CONTENT *The genus* Rosa *comprises some 200 species and is traditionally divided into 11 sections. With approximately 30 taxa, the section* Caninae*, the dog roses, dominates in Europe. All* Caninae *are allopolyploids – most are pentaploids – and evolved by multiple hybridization. They are characterized by a unique heterogamous meiosis. The egg cell contains four chromosome sets, whereas the pollen grain bears only one. During fertilization, the original constitution is restored, while the offspring is of maternal character, retaining 80% of the maternal genome. As a result of maternal-driven character inheritance, radiation of offspring is usually found within the maternal evolutionary constraints. Following the radiation of* Rosa*, two main parasitic groups, rust fungi and insects, unfold their diversity. The radiation process and the development of biodiversity in the parasitic groups depend on the genetic constitution of their hosts. Intensive reticulation of hosts prevents formation of host-specific races in parasites.*

Beauty and the bastards

Intensive hybridization controls the evolution of wild roses

Volker Wissemann*
Institut für Spezielle Botanik, Universität Jena, Jena, Germany

• It is the queen of the flowers, but also the Janus face of botany: the rose may be esteemed for its sheer beauty, but its genetic complexity is dreaded by evolutionary biologists. Mankind has been fascinated by the fragrance, blossoms and colours of all sorts of roses since times of old. At the same time, botanists were attracted by the evolution and the bewildering diversity of roses. The dominating wild roses in Europe, the dog roses (also referred to as *Caninae*) are hallmarked by intensive hybridization, a specific heterogamous meiosis, non-concerted evolution of gene families, non-Mendelian, mainly maternal inheritance of characters and imprinted character states.

The genus *Rosa*, in particular the dog roses, are of enormous diversity (*Figure 1A*). What makes research on roses even more difficult is that the origin of the oldest known cultivated roses (cultivars) is still a secret. They probably arose naturally by hybridization between different species. These plants were then cultured, protected, propagated and later bred to form new roses. New phenotypes of roses usually arise by so-called »sports«, natural mutations leading to new colours, doubling of petals etc. In the early phase of »rose breeding« these sports were propagated, cultivated and placed on the market. Soon after sexuality in plants was verified, first attempts were made to breed new roses by artificial hybridization between different species.

Around 1920, classical genetic research was breaking fresh ground and the chromosomal botany, geneticists and evolutionary biologists began to investigate the genus *Rosa*. They mainly focused on wild species, such as the dog roses. The ultimate goal was to gain insight into why such a diversity of wild roses exists and to comprehend the natural relationships between the different species.

In the 1960s, research on evolution of wild roses declined, due to technical limitations. At that time, it was not possible to verify the early geneticists' and cytologists' hypotheses. Among these were the hypothesis of the hybrid origin of the dog roses and the hypotheses of apomictic reproduction, which proposed that European roses had evolved by multiple hybridization events and that they could reproduce by asexual seed formation without prior pollination.

In the 1990s, these somewhat outdated beliefs again became the focus of attention. They were examined using new molecular techniques such as sequencing of both nuclear and chloroplast markers, fingerprint analyses or microsatellite studies. As a baseline, molecular data consolidated the rose taxonomy(1,2), determined the genetic constitution of the allopolyploid section *Caninae*(3) and their phylogenetic position within the genus(1). We also gained new insight into the levels of interaction between roses and rust fungi(4) and between insects and roses(5). All in all, the results revealed that the evolution of dog roses is completely different from the rest of the genus *Rosa*. Driven by intensive hybridization, maternally dominated inheritance of characters and the lack of species-specific co-evolutionary patterns, dog roses provide a unique postglacial

---

* Correspondence to volker.wissemann@uni-jena.de

evolutionary scenario not known in any other plant group.

Biodiversity – natural and man-made

• Today the genus *Rosa* comprises some 200 species and is traditionally taxonomically divided into 11 sections*. In Europe, the section *Caninae* dominates with approximately 30 species. The dog roses are – from the taxonomist's point of view – one of the most difficult groups of wild plants in Europe.

