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Two American *Sarracenia* Species as Neophyta in Central Europe

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With 4 Figures

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Summary

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The North American carnivorous pitcher plants *Sarracenia flava* L. and *S. purpurea* L. (*Sarraceniaceae*) are frequently introduced to European fens. This study reviews the recent distribution of *Sarracenia purpurea* in Central Europe, including sites in France, Switzerland, Germany, Austria, the Czech Republic and Denmark. Establishment is almost exclusively successful in foothill areas, e. g., at the borders of the Alps or the Bohemian Massif. Invasive tendencies are only observed in Western Switzerland. *S. flava* is restricted to isolated sites in France.

In this study, specimens of *S. flava* and *S. purpurea* were bedded out experimentally in two fens in Austria for two growing seasons. Most plants survived; *S. flava* produced flowers in the second year. The higher vitality of this species may predict increased immigration in Central Europe in the future. Both species were successfully trapping prey, mainly Coleoptera, Hymenoptera and Diptera. In *S. purpurea* trapping was partly inhibited by low precipitations. In all traps, phytotelm communities formed spontaneously, including bacteria (up to $6{\cdot}10^9$ cultivable units/ml), Dipteran larvae and Acari. The inquilines seem to be involved in prey degradation such as at the natural site.

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Zusammenfassung

ADLASSNIG W., MAYER E., PEROUTKA M., POIS W. & LICHTSCHEIDL I. K. 2010. Two American *Sarracenia* species as neophyta in Central Europe. [Zwei nordamerikanische *Sarracenia*-Arten als Neophyten in Mitteleuropa]. – Phyton (Horn, Austria) 49 (2): 279–292, mit 4 Abbildungen.

Die karnivoren Kesselfallenpflanzen *Sarracenia flava* L. und *S. purpurea* L. (*Sarraceniaceae*) stammen aus Nordamerika, werden aber oft in europäischen Mooren ausgepflanzt (angesalbt). Diese Studie gibt einen Überblick über die momentane Verbreitung von *S. purpurea* in Mitteleuropa. Diese umfaßt Standorte in Frankreich, Deutschland, Österreich, der Schweiz, Tschechien und Dänemark. Die Einbürgerung ist fast ausschließlich am Fuß größerer Gebirge erfolgreich, wie der Alpen oder der Böhmischen Masse. Invasive Tendenzen wurden nur in der westlichen Schweiz beschrieben. *S. flava* ist zur Zeit auf einzelne Standorte in Frankreich beschränkt.

Versuchspflanzen beider Arten wurden für zwei Vegetationsperioden in zwei Mooren im Waldviertel/Niederösterreich ausgesetzt. Die meisten Pflanzen überlebten die gesamte Versuchszeit; *S. flava* setzte sogar Blüten an. Die höhere Vitalität von *S. flava* läßt für die Zukunft eine verstärkte Einbürgerung befürchten. Beide Arten fingen erfolgreich Beutetiere, vor allem Käfer, Hautflüger und Zweiflügler; bei *S. purpurea* wurde der Beutefang jedoch durch zu geringe Niederschläge behindert. In den Fallen bildeten sich spontan Phytotelm-Gesellschaften, bestehend aus Bakterien (bis zu $6{\cdot}10^9$ Kultivierbare Einheiten/ml), Dipteren-Larven und Milben. Es ist zu vermuten, daß die Fallenbewohner wie am Naturstandort zum Abbau der Beute beitrugen.

1. Introduction

Sarraceniaceae are a family of carnivorous pitcher plants from North and South America. Asian members of the family are only known from fossil records (LI 2005). Two of the recent genera are restricted to small areas in California and Oregon (*Darlingtonia californica* TORR.) and northern South America (*Heliamphora* BENTHAM div. spec.). The third genus, *Sarracenia* L., is widespread in eastern North America from the Gulf of Mexico to Labrador (BARTHLOTT & al. 2004), inhabiting a great variety of peat bogs, fens, swamps and springheads (SLACK 2000).

The pitcher of *Sarracenia* consists of a peltate, cone-shaped leaf (Fig. 1). The escape of prey falling into the trap is impeded by fluid in the pitcher bottom and downward pointing hairs. After drowning, the soft tissues of the animals are dissolved and taken into the plant through the porous cuticle of the pitcher wall (CLARK & LEEGOOD 2004, JUNIPER & al. 1989).

