

Succession of Diptera on dead beech wood: A 10-year study

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Summary

This study describes the decomposition of dead beech wood and the succession of xylobiont Diptera. Branch wood ($\varnothing = 4.3\text{--}11.5\text{ cm}$) was sampled from two beech trees felled by wind in autumn 1984. In each spring (1987–1995) 6 to 8 logs were selected and placed individually in closed emergence traps to collect adult Diptera. Decay state of the logs was described by measuring relative density, water content, bark cover, moss cover, litter cover, carbon and nitrogen contents, C:N ratio, and residual weight. Overall, the environmental factors decreased or increased with log age as expected but variation within cohorts was considerable. For some common dipteran species clear temporal patterns of occurrence were identified, and it was also possible to relate abundances of some species to individual environmental factors. On the community level, mean number of individuals per log tended to increase with log age, suggesting that dead wood becomes a more rewarding food resource in the course of decomposition. Diversity of Diptera measured as the mean number of species per log increased with log age, indicating that resource heterogeneity increased with log age. Diversity of Diptera also increased with water content and moss cover but was negatively correlated with bark cover, C:N ratio, and relative density.

Key words: Dead beech wood, decomposition, succession, saproxylic Diptera, diversity

Introduction

Dead wood constitutes an important part of forest litter in deciduous woodlands (Bray & Gorham 1964), where it forms ‘centres of action’ (Elton & Miller 1954). Decomposition of woody litter is initiated by leaching and activity of microorganisms, later on, more or less specialized arthropods may invade followed by their predators and parasitoids (Harmon et al. 1986). Species depending essentially on dead wood as primary or higher order consumers during some part of their life cycle have been termed ‘saproxylic’ by

Speight (1989), but the fauna of dead wood often also includes species less strictly associated with this micro-habitat (Hövemeyer 1998).

Owing to its low content of nutrients (Swift 1977a) decomposition of dead wood takes many years in temperate forests. As decomposition proceeds, habitat properties change (Swift 1977a,b; Swift et al. 1976), and it is reasonable to assume that arthropod colonization is influenced by such changes resulting in successional patterns. For example, emergence abundances

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of many dipteran families increased with the age of dead beech wood (Kleinevoss et al. 1996).

Diptera form an important part of the saproxylic fauna but only few studies have looked at Diptera associated with dead wood (e.g., Derksen 1941; Irmeler et al. 1996; Kleinevoss et al. 1996; Haase et al. 1998; Hövemeyer 1998). These studies do not only differ in taxonomical resolution but also in the tree species considered and the methods used to assign dead wood to different stages of decay.

Basically, three kinds of classification can be distinguished: The state of decay and the types of dead wood are qualitatively classified (e.g., Irmeler et al. 1996; Hövemeyer 1998); (ii) The age of the dead wood studied is known, e.g., after fellings or windbreaks (e.g., Derksen 1941; Nicolai 1995); (iii) Quantitative measurements of certain properties of dead wood are taken; these may include relative density (Healey & Swift 1971; Swift et al. 1976; Christensen 1984), chemical analyses (Healey & Swift 1971; Swift 1977a), or determination of wood hardness using a resistograph (Kleinevoss et al. 1996; Haase et al. 1998).

Using dead branch wood collected from two beech trees felled by wind, the present study combines all three approaches with a sampling programme focussing on the succession of Diptera. This allowed us to study the relationship between the abundance of individual dipteran species and both the age of the dead wood and its environmental properties.

Feeding habits of dipteran larvae are highly diverse (Ferrari 1987; Hövemeyer 2000), and dead wood can mean different things to different species: it provides food for xylosaprophagous larvae and, indirectly, mycetophages and zoophages; it can be attractive to hygrophilous species, particularly after establishment of moss cushions; it may also form a pupation or hibernation site for species not related to wood decomposition (Hövemeyer 1998).

Owing to its low nutritive value when fresh, dead wood develops from a fairly homogeneous unfavourable habitat towards a more heterogeneous one with a moisture gradient establishing, colonizing fungi providing more rewarding food, and occasional moss cushions establishing. We, therefore, hypothesized that abundance and species richness of Diptera should increase with the age of the dead wood.

In summary, there are four aims to this study: (i) to describe the process of decomposition in rather small branches of dead beech wood, (ii) to look for successional patterns in Diptera associated with dead beech wood, (iii) to look at the relationship between the abundances of dipteran species and environmental factors, and (iv) to test hypotheses on the change in the abundance and diversity of Diptera during dead wood decomposition.

