Adv. Odonatol. 6 : 89-100 April, 1994

LARVAL DRAGONFLY COMMUNITIES IN DIFFERENT HABITATS OF A MEDITERRANEAN RUNNING WATER SYSTEM

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The species composition in dragonfly larvae of ten types of habitat situated at two sites in a Mediterranean irrigation canal was investigated by sampling these habitats at five dates in 1990 and 1991. A total of 28 species were found to be developing in the canal. Out of these 28 species, 19 were found in the larval stage and the rest during additional collections of exuviae along the water course. The types of habitat could be separated into five groups of different community structure. The distribution and larval densities of the most frequent species are described and niche selection discussed. It is stated that structural diversity is the main reason for high species diversity in the canal. It is suggested that this irrigation canal is a good example for consistency of human utilization and species richness of running waters.

INTRODUCTION

Community structure in larval dragonflies is affected by habitat and seasonal segregation (JOHNSON & CROWLEY, 1980 ; CROWLEY & JOHNSON, 1982), interspecific competition (e.g. BENKE, 1978 ; JOHNSON *et al.*, 1985), and predation (JOHNSON, 1991 ; BLOIS-HEULIN *et al.*, 1990).

Many investigations on larval community structure have been carried out in lentic systems (e.g. JOHANNSSON, 1978 ; JOHNSON & CROWLEY, 1980, 1989), but only a few in lotic habitats. JARRY & VIDAL (1960) and AGUESSE (1960) described typical dragonfly communities for Mediterranean running waters of different morphology and hydrology. FERRERAS-ROMERO (1984) distinguished three odonate community types based on physical and chemical parameters and water level in natural running water systems in Southern Spain.

Our study deals with community structure of different habitats in an irrigation canal, the Canal de Vergières (CdV), in Southern France. Canals of this type compared to natural streams of the same size generally show a reduction in the abundance of the invertebrate fauna due to uniformity along the watercourse (HYNES, 1970). However, in the system investigated, 39 dragonfly species occur (REHFELDT *et al.*, 1991). We tried to find out which of these species could develop in the system, and which were the sites preferred by the larvae.

STUDY AREA

The Crau is a 150 km² stony steppe in Southern France. It has high precipitation (570 mm) during the winter season, but a four months dry season in the summer (DEVAUX *et al.*, 1983) with temperatures frequently exceeding 40°C. The only running waters in the Crau are irrigation canals, some of which were already constructed in the 16th century -DEVAUX *et al.*, 1983).

Investigations were carried out at the Canal de Vergières, an irrigation canal, which is situated 20 km east of the city of Arles. Departement Bouches du Rhône. It has a total length of 12.4 km and crosses the steppe of the Crau from NE to SW, bordering the central part of the Crau, the natural reserve "Peau de Meau", to the north. The canal has an average width of 2.5 m and a depth varying between 10 and 40 cm (up to 1 m in some pools), and it flows almost at sea level, the total difference in altitude being 28 m and the mean resulting incline being 0.22%.

The current velocity is nonuniform, differeing from 1.2 m/s to a few cm/s near the edge and mostly overgrown parts (see Tab. I). Data on chemical and physical parameters of the water are given in REHFELDT *et al.* (1991).

METHODS

The investigation was carried out from April, 1990, to June, 1991, neglecting the winter period. A total of 96 samples were taken in April, July and October, 1990, and April and June, 1991, in ten types of habitat of different structure. The types of habitat were classified according to the following criteria: sediment particle size (categories according to WENTWORTH, 1922), presence and type of detritus, percent share and type of vegetation, current velocity, and section of the canal (Tab. I).

The sampler used was a modified surber-sampler designed to take samples both in lentic and lotic waters. For this purpose a cubic frame (side length : 35 cm, sampling area : 0.1225 m²) open on the bottom and top sides was closed with a net (mesh size : 1.4 mm) on three sides and a collecting net of 0.5 mm mesh size on the remaining side.

Substrate was whirled up using a paintbrush and washed into the sampling net. Samples were sorted by placing the debris in a sieve and manually searching for odonates. Larvae were identified immediately and then released. If determination was not possible under field conditions, larvae were preserved in 70% ethanol and determined in the laboratory. Additionally, collecting trips were made in search for exuviae in order to find also the rare species.