All species of *Sarracenia* are suitable for cultivation (D'AMATO 1998, ROMANOWSKI 2002), and numerous cultivars and hybrids have been produced by carnivorous plant enthusiasts all over the world (e.g., COOK 2004, HUMMER 2002 and many others). Most species of *Sarracenia* survive the winter in Western and Central Europe, therefore some plants are grown outdoors (BRAEM 2002). Many garden plants have the tendency to escape

Fig. 1. *Sarracenia purpurea*, growing in the Leckermoos in Lower Austria.

into natural habitats. Furthermore, carnivorous plant enthusiasts tried and still try to „enrich" the European flora by bedding out *Sarracenia* plants in European bogs.

This study evaluates the recent distribution of *Sarracenia* in Central Europe. Furthermore, we investigate growth, trapping activity and prey selection of *Sarracenia* plants cultivated temporarily in two Austrian bogs. The results are compared with the behaviour on primary sites in North America.

2. Material and Methods

The recent distribution of *Sarracenia* was reviewed using the current scientific literature as well as popular publications and personal contacts to breeders of carnivorous plants. For our experiments, we choose two of the most widespread and most generalist species of *Sarracenia*, i. e., *S. flava* L. and *S. purpurea* L. subsp. *heterophylla* Eaton. The test plants were grown in the greenhouses of the Faculty Centre for Ecology of the University of Vienna. The plants were bedded out for one and a half years in two peat bogs in Waldviertel, Lower Austria.

The first experimental site is „Schwarzes Moos" („Black Fen", no. 69090401 in the Austrian Fen Conservation Catalogue; Steiner 1992) next to the village Brand. It is an acid, mesotrophic ombrogenic fen (Steiner 1992) only partly preserved today. The second site is the fen „Gemeindeau" („Village Meadow", no. 69100302, Steiner 1992) next to the city of Heidenreichstein. This fen is also acidic and mesotrophic and has its origin in the aggradation of a lake (Steiner 1992). For a detailed description of flora and vegetation of both sites, compare Pranjić & al. 2006 and Steiner 1985.

Two specimens of *S. purpurea* and five specimens of *S. flava* were explanted in each bog in April 2004. In Schwarzes Moos, the plants were set out in a very wet cushion of *Sphagnum fallax* in an area of relatively intact fen vegetation between a bog and a *Pinus sylvestris* forest. In Gemeindeau, the plants were planted in the open fen. The surrounding vegetation consisted of *Sphagnum fallax, Drosera rotundifolia, Andromeda polifolia, Eriophorum latifolium* and *Carex echinata*.

Analysis of the plants took place once a month during the growing season from April 2004 to August 2005. After finishing of the experiments, all parts of the plants, including the underground rhizomes, were carefully removed. To avoid dispersal by seeds, plants were only bedded out after cutting off the inflorescence; flowers produced in 2005 were removed as well.

We examined the number and size of traps; monthly, one trap from each plant was removed. We determined the volume of pitcher fluid and the animal species trapped inside the pitcher. Bacteria inhabiting the trap were quantified by inoculation of pitcher fluid on Plate Count Agar (Merck 1.05463).

3. Recent Distribution of *Sarracenia* in Central Europe

The introduction of *Sarracenia* to Europe dates back about 100 years (COUVENBERG & JOOSTEN 2004). A rough survey of its recent distribution is given by the EU project DAISIE 2008. Concerning the British Isles, where *Sarracenia* proved to be most successful, detailed information is available: The first populations explanted in the late 19th century died out after some decades; today's populations go back to 1906 or 1907 (BUTCHER 1961, COUVENBERG & JOOSTEN 2004). Although *S. purpurea* is a poor competitor on its natural sites, it developed into a strong invader in Irish bogs, where it may form more than 50% of the vegetation; native communities may be driven out (COUVENBERG & JOOSTEN 2004, FOSS & O'CONNEL 1984).

Information concerning the established plants or populations in Central Europe is highly fragmented. As introduction of alien plant species is against the law in most countries, virtually no information is available on introduction events. The majority of data presented here comes from personal contacts. Fig. 2 shows the recent distribution of *Sarracenia* in Central Europe.