Materials and Methods

The study was conducted in a beech forest on limestone near Göttingen (Dierschke & Song 1982) and started after two beech trees had been felled by autumn storms in 1984. Eleven branches ($\text{Ø}=4.3\text{--}11.5\text{ cm}$) were selected, from which 65 logs (each some 30 cm long) were sawn off. Prior to exposure, diameter and volume (water displacement) of the fresh logs were recorded. Then the logs were placed individually on sheets of plastic gauze (mesh width = 0.3 mm) and arranged on the forest floor on a grid with 2m distance between and within rows.

During the following year (1985), the logs were left untouched in order to let dipteran females oviposit. However, in the next spring (1986), the logs did not show any sign of animal activity at all, so they were left in place for another year of exposure (1986). Sampling started in spring 1987, i.e. after roughly two years of exposure, and comprised the following steps:

(1) Six logs were randomly selected but care was taken not to select two logs from the same branch. For each log the percentages of bark cover, litter cover, and moss cover were estimated (The variable 'litter cover' describes the degree to which the logs were incorporated into the litter layer of the forest floor). Leaf litter and other loosely attached material was removed and wet weight of each log was determined.

(2) A hole ($\text{Ø}=1\text{ cm}$) was drilled vertically through each log and the bore-meal used for further analyses: (2a) The bore-meal was weighed fresh, then dried for 4 days at 60 °C, and weighed again in order to obtain an estimate of water content. (2b) Then the bore-meal was ground to dust and samples were analysed for carbon and nitrogen contents using a Carlo Erba analyzer.

(3) Each log was put into an emergence trap made of a conical plastic flower pot (max. $\text{Ø}=40\text{ cm}$) with a collecting vial at the top (preservative: picric acid). The traps were set up in the forest with the bottom closed using fine plastic gauze (mesh width = 0.3 mm). The collecting vials were emptied three times a year: in summer (June/July), autumn (September/October), and spring (March/April of the next year). These three collections were treated collectively giving the catch for "year 1". But the logs were left in the emergence traps for another year, in order to account for species larval development of which may take more than one year. During the second year, the traps were emptied on the same dates as for "year 1" giving the catches for "year 2".

Sampling as described above was repeated for nine years until 1995, however, in some years seven or eight logs were selected for sampling. So there were nine cohorts, which are defined by the number of years

of exposure, and two years of collecting within each cohort. Since some traps were destroyed by fallen branches the overall sample size reduced to $n = 62$.

Most families were identified to species and species were assigned to trophic groups according to larval feeding habits. These trophic groups have been defined elsewhere (e.g. Hövemeyer 1996), so only the abbreviations used will be given here: HyPi = hyphae piercers, PS = phytosaprophagous species feeding on leaf litter, PSx = phytosaprophagous species with a preference for dead wood according to the literature, X = xylosaprophagous species, MAMY = macro-mycetophages, Z = zoophages, Zx = zoophagous species with a preference for dead wood according to the literature, SS = surface scrapers, MI = microsaprophagous feeders, PaPs = parasitoids of phytosaprophagous hosts, ZS = zoosaprophages, PH = phytophages, PhPa = parasitoids of phytophages.

Precipitation rates during summer were calculated as the sum of monthly precipitation rates from May till August using data from the weather station at Göttingen (Deutscher Wetterdienst). This parameter was included because abundances of some dipteran species tend to increase with high precipitation rates in the summer preceding the year of emergence (Herlitzius 1987; Hövemeyer 1991).

Both MVSP 3.1. and CANOCO 4.02 were used to perform canonical correspondence analyses.

Results

Weather conditions

Summer precipitation (i.e., precipitation rates in the year prior to sampling) varied considerably during the study (Fig. 1) and three periods may be distinguished: The first two years were quite moist, followed by five fairly dry years, and the final two years were rather moist again.

The fate of the logs

Random sampling of the logs resulted in a fairly equal representation of differentially-sized logs within the cohorts, which did not differ significantly in this respect (Fig. 1; Kruskal-Wallis test: $H = 1.869$; n.s.). Therefore, species numbers and abundance values of Diptera for individual cohorts will be given as mean numbers per log below.

In the course of the study some of the environmental factors (litter cover, moss cover, water content, and nitrogen content) tended to increase while other factors decreased (Fig. 2). Moss cushions of reasonable size occurred only after six to seven years of exposure. Overall, trends were as expected, however, variation within cohorts was considerable.

