

Analysis of the spider fauna of the riverine forest nature reserve 'Walenbos' (Flanders, Belgium) in relation to hydrology and vegetation

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Abstract. The forest nature reserve 'Walenbos' is one of the major riverine forests in Flanders (Belgium). After a long history of agriculture (meadows) and forestry (coppice and coppice-with-standards) its management is now adapted towards a much more spontaneous development. In 1984 it was designated as a state nature reserve. To assess environmental factors affecting the arthropod communities living on the forest floor, eight stations were sampled for their spider fauna. Three pitfall traps per site were emptied at fortnightly intervals during a complete year cycle. A classification of the sampling stations by means of a TWINSPLAN analysis based on the captures of the 57 most abundant species revealed that mean groundwater level was the most important environmental factor, immediately followed by groundwater type (oligo- or mesotrophic). The composition of the tree layer was of minor importance.

INTRODUCTION

In comparisons of the spider faunas of forest stands distributed over the whole of our country (Maelfait et al., 1990b; Maelfait et al., 1992), we found that the composition of these faunas was highly dependent on the forest complex a particular stand is part of; there were also important zoogeographical influences. Hereafter, we analyse the variation of the spider fauna within a particular forest complex, i.e. of the 'Walenbos', a riverine forest in the northern part of Belgium; this is done in relation to the hydrology and the vegetation of the area.

STUDY SITE, MATERIAL AND METHODS

Our study area is the 'Walenbos', a forest state nature reserve. It is situated some thirty kilometers northeast of Brussels, along the right bank of the Motte (Fig. 1). This rivulet flows at 25 meters above sea level through a region of tertiary glauconite rich sands, which is at an altitude between 50–100 m. The forest is approximately 2.5 kilometer long with a width between approximately two and one kilometers. During the last century large parts of the area were used as meadows. Later on, forestry became more important, consisting of coppice, coppice-with-standards and plantation by fast growing trees such as Canadian poplar (*Populus x canadensis*) and Japanese larch (*Larix leptolepis*). At present, the area consists of some 350 hectares of forest and only some 20 hectares of open area, mainly meadows. Human use was only possible through a very labour-intensive drainage system. During the last decades this network was not maintained any longer and gradually filled up. The area is now largely left to a spontaneous development. The results we present here are part of an integrated monitoring of the developments of the ecosystem, including hydrology, vegetation and invertebrates (Batelaan et al., 1993a,b; Batelaan et al., in press; De Becker et al., 1993).

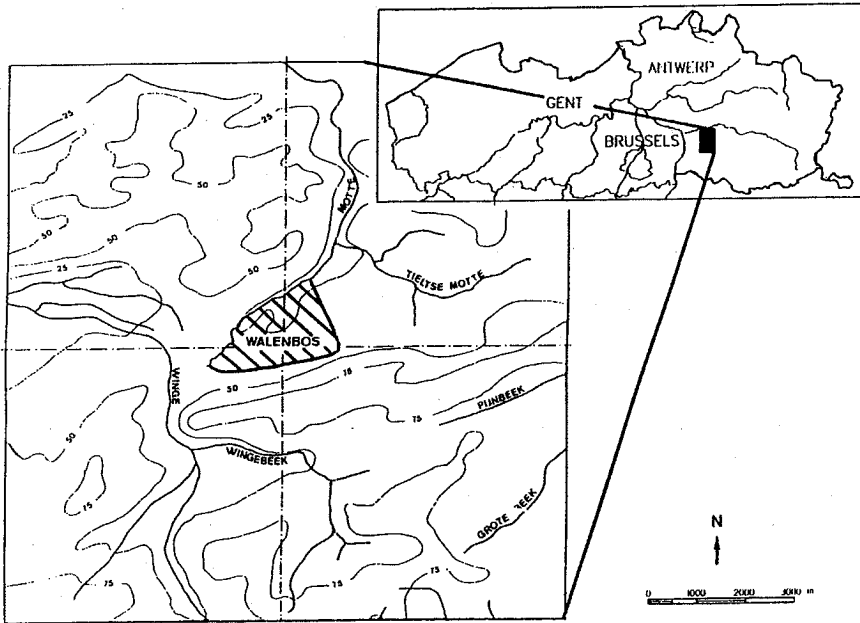


Fig. 1. Geographic and hydrographic setting of the Walenbos nature reserve.

