)	33904	1.43	0.67	0.96
Trifolio-Geranietea (TRI-GER)	2445	1.44	0.67	0.97
Thlaspietea (THL)	1302	0.98	1	0.98
Saginetea (SAG)	466	0.53	2	1.05
Robinietea (ROB)	552	1.10	1	1.10
Salicetea herbaceae (SAL H)	103	1.16	1	1.16
Franguletea (FRA)	3098	0.63	2	1.27
Epilobietea (EPI)	755	1.31	1	1.31
Rhamno-Prunetea (RH-PR)	4711	0.97	2	1.94

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Appendix S1. Central European taxa where seeds are to a large part produced by apomixis.

Anhang S1. Mitteleuropäische Taxa, bei denen Samen zu einem großen Teil durch Apomixis produziert werden.

Appendix S2. Taxa with (1) only low amount of apomictic seed production or prove of apomixis unsecured, (2) non-functional apomixis, (3) evidence for apomixis outside Central or Northern Europe, (4) nonspecific or wrong record of apomixis, or (5) apomictic taxa, which only occur as casuals in Central Europe.

Anhang S2. Taxa mit (1) nur einem geringen Ausmaß apomiktischer Samenproduktion oder Apomixis unsicher, (2) nicht-funktionaler Apomixis, (3) Hinweise auf Apomixis außerhalb Mittel- oder Nordeuropas, (4) nichtspezifische oder falsche Angabe von Apomixis oder (5) apomiktische Taxa, die nur als Unbeständige in Mitteleuropa auftreten.

Appendix S3. Phytosociological data with short commentaries on geographical scope and data quality.

Anhang S3. Pflanzensoziologische Daten mit kurzen Kommentaren zum geographischen Rahmen und zur Datenqualität.

Appendix S4. Grades for ecological traits for **W** (Water), **Ca/Mg** (Calcium and Magnesium Content), **N** (Nutrients), **D** (Dynamics), **Hem** (Hemeroby), **St** (Stress), **Salt**, **Al** (Altitude), **Hei** (Height), and **An** (Annuals).

Anhang S4. Ränge ökologischer Merkmale für **W** (Wasser), **Ca/Mg** (Calcium- und Magnesiumgehalt), **N** (Nährstoffe), **D** (Dynamik), **Hem** (Hemerobie), **St** (Stress), **Salt** (Salz), **Al** (Meereshöhe), **Hei** (Vegetationshöhe), und **An** (Annuelle).

Appendix S5. Life cycle, life form, and ploidy level of apomictic taxa.

Anhang S5. Lebenszyklus, Lebensform und Ploidiegrad apomiktischer Taxa.