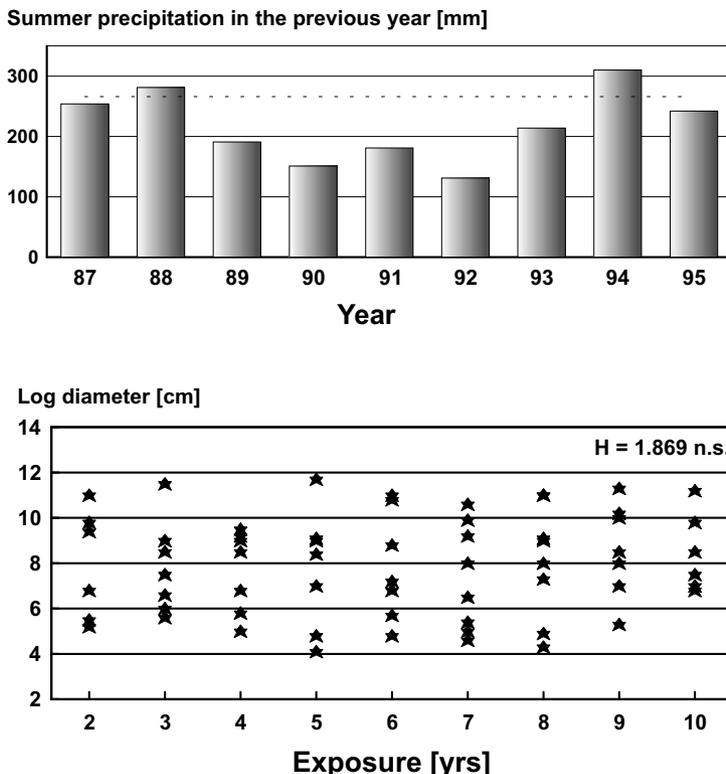


Fig. 1. Summer precipitation rates recorded for the years preceding the starting year of sampling for nine cohorts (upper panel; the stippled line indicates the long-term mean (1931–1980)) and size distribution of the logs selected in each cohort (lower panel)