The forest is highly influenced by groundwater discharges in specific zones of the forest. This groundwater results from infiltration in the surrounding areas of tertiary sand. Two different kinds of groundwater currents exfiltrate in the forest: (1) close to the southern valley wall, water poor in minerals discharges; the typical vegetation being here oligotrophic alder carr with extensive carpets of peat moss (*Sphagnum*), (2) closer to the rivulet there are seepages of alkaline groundwater (that is groundwater rich in Calcium, Magnesium and bicarbonate), resulting from a passage through a mineral rich geological aquifer; typically the vegetation here is a mesotrophic alder carr with a wide diversity of groundwater dependent plant species. For a complete description of the hydrology of that area see Batelaan et al. (in press).

To assess environmental factors affecting the arthropod communities occurring on the forest floor, eight stations were sampled for their spider fauna (Fig. 2). Station F is situated on the colluvial foot of the southern valley wall. It is an old forest stand of which the tree layer consists of standards of Oak (*Quercus robur*) with a coverage of 65%; a shrub layer of coppiced Hazel (*Corylus avellana*) (coverage 55%) and a herb layer of Blackberry (*Rubus spec.*) (coverage 5%). The soil consists of loamy sand. During summer the groundwater level is more than one meter below soil surface. Immediately north of this are the stations in the zone with an upwelling of oligotrophic groundwater: A, B and G. Of these sites groundwater level during summer is between -10 cm and -20 cm. Station A is virtually unaffected by drainage; there is no significant herb layer and a 80% coverage by peat moss. Its tree and scrub layer consist of Birch (*Betula pubescens*) (70%), Alder (*Alnus glutinosa*) (20%) and Oak (5%). Station G was somewhat drained, but it remained relatively untouched. During the sampling year it still had a coverage of 20% of peat moss; the herb layer was mainly composed of sedges (*Carex spec.*) (85% coverage). The tree layer was composed of Willow (*Salix cf. aurita*) (45%), Birch (35%)

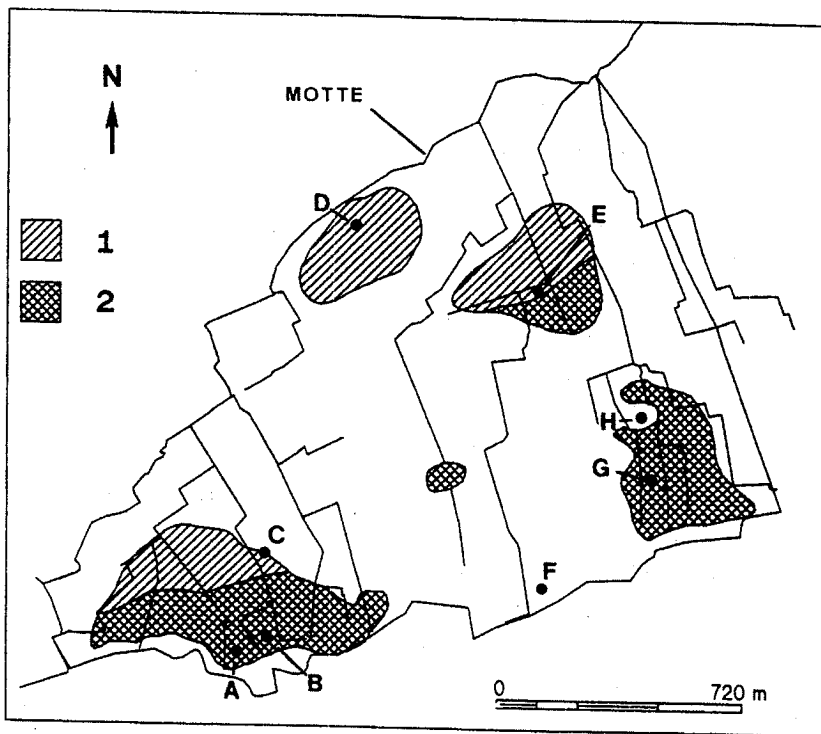


Fig. 2. Localisation of the eight sampling stations with indication of the seepage zones. (1) rich in minerals—mesotrophic, (2) poor in mineral content—oligotrophic.