Literature

- ASKER, S. (1979): Progress in apomixis research. – *Hereditas* 91: 231–240.
- ASKER, S. & JERLING, L. (1992): Apomixis in plants. – CRC Press, Boca Raton: 298 pp.
- BAKER, H.G. (1966): The evolution, functioning and breakdown of heteromorphic incompatibility systems. I. The Plumbaginaceae. – *Evolution* 20: 349–368.
- BAYER, R.J., PURDY, B.G. & LEBEDYK, D.G. (1991): Niche differentiation among eight sexual species of *Antennaria* Gaertner (Asteraceae: Inulae) and *A. rosea*, their allopolyploid derivative. – *Evol. Trends Plants* 5: 109–123.
- BICKNELL, R.A., BORST, N.K. & KOLTUNOW, A.M. (2000): Monogenic inheritance of apomixis in two *Hieracium* species with distinct developmental mechanisms. – *Heredity* 84: 228–237.
- BIERZYCHUDEK, P. (1985): Patterns in plant parthenogenesis. – *Experientia* 41: 1255–1264.
- BROCHMANN, C., GABRIELSEN, T.V., NORDAL, I., LANDVIK, J.Y. & ELVEN, R. (2003): Glacial survival or tabula rasa? The history of North Atlantic biota revisited. – *Taxon* 52: 417–450.
- BUTTLER, K.P. & HAND, R. (2008): Liste der Gefäßpflanzen Deutschlands. – *Kochia Beiheft* 1: 1–107.
- CAMPBELL, C.S., GREENE, C.W. & DICKINSON, T.A. (1991): Reproductive Biology in subfam. Maloideae (Rosaceae). – *Syst. Bot.* 16: 333–349.
- CARMAN, J.G. (1997): Asynchronous expression of duplicate genes in angiosperms may cause apomixis, bispority, tetraspority, and polyembryony. – *Biol. J. Linn. Soc.* 61: 51–94.
- CHOCHLOV, S.S. (1967): Apomiksis: Klassifikacija i rasprostranenie i pokrytosemennyh rastenij (Apomixis: classification and distribution in angiospermous plants) [in Russian]. – *Uspechi sovremennoj genetiki* (Achievements of modern genetics) 1: 43–105.
- CHOCHLOV, S.S., ZAJCEVA, M.I. & KUTRIJANOV, P.G. (1978): Vyjavlenie apomiktichykh form vo flore cvetkovykh rastenij SSSR. Programma, metodika, rezul'taty (Revelation of the apomictic forms in the flora of the angiosperms of USSR. Programs, methods and results) [in Russian]. – Saratovskogo Universiteta, Saratov: 223 pp.
- CHYTRÝ, M. (2001): Phytosociological data give biased estimates of species richness. – *J. Veget. Sci.* 12: 439–444.
- CHYTRÝ, M. (Ed.) (2007): Vegetation of the Czech Republic. 1. Grassland and Heathland Vegetation. [in Czech, with English summary] – Academia, Praha: 526 pp.
- CHYTRÝ, M. (Ed.) (2009): Vegetation of the Czech Republic. 2. Ruderal, Weed, Rock and Scree vegetation. [in Czech, with English summary] – Academia, Praha: 520 pp.
- CHYTRÝ, M., KUČERA, T. & KOČÍ, M. (Eds.) (2001): Katalog biotopů České republiky (Catalogue of biotopes of the Czech Republic) [in Czech]. – Agentura ochrany přírody a krajiny ČR, Praha: 304 pp.
- CHYTRÝ, M. & RAFAJOVÁ, M. (2003): Czech National Phytosociological Database: basic statistics of the available vegetation-plot data. – *Preslia* 75: 1–15.
- DEN NIJS H.C.M., KIRSCHNER, J., ŠTĚPÁNEK, J. & VAN DER HULST, A. (1990): Distribution of diploid sexual plants of *Taraxacum* sect. *Ruderalia* in east-Central Europe, with special reference to Czechoslovakia. – *Plant Syst. Evol.* 170: 71–84.
- DEN NIJS, H.C.M. & STERK, A.A. (1980): Cytogeographical studies of *Taraxacum* sect. *Taraxacum* (= sect. *Vulgaria*) in Central Europe. – *Bot. Jahrb. Syst.* 101: 527–554.
- DEN NIJS, H.C.M. & STERK, A.A. (1984): Cytogeography of *Taraxacum* sectio *Taraxacum* and sectio *Alpestris* in France and adjacent parts of Italy and Switzerland, including some taxonomic remarks. – *Acta Bot. Neerl.* 33: 1–24.
- DEN NIJS, H.C.M. (1997): *Taraxacum*: ploidy levels, hybridization and speciation. The advantage and consequence of combining reproductive systems. – *Lagascalia* 19: 45–56.