Densities per m² were calculated from the number of larvae per sample for each species. To compare community composition of the different habitats WARDS cluster-

Table I

Description of habitats investigated for occurence of dragonfly larvae

Habitat	Sediment	Organics (% on surface)	Vegetation (% of sample area)	Current Velocity (cm/s)	Section of the canal	Number of samples
mud	silty sand	fine detritus (100%)	-	0-3	lower reaches	4
submerged vegetation	sand	fine detritus (100%)	*Potamogeton coloratus* (100%)	4-7	»	9
sand	gravelly sand	leaf detritus (100%)	-	0-5	»	6
conglomerate	gravel*	-	*Rivularia* sp. (0-20%)	20-37	»	12
rapids	cobble/ coarse gravel	-	*Rivularia* sp. (0-30%)	60-100	upper reaches	15
conglomerate	gravel*	-	*Rivularia* sp. (5-60%)	30-56	»	15
conglomerate/ detritus	sandy gravel*	fine detritus (60-100%)	-	14-27	»	9
mud	silty sand	fine detritus (100%)	-	0-8	»	6
submerged vegetation	sand	fine detritus (100%)	*Chara* sp. *Mentha aquatica* *Berula angustifolia* (100%)	0-6	»	15
emergent rushes	silty sand	fine detritus (100%)	*Juncus effusus* (100%)	0-5	»	6

* the sediments did not completly cover the conglomerate in all samples

analysis (squared Euclidean distance) was used, considering the ten most frequent species. For each habitat the SHANNON-index of diversity (H_S) was calculated as discribed by MÜHLENBERG (1989).

RESULTS

A total of 44 dragonfly species were observed at the Canal de Vergières, 28 of which definitely completed their life cycles at the study site (Tab. II). Besides the 39 species already known form the CdV (see above) we found *Coenagrion scitulum, C. pulchellum, Enallagma cyathigerum, Pyrrhosoma nymphula*, and *Oxygastra curtisii.* Eight of these, *Sympetrum depressiusculum, Ischnura elegans, Ceriagrion tenellum*, and five aeshnid species were found only as exuviae during the collecting trips. The two species of *Platycnemis* could not be determined in the larval stage, but both, *P. latipes*

Table II

List of autochtonous damselfly and dragonfly species in the Canal de Vergières

Species	Exuviae	Larvae
Calopteryx splendens (Harris, 1782)	×	×
Calopteryx haemorrhoidalis (Vander Linden, 1825)	×	×
Platycnemis latipes Rambur, 1824 ([1])	×	×
Platycnemis accutipennis Sélys, 1841 ([1])	×	
Ischnura elegans (Vander Linden, 1820)	×	
Enallagma cyathigerum (Charpentier, 1840)		×
Coenagrion mercuriale (Charpentier, 1840)	×	×
Coenagrion caerulescens (Fonscolombe, 1838)	×	×
Coenagrion scitulum (Rambur, 1842)		×
Ceriagrion tenellum (Villers, 1789)	×	
Gomphus pulchellus Sélys, 1840	×	×
Gomphus simillimus Sélys, 1840	×	×
Ophiogomphus cecilia (Fourcroy, 1785)		×
Onychogomphus f. unguiculatus (Vander Linden, 1820)	×	×
Onychogomphus uncatus (Charpentier, 1840)	×	×
Brachytron pratense (O. F. Müller, 1764)	×	×
Boyeria irene (Fonscolombe, 1838)	×	
Aeshna mixta Latreille, 1805	×	
Anaciaeschna isosceles (O. F. Müller, 1764)	×	
Anax imperator Leach, 1815	×	
Anax parthenope (Sélys, 1839)	×	
Cordulegaster boltonii (Donovan, 1807)		×
Libellula fulva O. F. Müller, 1764	×	×
Orthetrum cancellatum (Linné, 1758	×	×
Orthetrum brunneum (Fonscolombe, 1837)	×	×
Orthetrum coerulescens (Fabricius, 1798)	×	×
Sympetrum fonscolombii (Sélys, 1840)	×	×
Sympetrum depressiusculum (Sélys, 1841)	×	×

([1]) Species that could not be identified in the larval stage.

and *P. acutipennis*, were observed emerging from the canal. Larvae of eight species, four of Anisoptera and four of Zygoptera, were caught in average densities of more than 10 individuals per m^2 (i/m^2) in at least one habitat (Tab. III) the most frequent being *Onychogomphus uncatus* and *Coenagrion mercuriale*. In each of these two species the maximum density exceeded 300 i/m^2. In most of the types of habitat, except of mud (lower reaches) and the two upstream vegetation habitats, anisopteran densities were higher than zygopteran.