and Alder (20%). Station B was heavily drained for a few years. This resulted in a breakdown of the superficial peat layers and a local enrichment. After the drainage stopped this breakdown of the superficial peat layers also led to very wet conditions. Only some 5% of *Sphagnum* coverage remained. There is a diversified herb layer with a maximal coverage of some 60%. Station H is situated very close to G, but the drainage of that area was much more successful. This was due to the presence of a very deep drainage ditch in the immediate vicinity of that stand and to the fact that its soil is relatively rich in sand. Its soil water level during summer was 45 cm below soil surface. The dominant tree species are Oak (65%) and Ash (35%); the herb layer is very comparable to that of G—85% coverage by sedges. Stations D and E are both situated in zones with an upwelling of alkaline groundwater; this makes that during summer groundwater level stays between -20 and -30 cm. Of both sampling sites the tree layer is dominated by Alder (some 65%) and they have a herb layer with sedges. Station C is comparable to the two former; it only differs from them by being situated at the outer limits of a groundwater seepage zone and by being planted by Canadian poplar, making up 60% of its tree layer.

The eight sampling stations were sampled by means of three pitfall traps each, which were emptied at fortnightly intervals during a complete year cycle; station F was sampled for two consecutive years (F1 and F2). In this way we obtained 27 sampling units.

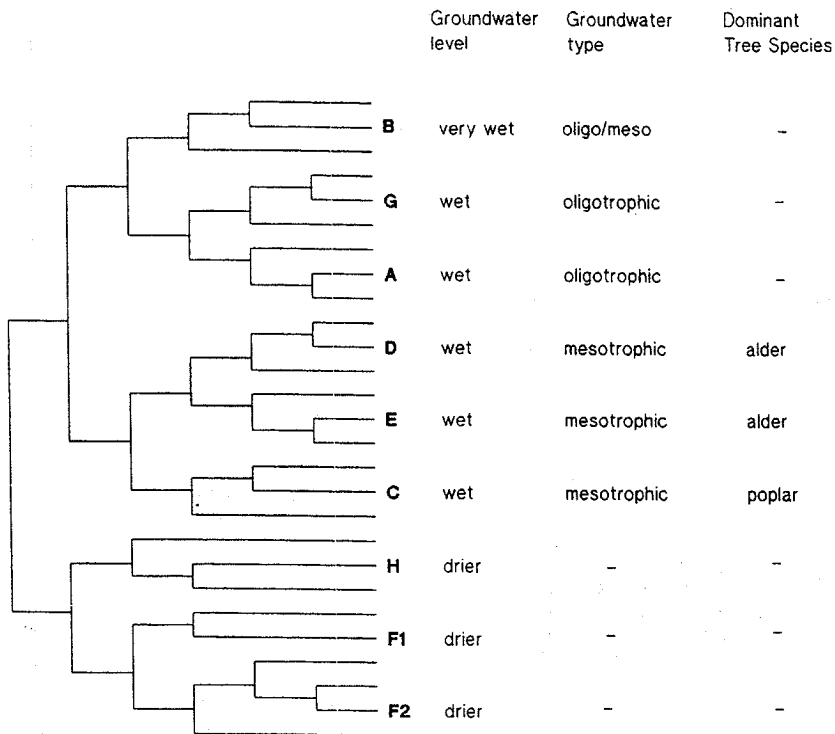


Fig. 3. Classification of the spider communities based on TWINSpan analysis.