- DICKINSON, T.A., LO, E. & TALENT, N. (2007): Polyploidy, reproductive biology, and Rosaceae: understanding evolution and making classifications. – *Plant Syst. Evol.* 266: 59–78.
- GADELLA, T.W.J. (1984): Cytology and the mode of reproduction of some taxa of *Hieracium* subgenus *Pilosella*. – *Proc. Kon. Ned. Akad. Wetensch. C* 87: 387–399.
- GADELLA, T.W.J. (1987): Sexual tetraploid and apomictic pentaploid populations of *Hieracium pilosella* (Compositae). – *Plant Syst. Evol.* 157: 219–245.
- GADELLA, T.W.J. (1991): Variation, hybridization and reproductive biology of *Hieracium pilosella* L. – *Proc. Kon. Ned. Akad. Wetensch. C* 94: 455–488.
- GRABHERR, G. & MUCINA, L. (1993): Die Pflanzengesellschaften Österreichs Teil II. – Ulmer, Jena: 523 pp.
- GRANT, V. (1981): *Plant speciation*. Ed. 2. – Columbia University Press, New York: XII + 563 pp.
- GUSTAFSSON, Å. (1946): Apomixis in higher plants. Part I. The mechanism of apomixis. – *Acta Univ. Lund* 42: 1–67.
- GUSTAFSSON, Å. (1947a): Apomixis in higher plants. Part II. The causal aspect of apomixis. – *Acta Univ. Lund* 43: 69–179.
- GUSTAFSSON, Å. (1947b): Apomixis in higher plants. Part III. Biotype and species formation. – *Acta Univ. Lund* 43: 181–370.
- HAAG, C.R. & EBERT, D. (2004): A new hypothesis to explain geographic parthenogenesis. – *Ann. Zool. Fenn.* 41: 539–544.
- HAGERUP, O. (1932): Über Polyploidie in Beziehung zu Klima, Ökologie und Phylogenie. Chromosomenzahlen aus Timbuktu. – *Hereditas* 16: 19–40.
- HOLM, S. (1995): Unexpected high levels of genetic variation in *Potentilla argentea* L. (s.l.) in southern Sweden. – *Hereditas* 123: 127–139.
- HOLM, S. & GHATNEKAR, L. (1996): Sexuality and no apomixis found in crossing experiments with diploid *Potentilla argentea*. – *Hereditas* 125: 77–82.
- HOLM, S., GHATNEKAR, L. & BENGTTSSON, B.O. (1997): Selfing and outcrossing but no apomixis in two natural populations of diploid *Potentilla argentea*. – *J. Evol. Biol.* 10: 343–352.
- HÖRANDL, E. (2006): The complex causality of geographical parthenogenesis. – *New Phytol.* 171: 525–538.
- HÖRANDL, E. (2008): Evolutionary implications of self-compatibility and reproductive fitness in the apomictic *Ranunculus auricomus* polyploid complex (Ranunculaceae). – *Int. J. Plant Sci.* 169: 1219–1228.
- HÖRANDL, E. (2009): Geographical parthenogenesis: Opportunities for asexuality. – In: SCHÖN, I., MARTENS, K. & DIJK, P. (Eds.): *Lost sex. The evolutionary biology of parthenogenesis*: 161–187. Springer, Heidelberg.
- HÖRANDL, E. (2010): Evolution and biogeography of alpine apomictic plants. – *Taxon* 60: 390–402.
- HÖRANDL, E., COSENDAL, A.-C. & TEMSCH, E.M. (2008): Understanding the geographic distributions of apomictic plants: a case of a pluralistic approach. – *Plant Ecol. Divers.* 1: 309–320.
- HÖRANDL, E., DOBEŠ, C., SUDA, J. VÍT, P., URFUS, T., TEMSCH, E.M., COSENDAL, A.-C., WAGNER, J. & LADINIG, U. (2011): Apomixis is not prevalent in subnival to nival plants of the European Alps. – *Ann. Bot. (Oxford)* 108: 381–390.
- HÖRANDL, E. & PAUN, O. (2007): Patterns and sources of genetic diversity in apomictic plants: implications for evolutionary potentials. – In: HÖRANDL, E., GROSSNIKLAUS, U., SHARBEL, T. & VAN DIJK, P. (Eds.): *Apomixis: Evolution, mechanism and perspectives*: 169–194. A.R.G. Gantner, Ruggel/Liechtenstein.
- HULTÉN, E. & FRIES, M. (1986): *Atlas of North European vascular plants north of the tropic of the Cancer*. Vol. I–III. – Koeltz, Königstein: (I) XVI + 498 pp., (II) XI + 499–968 pp., (III) 969–1172 pp.
- JENNISKENS, M.-J., DEN NIJS, H.C. M. & HUIZING, B.A. (1984): Karyogeography of *Taraxacum* sect. *Taraxacum* and the possible occurrence of facultative agamospermy in Bavaria and north-western Austria. – *Phyton* 24: 11–34.
- JERLING, L. (1986): Ecological aspects of agamospermy. – *Symb. Bot. Ups.* 27: 223–234.
- KIRSCHNER, J. & ŠTĚPÁNEK, J. (1998): *Monograph of Taraxacum sect. Palustria*. – Institute of Botany, Academy of Sciences of the Czech Republic, Průhonice: 281 pp.