In the wake of the botanical renaissance during the 16th century, the world of »rhodological« diversity was still very simple. In principle, four different groups of roses were recognized: wild species with single flowers growing naturally and tame species with doubled flowers, kept within the garden – both species were recorded as being either white or red. By the end of the 16th century, nature's own creativity had led to a total of 16 different roses recognized by scientists – as described in »The herbal or general history of plants« by John Gerard(6). The next century witnessed a decline in rose research. Typical for publications of that era, the florilegia – botanical books usually consisting of prints of flowers without text – showed more interest in representation rather than in scientific progress.

The first milestone of plant taxonomy and starting point for nomenclature, was Carolus Linnaeus' (Carl von Linné) work »Species Plantarum« in 1753. Linné claimed that »Rose species are difficult to distinguish, much more difficult to determine; for me nature seems to mix numerous species or to build just for fun multiples from a single species; for that all those which have seen a low number of species can distinguish rose species easier than those which have seen numerous species.«(7)

With this declarative statement, Linné pointed out a number of facts which still constitute the driving forces in evolutionary rose systematics: (i) roses are difficult to distinguish and therefore require a specialist's experience to attribute characters to species. Most characters are of great variability, rendering species delimitation and thus analysis of α-diversity (number of species) very complicated. (ii) Nature mixes species into new morphologically distinguishable species, in other words: intensive hybridization leads to more or less random distribution of chromosomes which becomes visible in the phenotype. Due to hybridization, a number of species share a considerable part of the same gene pool. This leads to overlapping character states (a character is e.g. the flower, a character state is the colour of this flower) among species, making delimitation of species even more difficult. (iii) Species determination is a tedious business, because a great deal of experience is required to understand the evolution of characters used for species delimitation.

In accordance with this, in 1762, Johann Herrman also made the observation that species are very difficult to determine. This was not only due to the lack of knowledge about suitable characters but also because man-made horticulture had already merged the species to such an extent that recognition of the »pure« species was no longer possible(8).

In the wake of Linné, who distinguished 12 rose species worldwide, botanists made every effort to take stock of the wild rose species(2) (*Figure 1B, Table 1*). By 1930, some 2000 names had been found for different taxonomic categories. This reflected the uncertainty about the genus rather than insight into the evolutionary history that had led to the diversity of recognizable forms. The different systems in use were personal preferences rather than observations

FIG. 1: Wild roses in Europe. (A) European wild roses – also referred to as dog roses or section Caninae *– are characterized by a great phenotypical variety. The picture shows the diversity of wild rose flowers. (B)* Rosa aciphylla *Rau. One of the numerous local forms in the early 19th century, today accepted as a morphotype from very hot sunny limestone soil, where leaves become small and brittle and flowers tend to be reduced in size.*

---

* *Taxonomists classify the diversity of life into categories, »taxonomic ranks«. These categories are nested. Thus within the large family* Rosaceae, *several smaller genera such as* Malus *(the apples),* Prunus *(the plums) or* Rosa *(the roses) exist. Within the genus* Rosa, *all roses are classified by morphology into different sections of which section* Caninae *comprises all dogroses. Within the section* Caninae *numerous species exist e.g.* R. canina *(the dog-rose),* R. rubiginosa *(the sweet briar) etc.*

in nature. In particular, the European-centred dog roses were prone to intensive splitting into new species, with only minor morphological differences between species. By 1886 the rhodologist Françios Crépin had castigated in one article the »buissonnomanie«. He accused the rhodologists of his time of giving a new name to each and every new rosebush they came across*(9)*. However, not all species within the genus *Rosa* faced the same problem.

The switch to an evolutionary understanding of the biological diversity of European wild roses began in 1873 by the Swiss rhodologist Hermann Christ, who applied a synthetic method of classification and reduced the European species to the number of 30. This synthetic classification applied combinations of correlated characters. Christ's approach circumscribed taxa, which are still recognized as natural groups and not artificial entities. However, recent molecular data clearly indicate that certain groups have to be revised.