In France, *Sarracenia purpurea* is established in the Elsass (Alsace; pers. comm. M.-S. SAMAIN), Franche-Comté (Frasne; pers. comm. F. MULLER and S. FILOCHE) and in Haute-Savoie (AESCHIMANN & al. 2004; pers. comm. J. FLIŠEK). Flowering populations of *S. flava* are also found in Haute-Savoie (pers. comm. J. FLIŠEK). In L'étang du Grand Lemps, populations of *S. purpurea* and *S. flava* have been bedded out (pers. comm. P. NAMOUR). The population of *S. purpurea* is vigorously growing and pro-

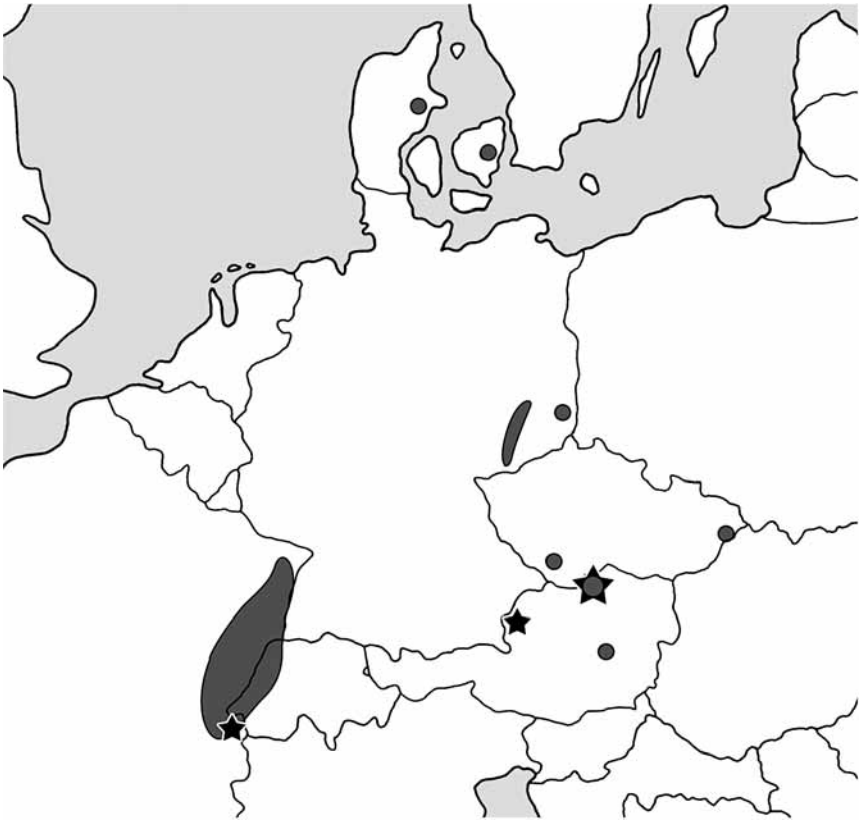

Fig. 2. Occurrence of *Sarracenia* in Central Europe; grey dots and areas indicate *S. purpurea*, asterices *S. flava*. The map includes sites where the plants were probably removed after successful establishment.

pagates asexually. The *S. flava* explants are too young for definite conclusions.

In Germany, *Sarracenia purpurea* seems to be established today in Bavaria, e. g. in Franken (MARABINI 1994) and the Bayerische Wald (FÜRSCH 2001). In Saxony, also several sites are known; in the Teufesmoor next to Wittichenau, *S. purpurea* is established since the 1970ies (JOHN & SCHNABEL 2005). Other Saxon populations are known from Bernsdorf (pers. comm. B. M. MÖSLER) and Hoyerswerda (pers. comm. H. SUKOPP). In Brandenburg, BERGEL 1991 carried out a series of explantation experiments with *S. purpurea* since 1964. In an unnamed subatlantic bog in the Lausitz, plants grew from seedlings up to a diameter of 60 cm and flowered within two years after bedding out; sexual reproduction is successful. In another fen in the Erzgebirge (about 700 m above sealevel) with a cooler

climate, first flowering occurred only after 15 years. BERGEL also bedded out *Darlingtonia californica (Sarraceniaceae)* in the Lausitz site which survived for several years in the peripheral part of the fen. In the central parts of the bog, the plants died of rotten roots.