- KNAPP, R. (1953): Über Zusammenhänge zwischen Polyploidie, Verbreitung, systematischer und soziologischer Stellung von Pflanzenarten in Mitteleuropa. – Z. Indukt. Abstammungs- Vererbungslehre 85: 163–179.
- KOLTUNOW, A.M. (1993): Apomixis: Embryo sacs and embryos formed without meiosis or fertilization in ovules. – Plant Cell 5: 1425–1437.
- KOLTUNOW, A.M. & GROSSNIKLAUS, U. (2003): Apomixis: a developmental perspective. – Annu. Rev. Plant Biol. 54: 547–574.
- KOPECKÝ, K. (1978): Die straßenbegleitenden Rasengesellschaften im Gebirge Orlické hory und seinem Vorlande. – Veg. ČSSR A10: 1–258, pl. 1–21.
- KOWARIK, I. (1988): Zum menschlichen Einfluß auf Flora und Vegetation. Theoretische Konzepte und ein Quantifizierungsansatz am Beispiel von Berlin (West). – Landschaftsentwickl. Umweltforsch. 56: 1–280.
- KRAHULCOVÁ, A. & KRAHULEC, F. (1999): Chromosome numbers and reproductive systems in selected representatives of *Hieracium* subgen. *Pilosella* in the Krkonoše Mts (the Sudeten Mts). – Preslia 71: 217–234.
- KRAHULCOVÁ, A., KRAHULEC, F. & CHAPMAN, H.M. (2000): Variation in *Hieracium* subgen. *Pilosella* (Asteraceae): What do we know about its sources? – Folia Geobot. Phytotax. 35: 319–338.
- KRAHULEC, F., KRAHULCOVÁ, A., FEHRER, J., BRÄUTIGAM, S., PLAČKOVÁ, I. & CHRTEK, J. jun. (2004): The Sudetic group of *Hieracium* subgen. *Pilosella* from the Krkonoše Mts: a synthetic view. – Preslia 76: 223–243.
- KRAHULCOVÁ, A. & ROTRKLIOVÁ, O. (2010): Use of flow cytometry in research on apomictic plants. – Preslia 82: 23–39.
- MARSHALL, D.R. & BROWN, A.H.D. (1981): The evolution of apomixis. – Heredity 47: 1–15.
- MARTIN, S.L. & HUSBAND, B.C. (2009): Influence of phylogeny and ploidy on species ranges of North American angiosperms. – J. Ecol. 97: 913–922.
- MASTERSON, J. (1994): Stomatal size in fossil plants: Evidence for polyploidy in majority of angiosperms. – Science 264: 421–424.
- MĚSÍČEK, J. & JAVŮRKOVÁ-JAROLÍMOVÁ, V. (1992): List of Chromosome Numbers of the Czech Vascular Plants. – Academia, Praha: 144 pp.
- MEUSEL, H. & JÄGER, E. (1992): Vergleichende Chorologie der zentraleuropäischen Flora 3. – Gustav Fischer, Jena: [Text] IX + 333 pp., [Karten] IX + 422–688 pp.
- MEUSEL, H., JÄGER, E. & WEINERT, E. (1965): Vergleichende Chorologie der zentraleuropäischen Flora. [1]. – Gustav Fischer, Jena: [Text] 583 pp., [Karten] 258 pp.
- MEUSEL, H., JÄGER, E. & WEINERT, E. (1978): Vergleichende Chorologie der zentraleuropäischen Flora 2. – Gustav Fischer, Jena: [Text] XI + 418 pp., [Karten] 259–421 pp.
- MOGIE, M. (1992): The evolution of asexual reproduction in plants. – Chapman & Hall, London: XIV + 276 pp.
- MRÁZ, P., CHRTEK, J. jun. & ŠINGLIAROVÁ, B. (2009): Geographical parthenogenesis, genome size variation and pollen production in the arctic-alpine species *Hieracium alpinum*. – Bot. Helv. 119: 41–51.
- MRÁZ, P., ŠINGLIAROVÁ, B., URFUS, T. & KRAHULEC, F. (2008): Cytogeography of *Pilosella officinarum* (Compositae): Altitudinal and Longitudinal differences in Ploidy Level Distribution in the Czech Republic and Slovakia and the General Pattern in Europe. – Ann. Bot. 101: 59–71.
- MUCINA, L., GRABHERR, G. & ELLMAUER, T. (1993a): Die Pflanzengesellschaften Österreichs Teil I. – Ulmer, Jena: 578 pp.
- MUCINA, L., GRABHERR, G. & ELLMAUER, T. (1993b): Die Pflanzengesellschaften Österreichs Teil III. – Ulmer, Jena: 353 pp.
- NOGLER, G.A. (1982): How to obtain diploid apomictic *Ranunculus auricomus* plants not found in the wild state. – Bot. Helvet. 92: 13–22.
- NOGLER, G.A. (1984): Gametophytic Apomixis. – In: JOHRI, B.M. (Ed.): Embryology of angiosperms: 476–518. Springer, Berlin.
- NOIROT, M., COUVET, D. & HAMON, S. (1997): Main role of self-pollination rate on reproductive allocations in pseudogamous apomicts. – Theor. Appl. Genet. 95: 479–483.
- NOYES, R.D. (2007): Apomixis in the Asteraceae: Diamonds in the Rough. – Funct. Plant Sci. Biotechn. 1: 207–222.