Botanist	**Year**	**Proposed number of species**
Forsyth	1794	28 species
Laicharding	1794	31 species
Willdenow	1811	34 species
Smith	1819	57 species
Trattinnick	1824	24 series >200 species
Seringe	1825	146 species
Lindley	1830	101 species ~ 300 synonyms
Reichenbach	1832	77 species ~ 200 synonyms
Döll	1855	114 species ~ 200 synonyms
Déséglise	1877	15 sections section Caninae: 329 species

TAB. 1: *Numbers of proposed botanical names for the genus* Rosa *through the centuries, reflecting both the increase of knowledge and the uncertainty as to how to categorize rose biodiversity.*

Maternal success

• In the early 20th century, the Swedish botanist and cytologist Gunnar Täckholm investigated the chromosomal setup of the genus *Rosa*, and a number of botanists from northern Europe soon followed suit. Täckholm discovered that the dominant roses in Central Europe, the dog roses, have a very peculiar mode of meiosis to form pollen and egg cells. He also noticed that dog roses were polyploids, meaning that they harbour more than the normal diploid set of chromosomes*(10)*. They are in fact pentaploid and usually contain five sets of chromosomes, making it impossible to split them equally into male and female sex cells.

Täckholm discovered that dog roses had »invented« a unique meiotic system to overcome the genetic burden of five chromosome sets*(11)*. Only two chromosome sets pair during meiosis, while three sets remain univalent and do not interact in meiosis. The fate of these univalent chromosome pairs is different during gamete formation. In the pollen grain, only the pairing set is kept, whereas the univalent sets seem to be eliminated. In the egg cell, one of the bivalent sets and all univalent sets are saved. The roses are heterogamous; they form gametes differing in chromosome numbers. While the egg cell retains four chromosome sets from the pentaploid genome, the pollen grain, which is haploid, harbours only one set. The original pentaploid constitution is restored by fusion of gametes. Offspring tends to have a greater similarity with the plant providing the egg cell, the »mother plant«, since it provides 80% of the genome – four of the five chromosome sets.

This discovery led Täckholm and later researchers to pose four main questions that will be discussed in the following chapters. (i) What causes the evolution of such a remarkable meiotic system? (ii) What effect does this heterogamy have on the sexual reproduction of this group? Is it still a functional system with normal sexual reproduction – albeit asymmetrically distorted – or do roses of the section *Caninae* reproduce by apomixis, seed formation without fertilization? (iii) What impact does heterogamous pentaploid reproduction have on character evolution and ecological niche differentiation? (iv): How does this specific mode of evolution in dog roses translate into interacting biodiversity, e.g. insects or phytopathogenic fungi?

Hybridization and the origin of European wild roses

• The immediate hypothesized explanation for the cause of the heterogamous meiosis was hybridization. Hybridization is defined as the cross breeding of plants which were generated by parents belonging to different species or subspecies etc.*(12)*. The scientific dispute relating to hybridization is much more recent than the discussion on sexuality in plants in general. It began around the middle of the 18th century. Up to the mid-19th century, the discussion focussed on the existence of hybrids in general, to gain an insight into the origin of biological diversity.

Since Darwin's Theory of Evolution (1859), one of the central questions was the importance of hybridization for the evolution of plants. Today, hybridization is accepted and understood as a major evolutionary factor in plants. Täckholm and colleagues argued that dog roses accumulated chromosome sets by multiple hybridization. In the 1920s, they observed that some chromosomal sets were divergent from each other. This led to the conclusion that these sets were just retained via egg-cell formation but did not participate in the active meiotic process.

Some 75 years later, we found molecular evidence for a hybridogenic constitution, the so-called allopolyploidy, of the dog roses. In 1999, we performed DNA-sequence analysis of the nuclear internal transcribed spacer nrITS(13). Normally all copies of nrITS within an organism are identical. Divergent copies are converted in a process called »concerted evolution«, which is known for a number of gene families. We demonstrated that this process is missing in dog roses. They thus maintain different copies of nrITS via »non-concerted evolution«(14). Since the diversity of nrITS is retained, its analysis enables us to identify the parents' source. Accordingly, we were able to show that in individual roses, these ITS-types were different, corresponding to the hybridization hypothesis. Six years later, a detailed analysis of the ITS-sequences proved that the dog roses were in fact of allopolyploid origin(15), as Gunnar Täckholm had postulated.

Seed formation: platonic love or bastards?

• After 1908, more and more of the evidence published, suggested a sexual reproduction of dog roses, meaning that seed formation required a fertile egg cell and a fertile pollen grain(16). However, experiments under controlled conditions were lacking. Thus, having detected the *Canina* meiosis, Täckholm stated that this system could not work as a functional meiosis. He postulated apomixis, the seed formation or somatic embryogenesis without fertilization, as a preferred, if not exclusive, mode of reproduction in dog roses.