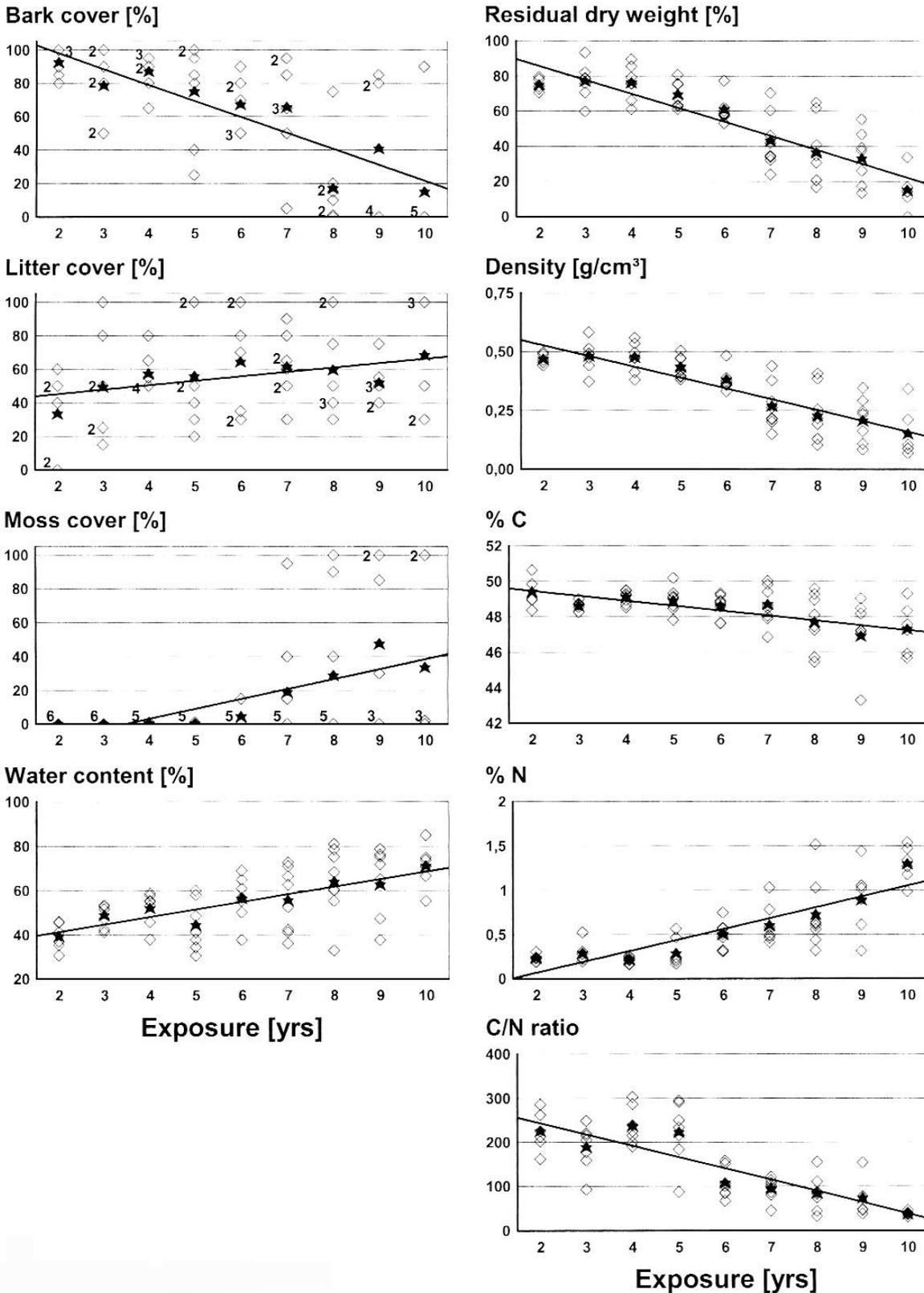


Fig. 2. Changes in environmental factors with time of exposure. Diamonds represent individual logs (identical values are indicated by numbers) and asterisks cohort means. Lines indicating trends are linear regressions for cohort means and significant ($p < 0.05$) in all cases excepting litter cover

Table 1. Correlations between environmental factors. Values given are Spearman rank correlation coefficients (r_s); $n=62$

	prec	diam	litt_c	expo	%N	water	moss_c	%C	bark_c	C/N	density	%rest
precipitation	1							-0.25				
log diameter		1	-0.63				0.36					
litter cover		-0.63	1		0.35	0.31			-0.22	-0.36		
exposure				1	0.81	0.59	0.44	-0.51	-0.65	-0.81	-0.83	-0.83
%N			0.35	0.81	1	0.64	0.36	-0.44	-0.49	-0.99	-0.79	-0.79
water content			0.31	0.59	0.64	1	0.41	-0.33	-0.43	-0.66	-0.66	-0.66
moss cover		0.36		0.44	0.36	0.41	1	-0.38	-0.36	-0.36	-0.44	-0.44
%C	-0.25			-0.51	-0.44	-0.33	-0.38	1	0.28	0.48	0.48	0.48
bark cover			-0.22	-0.65	-0.49	-0.43	-0.36	0.28	1	0.51	0.50	0.50
C:N ratio			-0.36	-0.81	-0.99	-0.66	-0.36	0.48	0.51	1	0.80	0.80
density				-0.83	-0.79	-0.66	-0.44	0.48	0.50	0.80	1	1.00
%residual dry weight				-0.83	-0.79	-0.66	-0.44	0.48	0.50	0.80	1.00	1
	p	<0.05	<0.01	<0.001								

Rank correlation was used to test for significant relationships between environmental factors (Table 1). Precipitation (in the previous summer), log diameter and litter cover were only rarely correlated with any of the other variables and if so at rather low significance levels. The highly significant negative correlation between litter cover and log diameter simply indicates that thick logs are less likely to be covered by leaf litter than thin ones. Relationships between all other factors are highly significant (positively or negatively) excepting moss cover.

Catches of Diptera – General results

Overall, 11,616 adult Diptera were caught, which represented 37 Families. 163 species were identified with Sciaridae and Mycetophilidae being the most species-rich families (see Appendix 1 for species names and abundance values). 46% of the species were represented by just one or two individuals in the total catch and more than two thirds of the species were recorded from no more than one or two logs. This renders most species unsuitable for an analysis of successional patterns.

Temporal patterns in dipteran emergence abundances

For all species the mean age of the logs from which the flies had emerged was calculated (Appendix 1: “mExp”): First, the mean number of individuals per log was calculated for each cohort, then the mean log age was determined using abundance values as weights, and for species recorded from more than one cohort standard deviations are also given (Usher 1970). The „mExp“-values (Appendix 1) give a rough

indication of the species’ temporal emergence patterns.