- NYBOM, H. (2007): Unique reproduction in dogroses (*Rosa* sect. *Caninae*) maintains successful and highly heterozygous genotypes. In: HÖRANDL, E., GROSSNIKLAUS, U., SHARBEL, T. & VAN DIJK, P.J. (Eds.): Apomixis: Evolution, mechanism and perspectives: 281–298. A.R.G. Gantner, Ruggel/Liechtenstein.
- NYGAARD, B. & LAWESSON, J. (1998): Systematics and ecology of Danish salt marsh communities. – *Ann. Bot.* 61: 53–72.
- NYGREN, A. (1954): Apomixis in the Angiosperms. II. – *Bot. Rev.* 20: 577–649.
- NYGREN, A. (1967): Apomixis in the angiosperms. – In: Ruhland, W. (Ed.): *Handbuch der Pflanzenphysiologie* 18. Sexualität Fortpflanzung Generationswechsel: 551–596. Springer, Berlin.
- OBERDORFER, E. (Ed.) (1977): *Süddeutsche Pflanzengesellschaften* 1. 2. Aufl. – G. Fischer, Stuttgart: 311 pp.
- OBERDORFER, E. (Ed.) (1978): *Süddeutsche Pflanzengesellschaften* 2. 2. Aufl. – G. Fischer, Stuttgart: 355 pp.
- OBERDORFER, E. (Ed.) (1983): *Süddeutsche Pflanzengesellschaften* 3. 2. Aufl. – G. Fischer, Stuttgart: 455 pp.
- OBERDORFER, E. (Ed.) (1992): *Süddeutsche Pflanzengesellschaften* 4. 2. Aufl. – G. Fischer, Jena: [Textband] 282 pp., [Tabellenband] 580 pp.
- OTTO, S.P. & WHITTON, J. (2000): Polyploid incidence and evolution. – *Annu. Rev. Genet.* 34: 401–437.
- PAULE, J. (2010): Evolutionary patterns and processes in the genus *Potentilla* L. (Rosaceae). – Dissertation Ruperto-Corola University of Heidelberg, Heidelberg: 146 pp.
- POGAN, E. & WCISLO, H. (1989): Cytological investigation on *Hieracium pilosella* L. from Poland. I. Karyological studies. – *Acta Biol. Cracov., Ser. Bot.* 31: 19–28.
- POGAN, E. & WCISLO, H. (1990): Chromosome numbers of Polish Angiosperms. – *Acta Biol. Cracov., Ser. Bot.* 32: 1–169.
- POGAN, E. & WCISLO, H. (1995): Embryological analysis of *Hieracium pilosella* L. from Poland. – *Acta Biol. Cracov., Ser. Bot.* 37: 53–61.