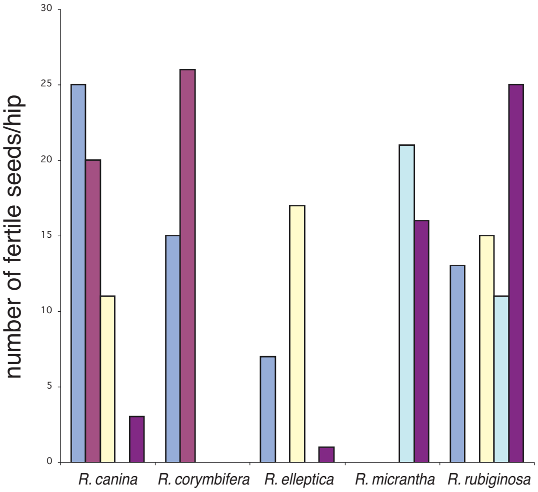

FIG. 2: Artificial crossings between species lead to differences in seed fertility. Increasing phylogenetic relationship causes an increase in investment (number of fertile seeds per hip). Note that pollination within species produces the highest number of seeds, whereas pollination between species reduces the number of fertile seeds depending on relatedness. (■: R. canina; ■: R. corymbifera; ■: R. elleptica; ■: R. micrantha; ■: R. rubiginosa)

Until the mid-1990s, artificial crossing experiments failed to clarify the dispute. However, between 1995(17) and 1997(18), we could clarify the situation (*Figure 2*). After 850 crossing experiments with more than 10,000 seeds, we could be certain that dog roses reproduce sexually. We also showed that apomictic reproduction is present, but is considerably less prevalent than outcrossing. Normal obligate outbreeding led to a seed set (number of seeds per hip) of 100%. By contrast, only 5% of the seed set was observed in crossing experiments which applied apomixis. Furthermore, dog roses were also shown to reproduce by autogamy (self-fertilization). This explains why, at a late stage of the flower period, anthers start to arch over their own pistil and disperse their own pollen on their own stigma to ensure that all egg cells are fertilized.

At this stage, the idea of platonic love declined. Instead, another question emerged: what happened to bastards formed by hybridization between different species of the hybrids? The assessment of plants regrown from the artificial crossing provided two results(20): (i) extensive hybridization between species is possible without a decline in ecological fitness or selection against hybrids; and (ii), remembering the maternally-dominated *Canina* meiosis, the offspring generated by reciprocal crossings is different. In a crossing of *R. rubiginosa* (seed parent) with *R. canina* (pollen parent) offspring did not look the same as the reciprocal crossing with the same individuals *R. canina* (seed parent) and *R. rubiginosa* (pollen parent), owed to maternal genetic contribution of 80%.

Evolution of character diversity

• The pentaploid constitution and maternally dominated reproduction has a great influence on the evolution of character diversity in dog roses. Thus, according to our text-book understanding of evolution based on Mendelian inheritance, dog roses are a model for evolutionary studies, pushing all concepts and theories to their limit. It is what the early botanists called the *»crux et scandalum botanicorum«* (botanist's cross and embarrassment). As far as we know now, in dog roses, the evolution of characters takes at least two pathways: sex-related inheritance and dominance. What is still missing, perhaps due to the 4/5 maternal contribution, is intermediate character inheritance. Most of the characters investigated are inherited in a maternally sex-related way. They include morphological traits such as glands, hairs, serration of the leaves and epicuticular waxes. Scent, as yet unpublished, is also transmitted maternally. On a molecular level, maternal inheritance was detected by microsatellite analysis and other fingerprint techniques(21).

To our great surprise, we also found characters that are inherited in an obligate paternally sex-related way, due to genomic imprinting. Examples are the diameter of the orifice in the hip and the persistence of sepals at hip ripening. Inheritance by epigenetic processes like genomic imprinting was described for genes involved in endosperm formation(22) – with the exception of the *MEDEA* gene in *Arabidopsis thaliana*. Since *Rosaceae* have no endoperm in their seeds, the diameter of the orifice in the hip and the performance of sepals at hip ripening are candidates for an additional non-endosperm related example for transmission by imprinting (*Figure 3*). There is no obvious reason why these rather unrelated characters should be controlled by imprinting. We currently assume that these characters are linked with other, hitherto unknown, characters which are targets for imprinting.