No evidence could be found that *Sarracenia* ever established successfully in the Netherlands, Luxembourg or in Belgium. In outdoor cultivation, at least *S. rubra* was shown to survive and flower in the Dutch climate (pers. comm. R. VAN DER MEIJDEN).

In Denmark, *Sarracenia purpurea* was found flowering in a bog in Gammel Rye (next to Århus/Midtjylland; ANDERSSON 2004) and in Bagholt Mose (Årløse/Sjælland; pers. comm. H. HEIDE-JØRGENSEN). K. DAMSHOLT (pers. comm.) tried to establish *S. purpurea* in many Danish and Swedish bogs from seeds. Nevertheless, these experiments were not successful in Denmark.

In Switzerland, *Sarracenia purpurea* is completely established today in the Waadt province (Jura; AESCHIMANN & al. 2004). Slow propagation can be observed in general, therefore *S. purpurea* is considered to be invasive (JEANMONOD 2001). The total number of *Sarracenia*-sites in Switzerland is unknown so far. Populations exist in the Rütliwald (Zürcher Oberland; pers. comm. E. URMI and R. FÜRST), Robenhauser Riet (Wetzikon; pers. comm. N. SCHNYDER), Les Embreux (Les Genevez; pers. comm. N. SCHNYDER), Boussens (Waadt; pers. comm. F. HOFFER), La Vraconne (Waadt; pers. comm. F. HOFFER), Tourbiere de Bellelay (Reconvilier; pers. comm. R. KRISAI), La Chaux de Fonds (Neuenburg; pers.com J. FLISEK), Marais de Fuet (Neuenburg; (HESS & al. 1970), Marais de Prantin (Vaud; (HESS & al. 1970), Vevey (Geneva; pers. comm. R. FÜRST) and Etang de la Gruère (Jura; pers. comm. R. FÜRST). Some of these sites have been recently reduced by nature conservation measures. HARTMEYER 1996 describes two populations of *S purpurea* subsp. *purpurea* next to Weil am Rhein (Jura) in more detail. In both populations, plants are healthy and do not differ significantly from plants on the natural sites. *S. purpurea* forms huge clonal individuals with more than 100 traps and a diameter of about one metre. Although flowers and seeds are produced, no seedlings or immature plants could be observed. The author estimates that the plants have been explanted more than 50 years ago. In other Swiss habitats, however, sexual propagation occurs; the genetic bottleneck effect on these small founding populations has been studied by PARISOD & al. 2005.

In the Principality of Liechtenstein, appropriate bogs and fens are available in abundance. However, *Sarracenia* was not found so far (pers. comm. E. WALDBURGER).

In Austria, wildly growing *Sarracenia* is a rare phenomenon as well. The catalogues of neophytes growing in Austria (ESSL & RABITSCH 2002, 2004) do not mention *Sarracenia*. One single plant of *S. flava* was growing

in the Ibmer Moos in Upper Austria for several years in the 1990ies (own observations). A specimen of *S. purpurea* was explanted in the Leckermoos (Göstling at the Ybbs/Lower Austria) in 1980 (pers. com. T. Ellmauer). In 2008, it was still alive, but did not propagate (own observation, Fig. 1). In 2008, a single flower was formed. Another individual of *S. purpurea* was reported in the 1980ies from the Hochschwab Mountains (Tragöß/Styria; pers. comm. H. Teppner); the plants could not be found again in 2008 by the authors.

Several attempts were made to introduce *Sarracenia purpurea* in the Czech Republic, e. g. in Beskydy Mountains (next to Frenštát/Moravskoslezský Kraj, pers. comm. V. Rybka), but the plants are constantly removed by the nature conservation authorities (pers. comm. M. Srba and V. Rybka). In 2006, at least one population of *S. purpurea* subsp. *purpurea* existed in Trijezerni Slat in Šumava National Park (Plzeň, pers. comm. M. Srba). M. Studnička (pers. comm.) bedded out *S. purpurea* for three years in Baronsky Rybnik (Středočeský Kraj) and removed them again after finding that the plants survived in the Czech climate.