- POTT, R. (1995): *Die Pflanzengesellschaften Deutschlands*. 2. Aufl. – Ulmer, Stuttgart: 622 pp.
- RENNWALD, E. (2000): Verzeichnis und Rote Liste der Pflanzengesellschaften Deutschlands. – *Schriften. Vegetationskd.* 35: 89–800.
- RICHARDS, A.J. (1996): Breeding systems in flowering plants and the control of variability. – *Folia Geobot. Phytotax.* 31: 283–293.
- RICHARDS, A.J. (1997): *Plant breeding systems*. Ed. 2. – Chapman & Hall, London: XII + 529 pp.
- ROBSON, N.K.B. (2002): Studies in the genus *Hypericum* L. (Guttiferae) 4(2). Sektion 9. *Hypericum* sensu lato (part 2): subsection 1. *Hypericum* series 1. *Hypericum*. – *Bull. Nat. Hist. Mus. London, Bot.* 33: 61–123.
- ROETMAN, E., DEN NIJS, J.C.M. & STERK, A.A. (1988): Distribution and habitat range of diploid, sexual dandelions (*Taraxacum* section *Vulgaria*), a Central European flora element in The Netherlands. – *Acta Bot. Neerl.* 37: 81–94.
- ROTKLOVÁ, O., KRAHULCOVÁ, A., MRÁZ, P., MRÁZOVÁ, V., MÁRTONFIOVÁ, L., PECKERT, T. & ŠINGLIAROVÁ, B. (2005): Chromosome numbers and breeding systems of some European species of *Hieracium* subgen. *Pilosella*. – *Preslia* 77: 197–195.
- RUTISHAUSER, A. (1967): Fortpflanzungsmodus und Meiose apomiktischer Blütenpflanzen. – Springer, Wien: 245 pp.
- SCHAMINÉE, J.H.J., STORTELDER, A.H.F. & WESTHOFF, V. (1996): *De vegetatie van Nederland* 3. – Opulus, Uppsala: 356 pp.
- SCHAMINÉE, J.H.J., WEEDA, E.J. & WESTHOFF, V. (1995): *De vegetatie van Nederland* 2. – Opulus, Uppsala: 360 pp.
- SCHAMINÉE, J.H.J., WEEDA, E.J. & WESTHOFF, V. (1998): *De vegetatie van Nederland* 4. – Opulus, Uppsala: 346 pp.
- SCHUHWERK, F. (2004): Some Thoughts on the Taxonomy of *Hieracium*. – *Ber. Bayer. Bot. Ges.* 73/74: 193–198.
- STEBBINS, G.L. (1941): Apomixis in the angiosperms. – *Bot. Rev.* 7: 507–542.
- STEBBINS, G.L. (1950): *Variation and evolution in plants*. – Columbia University Press, New York: XIX + 643 pp.