Our results might also influence the taxonomical studies in dog roses. Traditionally, the diameter of the orifice and the persistence of sepals are of importance for denomination of

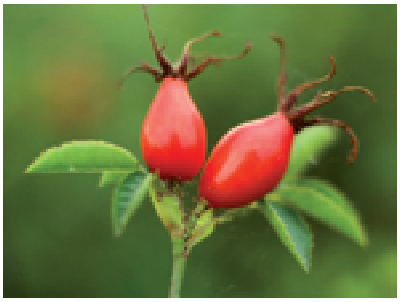

FIG. 3: Rosa rubiginosa *L., the Sweet briar. A glandular intensive scenting species with pronounced sepals which are erect at hip ripening.*

species. However, with the new knowledge of being imprinted, these characters are no longer reliable candidates for taxonomical studies.

Only recently, we identified a character which is dominantly expressed(23). We investigated the inheritance of growth form and mechanical characters in reciprocal polyploid hybrids of dog roses. The goal was to understand selection against or for hybrid offspring, to predict establishment of hybrids in different ecological niches as well as the adaptive radiation process.

By analysing bending patterns of young and old shoots, we tested the ability of roses to climb and therefore exploit new niches. In dog roses, two main growth types exist, an erect, dense type (D-type) and a lax growing, loose type (L-type). Interestingly enough, in crossing experiments, reciprocal hybrids of the F1-generation did not follow the sex-related line of character inheritance, but dominantly expressed the L-type. If in the next generation – which we will be able to examine in six years' time – the growth type splits into L- and D-types, it would be the first character ever found in dog roses to be transmitted according to the Mendelian laws.

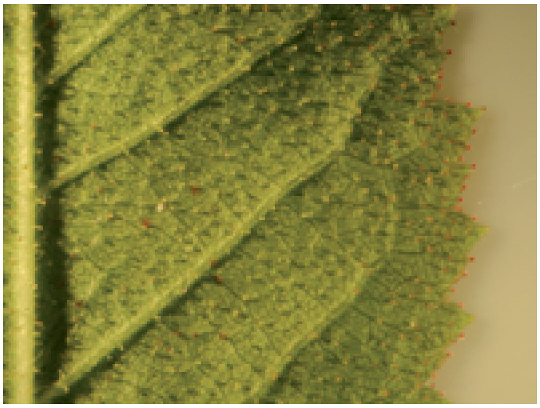

FIG. 4: Rosa rubiginosa *L., Underneath the leaf are numerous glands containing sesquiterpenoid-rich oil. These sesquiterpenoids presumably defend the plant against parasitic rust fungi.*

Meanwhile it is important to assess whether »growth« is indeed a character and not a syndrome of multiple interacting characters influenced by the environment. At present, we investigate the wood anatomy in detail to understand the role that each single anatomical part plays for the character »growth«.

Translating rose biodiversity into parasite evolution

• Apart from its influence in character diversity, the dog roses' heterogamous meiosis and the resulting diversity also has an effect on co-evolution of parasites. No organism lives in complete isolation. Thus the interactions between organisms and their biological as well as non-biological environment determine patterns and processes in ecosystems. A plant's ability to interact with this environment depends on its genetic ability to cope with the situation. The pronounced genetic mechanism and evolution in dog roses ultimately raises the question if and how rose evolution translates into evolutionary patterns of interacting organisms.

Our current aim is to ascertain how interactions between species influence the dynamics of evolutionary processes and enable radiation and unfolding of biological diversity in roses. The most important question in the interacting system of roses, fungi and insects is, how the radiation and diversity of the hosts translates into the radiation and diversity of the insect parasites and plant-fungus-insect interactions.

In this system, organisms that are hardly related to each other are connected in various and very complex, direct and indirect interactions. This »real-world complexity« has only recently been acknowledged by ecologists and evolutionary biologists. The focus in ecology and evolution is now changing from the traditional study of simple communities and interactions to approaches that consider the effects of multiple levels of trophism for the distribution and abundance of populations. The approaches include analyses of the genetic constitution, distance and phylogenetic relationships between rose species as well as their ability to create biodiversity via intensive hybridization.