Table 1. Number of individuals caught per three pitfall traps in (1) the drier stations (F and H), (2) the wet mesotrophic station planted with Canadian poplar (C), (3) the wet mesotrophic alder carrs (D and E), (4) the wet oligotrophic stations (A and G) and (5) the very wet station (B).

| | 1 | 2 | 3 | 4 | 5 |
|-----------------------------------|---|----|----|----|-----|
| <i>Gongylidiellum latebricola</i> | — | — | — | 31 | 15 |
| <i>Lophomma punctatum</i> | — | — | — | 1 | 31 |
| <i>Lepthyphantes ericaeus</i> | — | — | 1 | — | 44 |
| <i>Oedotheorax tuberosus</i> | — | 1 | 13 | 16 | 197 |
| <i>Centromerus dilutus</i> | 2 | — | 5 | 18 | 1 |
| <i>Antistea elegans</i> | 1 | 4 | 36 | 84 | 34 |
| <i>Agyneta subtilis</i> | — | 5 | 1 | 9 | 4 |
| <i>Dicymbium tibiale</i> | — | 20 | 17 | 9 | 26 |
| <i>Agyneta ramosa</i> | 1 | 4 | 21 | 3 | 8 |

Table 1. (cont.)

| | 1 | 2 | 3 | 4 | 5 |
|----------------------------------|-----|-----|-----|-----|-----|
| <i>Glyphesis servulus</i> | — | 3 | 17 | — | — |
| <i>Saloca dicerus</i> | — | 41 | — | — | — |
| <i>Bathypantes gracilis</i> | 2 | 3 | 2 | 5 | 27 |
| <i>Walckenaeria cuspidata</i> | 7 | 19 | 5 | 18 | 14 |
| <i>Pachygnatha clercki</i> | 2 | 6 | 8 | 14 | 9 |
| <i>Pirata hygrophilus</i> | 56 | 211 | 151 | 299 | 259 |
| <i>Lepthyphantes zimmermanni</i> | 15 | 56 | 37 | 16 | 46 |
| <i>Centromerus sylvaticus</i> | 12 | 75 | 25 | 19 | 56 |
| <i>Diplostyla concolor</i> | 32 | 169 | 51 | 19 | 64 |
| <i>Walckenaeria nudipalpis</i> | 3 | 12 | 17 | 8 | 28 |
| <i>Ceratinella scabrosa</i> | 2 | 2 | 14 | — | 3 |
| <i>Robertus lividus</i> | 3 | 11 | 17 | 4 | 9 |
| <i>Walckenaeria acuminata</i> | 21 | 112 | 34 | 11 | 2 |
| <i>Gonatum rubellum</i> | 7 | 6 | 19 | 1 | 3 |
| <i>Cicurina cicur</i> | 5 | 11 | 14 | 3 | 1 |
| <i>Clubiona lutescens</i> | 4 | 6 | 2 | 1 | 4 |
| <i>Lepthyphantes pallidus</i> | 7 | 6 | 10 | 1 | 8 |
| <i>Diplocephalus picinus</i> | 77 | 60 | 110 | 32 | 41 |
| <i>Clubiona compta</i> | 9 | 6 | 4 | 6 | 8 |
| <i>Centromerus aequalis</i> | 20 | 16 | 1 | 18 | 13 |
| <i>Saaristoa abnormis</i> | 7 | 3 | 8 | 11 | 6 |
| <i>Bathypantes nigrinus</i> | 17 | 6 | 16 | 20 | 18 |
| <i>Lepthyphantes tenebricola</i> | 4 | 5 | 1 | 27 | — |
| <i>Pachygnatha listeri</i> | 48 | 53 | 19 | 17 | 17 |
| <i>Microneta viaria</i> | 28 | 29 | 13 | 10 | 9 |
| <i>Lepthyphantes tenuis</i> | 6 | 4 | 1 | 3 | 5 |
| <i>Walckenaeria atrotibialis</i> | 3 | 12 | 6 | — | — |
| <i>Maso sundevalli</i> | 8 | 12 | 16 | — | 1 |
| <i>Walckenaeria dysderoides</i> | 8 | 3 | 6 | 2 | — |
| <i>Oxyptila trux</i> | 15 | 23 | 4 | — | 1 |
| <i>Gongylidium rufipes</i> | 16 | 5 | 4 | 1 | — |
| <i>Hahnia helveola</i> | 13 | 1 | — | 13 | 5 |
| <i>Hahnia montana</i> | 11 | — | — | 5 | 1 |
| <i>Lepthyphantes cristatus</i> | 55 | 1 | 2 | 10 | 2 |
| <i>Macrargus rufus</i> | 235 | 8 | 3 | 26 | 4 |
| <i>Coelotes terrestris</i> | 136 | 13 | 26 | 40 | 4 |
| <i>Micrargus herbigradus</i> | 20 | 6 | 6 | 8 | 1 |
| <i>Monocephalus fuscipes</i> | 24 | 8 | 1 | 2 | 2 |
| <i>Pardosa amentata</i> | 12 | — | 5 | 1 | — |
| <i>Lepthyphantes flavipes</i> | 71 | 28 | 13 | 10 | 2 |
| <i>Agroeca brunnea</i> | 69 | 38 | 2 | 7 | 2 |
| <i>Hahnia pusilla</i> | 24 | 2 | 1 | 6 | — |
| <i>Trochosa terricola</i> | 8 | — | 1 | — | 4 |
| <i>Xysticus lanio</i> | 11 | — | — | — | — |
| <i>Pardosa lugubris</i> | 28 | — | 2 | — | — |
| <i>Linyphia clathrata</i> | 24 | 4 | — | 1 | — |
| <i>Walckenaeria cucullata</i> | 16 | — | — | 1 | — |
| <i>Tegenaria picta</i> | 9 | — | 1 | — | — |