- STEBBINS, G.L. (1984): Polyploidy and the distribution of the arctic-alpine flora: new evidence and a new approach. – *Bot. Helv.* 94: 1–13.
- STEBBINS, G.L. & DAWE, J.C. (1987): Polyploidy and distribution in the European flora: A reappraisal. – *Bot. Jahrb. Syst.* 108: 343–354.
- ŠTĚPÁNEK, J., KIRSCHNER, J., JAROLÍMOVÁ, V. & KIRSCHNEROVÁ, L. (2011): *Taraxacum nigricans*, *T. alpestre* and allies in the *Taraxacum* sect. *Alpestris*: taxonomy, geography and conservation status. – *Preslia* 83: 537–564.
- STERK, A.A. (1987): Paardebloemen. Planten zonder vader (Dandelions. Plants without a father.) [in Dutch]. – Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht: 348 pp.
- STORTELDER, A.H.F., SCHAMINÉE, J.H.J. & HOMMEL, P.W.F.M. (1999): De vegetatie van Nederland 5. – *Opulus*, Uppsala: 376 pp.
- SUKOPP, H. (1976): Dynamik und Konstanz in der Flora der Bundesrepublik Deutschland. – *Schriftenreihe Vegetationskd.* 10: 9–26.
- TISCHLER, G. (1935): Die Bedeutung der Polyploidie für die Verbreitung der Angiospermen, erläutert an den Arten Schleswig-Holsteins, mit Ausblicken auf andere Florengebiete. – *Bot. Jahrb. Syst.* 67: 1–36.
- TUTIN, T.G., HEYWOOD, V.H., BURGESS, N.A., CHATER, A.O. (Ed. 1–2), EDMONDSON, J.R. (Ed. 1–2), MOORE, D.M., VALENTINE, D.H., WALTERS, S.M. & WEBB, D.A. (1968–1993): *Flora Europaea* 2–5, 1 ed. 2. – Cambridge University Press, Cambridge: (1 ed. 2, 1993) XLVI + 581 pp., (2, 1968) XXVII + 469 pp., (3, 1972) XXIX + 370 pp., (4, 1984) XXIX + 505 pp., (5, 1980) XXXVI + 452 pp.
- UHLEMANN, I. (2001): Distribution of reproductive systems and taxonomical concepts in the genus *Taraxacum* F.H. Wigg. (Asteraceae, Lactuceae) in Germany. – *Feddes Repert.* 112: 15–35.
- VAN DIJK, P.J. (2007): Potential and realized costs of sex in dandelions, *Taraxacum officinale* s.l. – In: HÖRANDL, E., GROSSNIKLAUS, U., SHARBEL, T. & VAN DIJK, P. (Eds.): *Apomixis: Evolution, mechanism and perspectives*: 215–233. A.R.G. Gantner, Ruggel/Liechtenstein.
- VAN DIJK, P.J. & VIJVERBERG, K. (2005): The significance of apomixis in the evolution of the angiosperms: a reappraisal. – In: Bakker, F.T., Chatrou, L.W., Gravendeel, B. & Pelsner, P.B. (Eds.): *Plant Species-Level Systematics: New Perspectives on Pattern & Process*: 101–116. A.R.G. Gantner, Ruggel/Liechtenstein.
- VANDEL, A. (1928): La parthénogenèse géographique. Contribution à l'étude biologique et cytologique de la Parthénogenèse Naturelle. Première partie (The geographical parthenogenesis. Contribution to the biological and cytological study of the natural parthenogenesis. First part). [in French] – *Bull. Biol. France Belgique* 62: 164–281.
- VANDEL, A. (1940): La parthénogenèse géographique. IV. Polyploidie et distribution géographique (The geographical parthenogenesis. IV. Polyploidy and geographical distribution). [in French] – *Bull. Biol. France Belgique* 74: 94–100.
- WEBER, H.E. (1995): 4. *Rubus*. – In: Weber, H.E. (Ed.): *Gustav Hegi. Illustrierte Flora von Mitteleuropa* 4(2a). 3. Auf.: 284–587. Blackwell, Oxford.
- WINKLER, H. (1908): Über Parthenogenesis und Apogamie im Pflanzenreiche. – *Progr. Rei Bot.* 4: 293–454.