Analysis of the dog roses' radiation process and the unfolding of biological diversity in this group gives insight into the level of co-evolution, co-specification and interaction of rust fungi and insects. For dog roses, the following hypothesis was formulated(24): in the last postglacial period – following a single event into which the peculiar mode of *Canina* meiosis developed – this group of roses managed to take Central Europe by storm on account of a very fast and explosive radiation process. Its genetic variability, together with polyploidy and great homology between genomic parts, as well as the ability to hybridize and maternal-driven character inheritance, is more than one reason for the morphological variation. It explains numerous local forms and phenotypic plasticity. Subsequent to the radiation of *Rosa*, numerous pathogens interacted with their hosts.

At present, both fungi and insects are found on all species within the genus *Rosa*. However, little is known about the evolutionary process of the two main and commercially important rust fungi on roses: *Phragmidium mucronatum* and *P. tuberculatum*. We sequenced a number of accessions of parasitic rose rust fungi and plotted the phylogenetic tree of these fungi on the tree of wild roses. Preliminary results(4) provided clear evidence that an antagonistic parasitism of the two rust species is not host-specific at species level, but may be at the level of the sections in the genus *Rosa*.

We also collected insect samples from rose bushes throughout Europe with a focus on hip-parasitizing insects and gall-forming insects. We counted infection rates per plant and analysed genetic diversity within populations by genetic fingerprints. Preliminary results on rose-insect interactions(5) showed that densities of the fungus, the hip-inhabiting tephritid fly *Rhagoletis alternata* and the gall-inducing cynipid wasp *Diplolepis rosae* changed with the geographic gradient in a species-specific way. Further, feeding experiments, in which a generalist caterpillar was given the choice of feeding on different rose species, revealed clear preferences in consumption, depending on the *Rosa* species or hybrid presented (Klinge, K *et al.*, unpublished data).

We still have little information on how a systemic rust infection may influence herbivore distribution, e.g. in *Diplolepis* rose galls. First results (Klinge, K *et al.*, unpublished data) from the interaction studies showed that the attack rate of the gall wasp was highest with the glandular host *Rosa rubiginosa*. Rust infection showed a preference for the non-glandular *R. canina*, which might be explained by the high degree of sesquiterpenoids in *R. rubiginosa* (*Figure 4*), known to interact in fungus defence (Degenhardt, J & Wissemann, V, unpublished data). These results contrasted with a more homogeneous distribution of hip-inhabiting tephritid fly *R. alternata*, indicating a non-specific interaction with roses. Further data are required and should be available by the end of 2007.

All in all, more than in any other reproduction system, the dog roses' specific meiosis allows for a diversification and radiation process controlled by maternal evolutionary constraints. The *Canina* meiosis directly translates the genetic constitution of the rose into the interaction process. But at the same time, intensive hybridization between species does prevent species specific coevolution of hosts and parasites in dog roses.

Acknowledgements

• Radiation, biological diversity and host-parasite interactions in wild roses, rust fungi and insects is a Priority programme (Spp 1127) funded project by the Deutsche Forschungsgemeinschaft (DFG) of a network of scientists from the Universities of Jena: V. Wissemann (Systematic Botany), G. Theissen (Genetics), Marburg: R. Brandl (Ecology, Zoology), Göttingen: T. Tscharntke (Agroecology) and Tübingen: F. Oberwinkler (Mycology).