RESULTS AND DISCUSSION

The 27 sampling units were classified by means of TWINSPAN analysis (Hill, 1979) based on the captures of the 57 most abundantly caught species (Fig. 3). In this analysis, each species was given equal weight by expressing the capture made in each trap as a percentage of the total catch in the 27 sampling units. The groups in the dendrogram can be understood as follows. The most important division is in agreement with the mean groundwater level: at one side we have the very wet station B; at the other we have the dryer stations F and H, lacking an upwelling of groundwater. In between these two extremes the remaining stations are situated. At the next level the sampling stations are classified in accordance with the quality of the groundwater: the oligotrophic ones at the one side, the mesotrophic ones at the other. Only at the third level we see a separation in the mesotrophic stations between the Poplar stand and the two habitats dominated by Alder trees. We can conclude that the composition of the tree layer does not seem to be very important for the distribution and abundance of the spiders of the ground surface; much more important are groundwater level and quality. Even so, the observed difference between the Poplar and the Alder stands may also result from subtle differences in groundwater regime as indeed station C is at the outer limits of a seepage zone (cf. Fig. 2).

Now we will look somewhat more closely to the species which are responsible for the differences we observe between the forest types. To do that we have ordered the sampling stations and the species in agreement with their clustering resulting from the TWINSPAN analysis in Table 1, i.e. from column 1: the mean number in three pitfalls of the drier stations F and H (cf. Fig. 2) to column 5: the number of individuals in three pitfalls of the very wet station B.

A first species to discuss is *Gongylidiellum latebricola*. This species was only caught in the oligotrophic sampling stations. Almost all individuals, 70 males and seven females, were caught in May, June and July. In Belgium as well as in neighbouring countries the species is indeed only found in wet woodlands (Lockett & Millidge, 1953; Wiehle, 1960; Palmgren, 1976; Roberts, 1987; Tips, 1978; Maurer & Hänggi, 1990; Heimer & Nentwig, 1991). Its presence seems to be correlated with the presence of *Sphagnum* mosses. The reason for that very specific habitat binding is, as far as we are aware of, not known. That lack of understanding of the habitat features of essential importance for the occurrence of a particular species, goes through for very many spider species. In arachnology important gaps remain in our understanding of the habitat binding and autecology of species.

Two other species, *Lophomma punctatum* and *Lepthyphantes ericaeus*, were almost only and in quite large numbers caught in the very wet oligotrophic station B. Adults, mostly males of *Lepthyphantes ericaeus* were observed all year round, while adult males of *L. punctatum* were by far the most caught in March, only a few in February and April. *Lophomma punctatum* is indeed known as a species bound to very wet habitats, like wet grasslands and marshes; the habitats in which it occurs may not be too rich in shadow, it seems to prefer more open habitats (Lockett & Millidge, 1953; Wiehle, 1960; Palmgren, 1976; Roberts, 1987; Maurer & Hänggi, 1990; Heimer & Nentwig, 1991). Station B was indeed the most open wet woodland we sampled.