The family group of the gomphids, with five species, played a dominant role in the CdV. Gomphidae were found in frequencies of more than 66% of all species in five habitats and reached a frequency up to 50% in one other (Fig. 1). *Gomphus simillimus* and *G. pulchellus* were mostly, and regularly, caught in the downstream habitats, especially in sand. No habitat preference could be found for *Ophiogomphus cecilia* which was rare, and only found in low densities, or *Onychogomphus forcipatus unguiculatus* which occured in slightly higher densities in seven types of habitat. The most abundant species, *O. uncatus*, was caught in all habitats except mud (lower reaches), mostly at densities of more than 10 i/m^2 on average. It was found regularly in very high densities (Tab. III) in gravelly to stony habitats and in conglomerate/detritus. In the muddy substrate larvae were caught only in June 1991, when emergence began. In submerged vegetation 41 young instar larvae (334.7 i/m^2) were caught in only one sample in April 1990, but in this habitat such high numbers of *O. uncatus* were never found again.

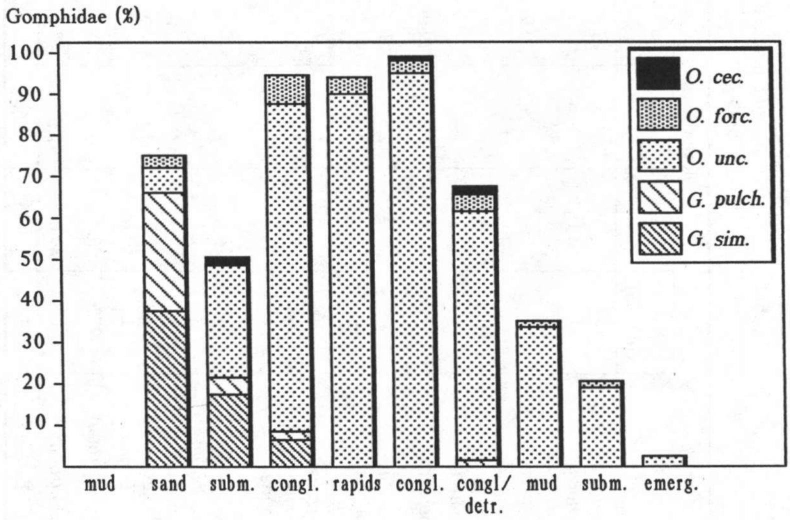

Fig. 1. Percent share of Gomphidae in total dragonfly population densities of ten investigated types of habitat in the Canal de Vergières.

Table III

Densites of dragonfly species found in 10 different haibats of the Canal de Vergières and indices of diversity for the habitats. Average number/m² and standard deviation (small numbers) are given.