In spite of intensive research, no evidence for an establishment of *Sarracenia* in Eastern Europe could be found, i. e. Poland, Belorussia, Estonia, Latvia, Lithuania, Hungary, Slovakia, Slovenia, Romania, Moldova, Ukraine and Russia.

4. Bedding out of *Sarracenia* in Waldviertel/Austria

In Gemeindeau, all plants grew well and survived the winter. Like in the natural habitat, trap leaves were formed in spring and summer, in autumn phyllodes followed. In spring, growth began in May. In summer 2005, one individual of *S. flava* formed an inflorescence. In Schwarzes Moos, several plants were dug out by wild boars within the first weeks, but not eaten. To continue the experiment, we reimplanted them. Here, in a waterlogged habitat, we observed only poor growth. *S. purpurea* did not survive the winter, only two of five plants of *S. flava* produced new leaves in June 2005 – one month later than in Gemeindeau.

All traps formed in Waldviertel were smaller than under controlled greenhouse conditions (Fig. 3; the leaf size of the plants in the greenhouse used in this study is approximately the same as at the natural site, according to Slack 2000). The Mann-Whitney test showed that the traps of *S. purpurea* were significantly smaller in both bogs ($P < 0.05$). The leaves of *S. flava* were highly significant smaller in Schwarzes Moos ($P < 0.01$), but only insignificantly smaller in Gemeindeau. *S. flava* formed highly significant larger leaves in Gemeindau than in Schwarzes Moos ($P < 0.01$), whereas no difference was found in *S. purpurea*.

All plants successfully captured animal prey, but in different amounts. In Waldviertel, *S. flava* was much more successful than *S. purpurea*. In *S.*

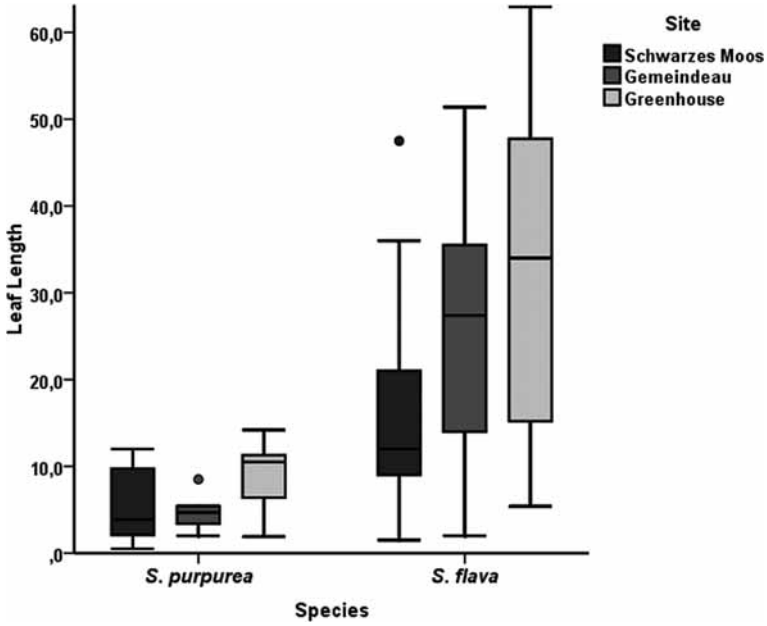

Fig. 3. Comparison of the lenght of leaves [cm], developed either in the greenhouse or in Waldviertel.

flava, all traps were crammed with insects, whereas in many traps of *S. purpurea* only single animals could be found (in Leckermoos, however, *S. purpurea* traps contained numerous animals as well; Fig. 4). Most captured animals were more or less decayed, making quantification impossible. In general, prey was degraded more completely in traps of *S. purpurea*, which contained several millilitres fluid in periods of rain, but fell dry during sunny weather. In *S. flava*, traps are protected by a lid; all traps investigated contained less than 0.1 ml fluid, and the dry prey was at least partly preserved. All trapped animals belonged to the insects. A list of taxa is given in Table 1.