Because of its habitat choice the species is vulnerable in the northern part of Belgium. Very comparable in habitat choice in our country is *Lepthyphantes ericaeus*; because of that, it is not widely distributed. It is therefore surprising to read in the British literature (Locket & Millidge, 1953; Roberts, 1987) that it is a widely distributed species preferring dry habitats. That is really exceptional because in general the habitat descriptions found in Locket & Millidge (1953) for example agree very well with what we observe in Belgium. It would be interesting to study this difference a bit more closely.

The next species worth of discussing in more detail is *Oedothorax tuberosus*. In agreement with other observations of the species in our country (Maelfait & De Keer, 1988; De Keer & Maelfait, 1989) and with the literature (Locket & Millidge, 1953; Palmgren, 1976; Roberts, 1987; Maurer & Hänggi, 1990; Heimer & Nentwig, 1991) we only caught the species in the oligotrophic habitats and especially in the very wet sampling site B. The males of that species occur in two genetically determined morphs: forma *tuberosus* and forma *gibbosus* (De Keer & Maelfait, 1988; Maelfait et al, 1990a). In all populations we investigated we found the two forms mixed together. We, however, also observed changes in their relative abundance, in the ratio between the abundances of both forms. The reasons for this variation need to be further investigated. A possible reason is suggested in our data. Indeed, the percentages the captures of *gibbosus*, made during spring, respectively during summer, make up of the total catch of the complete year cycle are 6 and 83% (total catch: 66 individuals); for the *tuberosus*-form these percentages are: 33 and 49% (total number of individuals: 96). This means that *tuberosus*-males are active earlier in the year, while *gibbosus*-activity starts later but goes on for longer. This difference in activity pattern may be the result of a difference in developmental rate between both morphs. This would explain the co-occurrence of both types, be it in variable proportions: in a warm year or in a warm habitat the faster developing, the earlier female seeking males may be in a selective advantage (more fertilisations); in the reverse situations, the slower developing males would be in a selective advantage. However, as we already mentioned, more field and especially laboratory observations would be needed to solve this problem.

A clearly pronounced preference for the oligotrophic woodlots is also shown by *Centromerus dilutus* and *Antistea elegans*. *Centromerus dilutus* seems to be confined to this kind of habitat in Belgium (Maelfait et al., 1992). *Antistea elegans* can also be found in open habitats, like wet, unmanaged grasslands, dune slacks and marshlands (Dahl, 1937; Locket & Millidge, 1953; Palmgren, 1977; De Blauwe & Baert, 1981; Jones, 1984; Roberts, 1987; Maurer & Hänggi, 1990; Heimer & Nentwig, 1991).

Occurring in the four wet woodland types are the following species we sampled: *Agneta subtilis*, *Dicymbium tibiale* and *Agneta ramosa*. *A. ramosa* is quite rare (Locket & Millidge, 1953; Palmgren, 1975; Bosmans & Pollet, 1986; Pollet & Hublé, 1987; Roberts, 1987; Maurer & Hänggi, 1990; Van Keer & Van Keer, 1990; Heimer & Nentwig, 1991). Here it seems to prefer the mesotrophic alder carr. An open habitat in which we also found the species in large numbers is a lime rich dune slack with a well developed moss layer (Maelfait et al., 1990).

Only found in the mesotrophic woodlots and with a preference for the mesotrophic alder carr is *Glyphesis servulus*, a rare species, which can also be found in nutrient

poor, more open habitats like wet *Molinia* vegetation and nutrient poor wet grasslands (Locket et al., 1974; Roberts, 1987; Janssen & Maelfait, 1990; Maurer & Hänggi, 1990; Heimer & Nentwig, 1991).

The species which makes the difference between the mesotrophic sites dominated by Alder and the mesotrophic site planted by Poplar is *Saloca diceros*. This is a quite rare species (Locket & Millidge, 1953; Locket et al., 1974; Tips, 1978; Bosmans & Pollet, 1986; Pollet & Hublé, 1987; Roberts, 1987; Maurer & Hänggi, 1990; Heimer & Nentwig, 1991), which has in our country only been found in a few woodland habitats and a wet dune slack overgrown by Sea buckthorn (Maelfait et al., 1990; Segers & Heirman, 1991).