Species		lower reaches				upper reaches					
	No. collected	mud	sand	subm.	congl.	rapids	congl.	congl./ detr.	mud	subm.	emerg.
C. haemorrhoidalis	143	–	–	5.5 8.2	1.4 3.2	6.0 12.5	–	1.8 3.6	–	34.8 57.5	72.1 57.8
C. splendens	1	2.1 4.1	–	–	–	–	–	–	–	–	–
Platycnemis	37	24.5 14.9	5.5 6.7	5.4 9.1	–	–	0.6 2.2	4.5 8.3	1.4 3.3	1.1 2.9	8.2 20.0
E. cyathigerum	1	–	–	0.9 2.7	–	–	–	–	–	–	–
C. mercuriale	334	2.1 4.1	–	7.3 2.4	0.7 2.4	–	0.6 2.2	2.7 5.7	12.3 16.9	135.9 89.6	83.0 49.9
C. caerulescens	19	–	–	–	–	–	–	–	–	10.3 16.6	–
C. scitulum	1	–	1.4 3.3	–	–	–	–	–	–	–	–
Zygoptera (total)	*536*	*28.6 17.0*	*6.8 9.5*	*19.0 17.3*	*2.1 3.7*	*6.0 12.5*	*1.2 3.0*	*7.3 10.3*	*13.6 16.0*	*183.4 118.0*	*163.2 91.4*
G. pulchellus	13	–	12.3 11.2	1.8 3.6	0.7 2.4	–	–	0.9 2.7	–	–	–
G. simillimus	25	–	16.3 10.3	8.2 10.8	2.7 5.3	–	–	–	–	–	–
O. cecilia	6	–	–	0.9 2.7	–	–	1.2 4.4	2.7 5.8	–	–	–
O.f. unguiculatus	30	–	1.4 3.3	–	3.4 7.4	3.3 8.6	4.1 5.3	5.5 8.2	1.2 3.1	2.2 6.5	–
O. uncatus	707	–	2.7 6.7	12.7 21.2	33.3 32.3	71.8 38.0	179.0 67.6	80.7 47.3	24.5 32.1	52.8 86.1	5.5 9.9
B. pratense	1	–	–	–	–	–	–	–	–	–	1.4 3.4
C. boltonii	1	–	–	–	–	–	–	–	1.4 3.4	–	–
L. fuila	3	6.1 12.3	–	–	–	–	–	–	–	–	–
O. cancellatum	3	2.1 4.4	–	–	–	–	–	–	–	–	–
O. brunneum	9	–	–	–	–	–	–	6.4 6.8	5.4 13.1	–	–
O. coerulescens	173	12.2 8.2	4.1 6.8	3.6 5.9	–	–	3.5 10.9	30.9 30.5	27.2 32.5	38.4 24.3	44.9 20.5
S. fonscolombii	1	–	–	–	–	–	–	–	–	–	1.4 3.4
Anisoptera (total)	*972*	*20.4 16.9*	*36.7 21.1*	*28.1 27.7*	*40.2 31.8*	*74.6 43.6*	*187.8 71.8*	*127.0 39.8*	*61.4 36.6*	*92.0 90.5*	*53.2 28.4*
Odonata (total)	**1508**	**49.0 29.0**	**43.5 21.0**	**47.2 33.9**	**42.2 31.5**	**80.0 43.2**	**188.9 72.2**	**134.3 33.2**	**73.5 42.6**	**274.8 172.3**	**216.3 102.2**
Index of Diversity	H_s	1.36	1.60	1.92	0.74	0.41	0.20	1.28	1.44	1.39	1.34

Most larvae of Zygoptera, except *Platycnemis* spp., were found predominantly in the upstream vegetation habitats. In the similar downstream vegetation habitat, with *Potamogeton coloratus* (Tab. I), zygopteran densities were relatively low. The most frequent species, *Calopteryx haemorrhoidalis* and *Coenagrion mercuriale*, were caught at similar densities in the rushes habitat, but in the submerged vegetation the density of *C. mercuriale* was much higher.

The libellulids, the third large group of dragonflies in the CdV, were represented mostly by species of the genus *Orthetrum*, especially *O. coerulescens*. They were caught predominantly in muddy or detritus-containing habitats, with or without vegetation. The two larger species of libellulids *Libellula fulva* and *Orthetrum cancellatum* were caught only in the downstream mud habitat.

Comparing the types of habitat present both in the downstream and the upstream part of the canal, namely mud, submerged vegetation, and conglomerate, revealed some general differences. In the downstream habitats total larval densities were lower but species diversity was higher (Tab. III). Species composition too, differed between upstream and downstream habitats. While the most abundant species were found in both parts of the canal, six species were caught exclusively in the lower reaches and five others were restricted to the upper reaches.

Whereas nine species were found in the lower reaches submerged vegetation habitat and in conglomerate with detritus, there were only three species in the rapids. In the remaining types of habitat six or seven out of the total number of 19 species were found.

Using WARDS cluster-analysis, based on larval distribution patters, groups with typical dragonfly communities could be separated out of the ten habitats investigated (Fig. 2).

The community structure in the lower reaches mud habitat was widely different from that of all other habitats. It was dominated by larvae of *Platycnemis* spp. and *Orthetrum coerulescens*. Three out of the six species, *Calopteryx splendens, Libellula fulva*, and *Orthetrum cancellatum*, were restricted to this habitat. The total population density was the highest of the lower reaches types of habitat.