As in the natural habitat, the traps of both *Sarracenia* species did not only kill animals, but also hosted living organisms. The numbers of cultivable bacteria per ml (CU/ml) could be determined only in pitchers containing fluid. In *S. purpurea* we found $3.5 \pm 5.1 \cdot 10^6$ CUs/ml; in *S. flava* $2.4 \pm 2.8 \cdot 10^9$ CUs/ml. Trap inquilines were not restricted to microorganisms. In traps of *S. purpurea*, living Acari were frequently found which were able to move the trap wall upwards and downwards. In three traps of *S. flava*, large Dipteran larvae fed on the dead prey, like *Sarcophagus sarraceniae* on the primary sites (Barthlott & al. 2004, Riley 1874).

Fig. 4. Trap of *Sarracenia purpurea* in Leckermoos, completely filled with carcasses of Necrophorus vespilloides.

5. Discussion

5.1. *Sarracenia* is Restricted to Oceanic Climate or Foothill Areas

The distribution of *Sarracenia purpurea* in Europe correlates with the climatic conditions of the peat bogs: The highest abundance, the best growth and the most successful reproduction can be found in an oceanic climate, either in Atlantic Western Europe (Great Britain, Ireland), at the North-western border of the Alps (populations in France or Switzerland) or at the coast of the Baltic sea (Denmark). Here it is sometimes reported that *S. purpurea* may drive out the natural vegetation. In suboceanic regions (Bavaria, Saxony, Austria, Czech Republic) *Sarracenia* is found only occasionally and shows no invasive tendencies; sexual reproduction fails. Here, as in France or Switzerland, *Sarracenia* is found almost exclusively at foothills, e. g., of the Eastern Alps, the Bohemian Massif, the Beskydy Moutains or the Erzgebirge. In continental (Poland, Hungary, Slovakia and Eastern European countries) climate, *Sarracenia* is missing completely, though rainfalls still allow the formation of ombrotrophic bogs (Steiner 2005). As expected, *Sarracenia* is not found in submediterranean climate (Slovenia) as well.

Table 1: Animals trapped in Austrian *Sarracenia* pitchers. Specimen marked with * could not be determined to the genus level due to strong degradation.

Order	Species (Family)	*Sarracenia* species
Collembola	div. Isotomidae*	*S. purpurea*
Hemiptera	Elasmucha ferrugata (Acanthosomidae)	*S. flava*
Diptera	div. Culicidae*	*S. flava* *S. purpurea*
	div. Muscidae*	*S. flava*
	div. Sciophilinae (Mycetophilidae)*	*S. flava*
	div. Chironomidae*	*S. flava*
	div. Simuliidae*	*S. flava*
	Episyrphus spec. (Syrphidae)	*S. flava*
	Pelecocera spec. (Syrphidae)	*S. flava*
	Myopinae spec. (Conopidae)	*S. flava*
Hymenoptera	Formica div. spec. (Formicidae)	*S. flava* *S. purpurea*
	div. Formicidae*	*S. flava* *S. purpurea*
	div. Bracionidae*	*S. flava*
	Vespa crabro (Vespidae)	*S. flava*
Coleoptera	Lampyris noctiluca (Lampyridae)	*S. flava*
	Necrophorus vespilloides (Silphidae)	*S. flava* *S. purpurea* (Leckermoos)
	Propylaea quatuordecimpunctata (Coccinellidae)	*S. flava*
	Coccinella septempunctata (Coccinellidae)	*S. flava*
	Adonia variegata (Coccinellidae)	*S. flava*
	Anistosticta novemdecimpunctata (Coccinellidae)	*S. flava*
	Adalia decempunctata (Coccinellidae)	*S. flava*
	div. Buprestidae*	*S. flava*
	Mordellistena brevicauda (Mordellidae)	*S. flava*
	Rhynchites spec. (Attelabidae)	*S. flava*
	Apion spec. (Apionidae)	*S. flava*
	Typhaca stercorea (Mycetophagidae)	*S. flava*
	Cytilus spec. (Byrrhidae)	*S. flava*
	Oedemera virescens (Oedemeridae)	*S. flava*
	Gastroidea polygoni (Chrysomelidae)	*S. flava*
	Phytodecta spec. (Chrysomelidae)	*S. flava*