References

1. *Wissemann, V, Ritz, CM* (2005) The genus Rosa (Rosoideae, Rosaceae) revisited: molecular analysis of nrITS-1 and *atp*B-*rbc*L intergenic spacer (IGS) versus conventional taxonomy. ***Bot. J. Linn. Soc. 147, 275–290***
2. *Wissemann, V* (2003) Conventional taxonomy of wild roses. In: Roberts, A, Debener, T, Gudin, S (eds.) Encyclopedia of Rose Science. ***London, UK: Elsevier, 111–117***
3. *Ritz, CM, Schmuths, H, Wissemann, V* (2005) Evolution by reticulation: European dogroses originated by multiple hybridization across the genus Rosa. ***J. Heredity 96, 4–14***
4. *Ritz, CM, Maier, W, Oberwinkler, F, Wissemann, V* (2005) Different evolutionary histories of two Phragmidium species infecting the same dog rose hosts (Rosa L. sect. Caninae (DC.) Ser.). ***Mycol. Res. 109, 603–609***
5. *Vaupel, A, Klinge, K, Brändle, M, Wissemann, V, Tscharntke, T, Brandl, R* (2006) Genetic differentiation between populations of the European rose hip fly Rhagoletis alternata (Diptera: Tephritidae). ***Biol. J. Linn. Soc. (In press)***
6. *Gerard, J* (1633) The herbal or general history of plants. ***London***
7. *Linnaeus, C* (1753) Species plantarum. ***Holmiae, 1, 491–492***
8. *Herrmann, J* (1762) Dissertatio inauguralis botanico-medica de Rosa. ***PhD-Thesis, Straßburg: Officina J.H. Heitz***
9. *Crépin, F* (1886) Le rôle de la buissonnomanie dans la genre Rosa. ***Bull. Soc. Roy. Bot. Belgique. 25, 53–61***
10. *Täckholm, G* (1920): On the cytology of the genus Rosa. A preliminary note. ***Svensk Bot. Tidskr. 14, 300–311***
11. *Täckholm, G* (1922): Zytologische Studien über die Gattung Rosa. ***Acta Horti Berg. 7, 97–381***
12. *Wagenitz, G* (2003) Wörterbuch der Botanik. ***Heidelberg, Berlin, Germany: Spektrum Akademischer Verlag, 150***
13. *Wissemann, V* (1999) Genetic constitution of Rosa sect. Caninae (R. canina, R. jundzillii) and sect. Gallicanae (R. gallica). ***Angew. Bot. 73, 191–196***
14. *Wissemann, V* (2003) Hybridization and the evolution of the nrITS spacer region. In: Sharma, AK, Sharma, A (eds.): Plant Genome, Biodiversity and Evolution Vol.1. Part A. ***Enfield, New Hampshire: Science Publishers, Inc. 57–71***
15. *Ritz, CM, Schmuths, H, Wissemann, V* (2005) Evolution by reticulation: European dogroses originated by multiple hybridization across the genus Rosa. ***J. Heredity 96, 4–14***
16. *Wissemann, V* (2002) Molecular evidence for allopolyploid origin of the Rosa canina – complex (Rosaceae, Rosoideae). ***J. Appl. Bot. 76, 176–178***
17. *Dingler, H* (1908) Neuere Beobachtungen in der Gattung Rosa. ***Bot. Jahrbücher 4, 100–108***
18. *Wissemann, V* (1995) Kreuzungsverhalten und Merkmalsvariation an ausgewählten Wildrosenpopulationen der Sektion Caninae (Ser.) Rehd. in Südniedersachsen. ***Diplomarbeit, Georg-August-Universität Göttingen***
19. *Wissemann, V, Hellwig, FH* (1997) Reproduction and Hybridisation in the Genus Rosa, Section Caninae (Ser.) Rehd. ***Bot. Acta 110, 251–256***
20. *Ritz, CM, Wissemann, V* (2003) Male correlated non-matroclinal character inheritance in reciprocal hybrids of Rosa, section Caninae (DC) Ser. (Rosaceae). ***Pl. Syst. Evol. 241, 213–221***
21. *Wissemann, V, Ritz, C* (2006) Evolutionary patterns and processes in the genus Rosa (Rosaceae) and their implications for host-parasite co-evolution. ***Pl. Syst Evol. (In press)***
22. *Alleman A, Doctor, J* (2000) Genomic imprinting in plants: observations and evolutionary implication. ***Pl. Mol. Biol. 43, 147–161***
23. *Wissemann, V, Gallenmüller, F, Ritz, C, Steinbrecher, T, Speck, T* (2006) Inheritance of growth form and mechanical characters in reciprocal polyploid hybrids of Rosa sect. Caninae – implications for the ecological niche differentiation and radiation process of hybrid offspring. ***Trees – Structure and Function 20, 340–347***
24. *Zielinski, J* (1985) Studia nad rodzajem Rosa L. - Systematyka sekcji Caninae DC. em Christ. ***Arboretum Kórnickie. Polska Akademia Nauk. Instytut Dendrologii. Panstwowe wydawnictwo Naukowe. Warszawa & Poznan 1986. Rocznik XXX, 3–109***