The vegetation habitats of the upper reaches formed a second group separated from the others. These habitats were characterised by the highest larval densities (Tab. III) with calculated maximum values up to 710 i/m^2 from a single sample. The dominant species were the zygopterans *Coenagrion mercuriale* and *Calopteryx haemorrhoidalis*, and the libellulid *Orthetrum coerulescens*. Whereas numbers of the two damselflies differed (see above), numbers of *O. coerulescens* were similar in both habitats. Larvae of three species *Coenagrion caerulescens, Brachytron pratense* and *Sympetrum fonsco-*

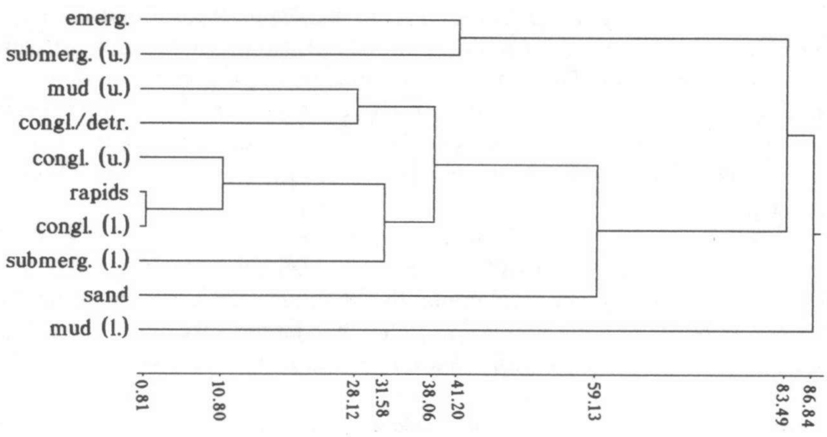

Fig. 2. Associated groups of habitats in the Canal de Vergières (CdV), based on cluster-analysis (WARD) on larval dragonfly distribution patterns in the CdV. u = upper reaches; l = lower reaches.

lombii, were caught only in these habitats. *C. caerulescens* was restricted to the submerged vegetation where it was found in a relatively high density.

All other habitats were more or less dominated by the gomphids (Fig. 1) and because of this they formed a big group containing some smaller groups of habitat with different community structures. The dragonfly communities of the three habitats of gravelly to stony bottom and high current velocity (Tab. I) were closely related. *O. uncatus* made up more than 80% of all larvae caught in these habitats. The only other species found regularly and in somewhat higher densities was *Onychogomphus forcipatus unguiculatus*. In the upstream conglomerate, where a high total larval density of 188.9 i/m^2 was found, the dominance of *O. uncatus* was even higher (95%). Another group comprised the remaining upstream habitats with more or less high amounts of detritus on the bottom. Here, the larval density in *Orthetrum coerulescens* equalled that of *Onychogomphus uncatus*. Two species, *Orthetrum brunneum* and *Cordulegaster boltonii*, were mostly restricted to these habitats. The downstream vegetation habitat had the highest diversity and highest number of species, most of them being found at similar densities. The sand habitat was dominated by the two species of the genus *Gomphus*. Both of them reached their highest densities in this habitat.

DISCUSSION

The Canal de Vergières is a good example of the capacity of a man-made water system to support a high species diversity. More than 70% of the odonate species known to occur in Provence (AGUESSE, 1960 ; PAPAZIAN, 1989) can be found there. Almost 80% of the reophilous species of this region, and one species, *Ophiogomphus cecilia*, newly recorded in Southern France (REGFELDT *et al.*, 1991), develop in this irrigation canal. Similar numbers of riverine dragonfly species are known from some undisturbed rivers and streams in Southern Europe (AGUESSE, 1960 ; BALESTRAZZI & BUCCIARELLY, 1979 ; CARCHINI & ROTA, 1985 ; FERRERAS-ROMERO, 1985, 1988 ; JARRY & VIDAL, 1960), but most of these are much larger water systems.

It has long been known that in artifical ponds, especially in gravel pits, similar and sometimes higher numbers of dragonfly species can be found than in more natural systems (e.g. MARTENS, 1983, 1991 ; WILDERMUTH, 1986 ; WILDERMUTH & KREBS, 1983). However, no other man-made canal of a species richness similar to that of the CdV is known. In some regions of central Europe many of the small streams used as drainage ditches are totally free of reophilous odonates, only insensitive, ubiquitous species such as *Ischnura elegans* occuring in them (LIESS, 1986).