Possible reasons for this behaviour include protection by snow in winter and improved prey capture in wet climates (see below). Extreme wetness of the soil or even waterlogging, however, are no prerequisite, as *Sarracenia* showed poorer survival and growth in the wet Schwarzes Moos than in the comparatively dry Gemeindeau. Mild winters are not necessary as well, since the cold winters of the Erzgebirge (discussed in more detail by BERGEL 1991) and the Waldviertel (about 130 $d \cdot a^{-1} < 0$ °C, mean temperature –2.4 °C in January, Zentralanstalt für Meteorologie und Geodynamik 2009) are survived. Low nutrient supply, on the other hand, seems to be a prerequisite for establishment: Industrialised regions with high nitrogen deposition (Normandy, Belgium, Netherlands, Luxemburg) lack *Sarracenia* – in Europe as in America (GOTELLI & ELLISON 2002).

Sarracenia flava is very rare in the European flora so far. Only three sites, two in France and one in Austria, are reported. To our knowledge, no other species or hybrids of *Sarracenia* are established in Europe.

The experiment described here took place in Waldviertel, i. e., at the borderline between suboceanic and subcontinental climate (RICEK 1982), next to the Mühlviertel mountains. *Sarracenia purpurea* survived only in one of two bogs. *S. flava* is much less frequent in Europe, but showed better growth on both sites; in Gemeindeau it even started flowering. Thus we expect an enhanced invasion of *S. flava* in Europe for the future.

5.2. Prey Capture and Pitcher Inquilines

Both species were trapping animals successfully, but to a very different extent. *Sarracenia flava* caught so much prey that the pitchers were usually completely full and sometimes died because of fungal infections. These infections do not indicate general weakness, but are common in overfed traps (MACMILLAN 1891). In *S. purpurea* only few animals could be found. The prey was somewhat different to the spectrum observed on primary sites.

Sarracenia purpurea catches mainly ants (NEWELL & NASTASE 1998), snails (HEARD 1997) and flies in North America (CRESSWELL 1991) as well as in Ireland (SLACK 2000) In Waldviertel we found mainly ants, Collembolae and only few Diptera. Overall, we found only individuals from three families, instead of 49 in one single fen in America (CRESSWELL 1991). Some taxa important as prey in the natural habitat, like Gastropoda, Diplopoda or Orthoptera (CRESSWELL 1991, HEARD 1997, NEWELL & NASTASE 1998) were missed completely, although they occur in Austria as well as in North America. A possible explanation may be that in Waldviertel pitchers of *S. purpurea* often fell dry, which is usually not the case in the natural habitat (KINGSOLVER 1979; 1981). Trapping and retention of prey therefore are less efficient (SLACK 2000). This is confirmed by traps of *S. purpurea* from Leckermoos, growing in a more humidic climate

(1,200 mm · a^{-1} versus 680 mm · a^{-1} in Western Waldviertel; Zentralanstalt für Meteorologie und Geodynamik 2009), which are usually completely filled with prey at the end of the growing season. The need for high precipitations for successful prey capture is probably one reason for the observed preference for oceanic climates.

Sarracenia flava was more successful in trapping than *S. purpurea*. In this species, prey is rather retained by downward pointing hairs, working even without pitcher fluid (ADLASSNIG 2007). We detected individuals from 25 families. In the natural habitat, mainly ants are trapped (CHRISTENSEN 1976). In Waldviertel, we found Diptera, Hymenoptera and Coleoptera in equal proportions. The odour of decaying prey seems to serve as an attractant, since we found several sarcophagous animals, especially Necrophorus (Burying beetle), among the trapped animals. The explanted specimens trapped prey up to a size of 2 cm.

Like in the natural habitat, the traps did not only kill animals but also hosted living organisms. In the traps of *S. flava*, living maggots occurred. We did not find evidence that these maggots are eating plant tissue, they are rather scavengers. The nitrogen in the faeces of the animals may be easier available than in the intact prey. Similarly, the abundant bacteria in the pitcher fluid of both species probably take part in prey degradation. Parasitic spiders were found catching trapped insects in about 10% of the pitchers in America (CRESSWELL 1991) as well as in naturalised populations in Switzerland (HARTMEYER 1996). In Waldviertel, this was never observed.

6. Acknowledgements

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