Species found in all sampled habitats but occurring in larger abundances in the wet ones are: *Bathyphantes gracilis*, *Walckenaeria cuspidata*, *Pachygnatha clercki*, *Pirata hygrophilus*, *Lepthyphantes zimmermanni*, *Centromerus sylvaticus*, *Diplostyla concolor* and *Walckenaeria nudipalpis*; none of these species is really rare.

Species found in all types, most of them without a preference for one or combinations of several types are: *Ceratinella scabrosa*, *Robertus lividus*, *Walckenaeria acuminata*, *Gonatum rubellum*, *Cicurina cicur*, *Clubiona lutescens*, *Lepthyphantes pallidus*, *Diplocephalus picinus*, *Clubiona compta*, *Centromerus aequalis*, *Saaristoa abnormis*, *Bathyphantes nigrinus*, *Lepthyphantes tenëbricola*, *Pachygnatha listeri*, *Microneta viaria* and *Lepthyphantes tenuis*.

Absent or almost absent from the oligotrophic sites are the following species: *Walckenaeria atrotibialis*, *Maso sundevalli*, *Walckenaeria dysderoides*, *Oxyptila trux* and *Gongylidium rufipes*.

Rather special distribution patterns are found in *Hahnia helveola*, *Hahnia montana*, *Lepthyphantes cristatus* and to a lesser degree in *Macrargus rufus* and *Coelotes terrestris*. These species occur in high number in the driest stations F and H, but also in relatively high numbers in the wet oligotrophic station. A possible explanation for this would be that in even these wet sites drier microhabitats occur like for instance the drier patches resulting from upgrowing *Sphagnum* carpets.

Found in all or almost all types but with a higher abundance in the drier habitats are: *Micrargus herbigradus*, *Monocephalus fuscipes*, *Pardosa amentata*, *Lepthyphantes flavipes*, *Agroeca brunnea*, *Hahnia pusilla* and *Trochosa terricola*.

Only or almost only found in the drier habitats are: *Xysticus lanio*, *Pardosa lugubris*, *Linyphia clathrata*, *Walckenaeria cucullata* and *Tegenaria picta*.

Xysticus lanio is a thomisid living on low scrubs in woodlands; it is only rarely found in our country (Jocqué, 1973; Janssen, 1993). Other special species found in these drier woodland types but in low numbers are: *Scotina celans* (cf. Locket & Millidge, 1951; Jones, 1984; Ransy et al., 1987), *Dysdera erythrina* (cf. Ransy & Baert, 1987), *Meioneta innotabilis* (cf. Denis, 1962; Wunderlich, 1971; Palmgren, 1975; von Broen, 1985; Roberts, 1987; Maurer & Hänggi, 1990; Heimer & Nentwig, 1991), *Hahnia ononidum* (cf. De Blauwe & Baert, 1981) and *Centromerus leruthi* (cf. Fage, 1933; Miller, 1958; Wunderlich, 1972; Maurer & Walter, 1980; Thaler, 1983; Thaler & Plachter, 1983; Bauchhenss et al., 1985; Maurer & Hänggi, 1990; Heimer & Nentwig, 1991; Maelfait et al., 1992). Faunistically interesting species found in low numbers in the wet stations are: *Theridiosoma gemmosum* (cf. Dahl, 1931; Locket

& Millidge, 1953; Bristowe, 1958; Jones, 1984; Roberts, 1985; Maurer & Hänggi, 1990; Van Keer & Van Keer, 1990; Heimer & Nentwig, 1991; Van Keer & Vanuytven, 1993) and *Maro sublestus* (cf. Saaristo, 1971; Moritz, 1973; Lockett et al., 1974; Merrett & Snazel, 1975; Palmgren, 1975; Merrett, 1982; Heimer & Nentwig, 1991).

CONCLUSION

The above given results show that in spite of artificial tree layers our riverine forests still contain very interesting spider assemblages. Their composition is highly influenced by the hydrology of a particular stand. The composition of the tree layer is of minor importance. In our opinion, this result gives hope for the future: in spite of tree layers with a low diversity, there still remains a high biodiversity in the ground-living spider communities of these forests. These communities will develop themselves even more when more opportunities will be given to spontaneous developments in forest management.

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