In many of the species which develop in the CdV, larval densities exceed the numbers found by JOHNSON & CROWLEY (1980) who recorded a similar amount of species (28) in Bays Mountain Lake, but found only two species, *Enallagma traviatum* and *Tetragoneuria cynosura*, at densities higher than 10 individuals per m^2. Whereas the densities of the Zyoptera, especially *Coenagrion mercuriale* are comparable to results from fish free ponds (MACAN, 1964 ; JOHNSON & CROWLEY, 1980) the densities of *Onychogomphus uncatus* exceed by far those found for gomphids of this genus in other studies (e.g. DUDGEON, 1989 ; PREVOT & PREVOT, 1986) and for *O. uncatus* in other streams (SCHRIDDE & SUHLING, unpublished data). On the other hand maximum densities of *Gomphus pulchellus* and *G. simillimus* are approximately the same as those of *Gomphus externus* (HUGGINS & DUBOIS, 1982), *G. vulgatissimus* (TITTIZER *et al.*, 1989) and *G. pulchellus* in other surroundings (SUHLING, 1992). One might ask if the density of about 20 individuals per m^2 is the upper limit for larvae of this genus.

The spatial distribution of the species of the family group of the Gomphidae in the canal gives a food example of the role of habitat as niche in odonate communities as stated by CROWLEY & JOHNSON (1982). According to HUGGINS & DUBOIS (1982) the differences in microdistribution between *Progomphus obscurus* and *Gomphus externus* are affected by their specialisation to specific sediments. This may be similar in the two morphological "types" *Onychogomphus* spp. and *Gomphus* spp., but probably competition has a great influence, too. The rarity of *Onychogomphus forcipatus* in comparison to *O. uncatus* may be affected by competitive advantage of the latter. The larvae of *O. forcipatus unguiculatus* occur in waters of lower current velocity (AGUESSE, 1958) but higher temperatures (FERRERAS-ROMERO, 1988) than do those of *O. uncatus*.

Another factor affecting community composition is the presence or absence of plants. Our findings that average larval densities are highest in the upstream vegetation habitats but are comparatively low in the downstream habitat of submerged vegetation confirm the general thesis that aquatic plant substrates support higher densities of insects than do mineral substrates, and that plant species may differ considerably in this regard (MINSHALL, 1984). However, the results for the upstream conglomerate habitat with maximum densities almost equalling the respective values of the upstream plant habitats and even exceeding those in the lower reaches partly contradict this thesis.

In agreement with our results, in downstream habitats of a subtropical black-water river densities of predators are lower in comparison to equally structured upstream habitats (BENKE *et al.*, 1984). But comparing the distances between the upper and lower sites of the running waters in the two investigations, there is a great difference : whereas in the study of BENKE *et al.* (1984) the distance was 160 km, the upper site in the CdV is only 5 km from the lower site. The dragonfly assemblages between these relatively close habitats are different too. Possible explanations for these differences in species composition may be the reduced current velocity and oxygen content in the downstream part and differences in water temperature. Additionally, as stated above, the difference in community structure between the submerged vegetation habitats may be affected by the various plant species and statures.

According to AGUESSE (1960) the change of odonate assemblages along the course of running waters depends on varying current velocity and depth. Based on this statement he describes three types of odonate assemblages colonising rivers, streams and brooks. He points out that there are no strict separations but transitions are rather common, especially at confluences. The CdV must at least partly have characters of all three types of running waters, as most of the typical species of all of the three assemblages occur together, though they live in distinct habitats. Because of this fact we consider the high structural diversity of this system to be the main reason for its species richness.

Another aspect that gives special importance to the CdV is the fact that nine out of its 28 autochthonous species are endangered or vulnerable for Europe (VAN TOL & VERDONK, 1988).

These findings show that human utilisation does not necessarily mean ecological uniformity as stated by HYNES (1970) and that irrigation canals can partly take the place of natural running waters, provided that the design and management are planned carefully.

ACKNOWLEDGEMENTS

We are very grateful to the C.E.E.P. and the Ecomusée de la Crau, St. Martin, for supporting our studies at the Canal de Vergières. Special thanks to Marte Busse, who did a lot of organising work for us in the Crau. We thank Dr. Andreas Martens and Dr. Gunnar Rehfeldt for helpful comments. We are particularly grateful to Dr. Peter Miller for kindly revising this paper. Our work was supported by the DFG.

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