Temporal patterns of emergence abundances of a few selected taxa are shown in Fig. 3: *Medetera* species (Fam. Dolichopodidae) and *Xylophagus compeditus* (Fam. Xylophagidae) appeared to be associated with fairly young logs.

Tipula flavolineata emerged from the logs only after 3–4 years of exposure. This species is associated with white rot branches (Brauns 1954; Hövemeyer 1998). Some adults occurred in the catches from “year 2” in cohorts 3 to 7 (Fig. 3). It is possible that nutritive quality of the logs was still too low and/or that drought (Fig. 1) reduced food availability, both resulting in prolonged larval development.

Symmerus annulatus (Ditomyiidae) occurred only on medium-aged logs, but no ecological information explaining this pattern seems to be available.

Some species appeared to be largely restricted to later stages of wood decay (Fig. 3): *Caenosciara lucifuga* (Sciaridae), *Euthyneura myrtilli* (Hybotidae), *Cordyla fissa* (Mycetophilidae; not shown), and *Neolimonia dumetorum* (Limoniidae).

Other quite abundant taxa such as the Lestremiinae (Cecidomyiidae), the sciarids *Lengersdorfia flabelata*, *Epidapus atomarius*, *Scatopsciara pusilla*, and *Bradysia fungicola*, and the mycetophilid *Brevicornu crassicornis* did not exhibit any clear temporal pattern (not shown).

Finally, there are some species with a bi-modal pattern: *Corynoptera clinochaeta* (Sciaridae) is a litter-dwelling species, the abundance pattern of which (Fig. 3) clearly reflects the positive effect of moist summers (Fig. 1) on population size. High moisture can account for the first peak in the abundance graphs of *Atricho-*

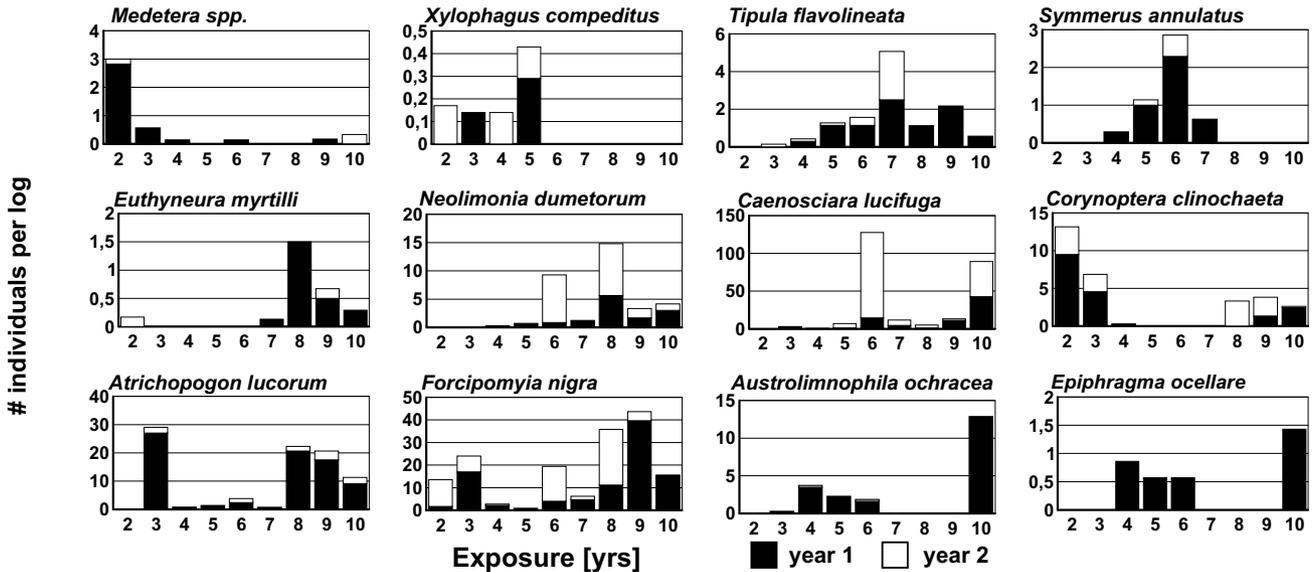


Fig. 3. Mean emergence abundances of selected dipteran species in the course of succession. Catches from “year 1” and “year 2” (see Materials and Methods) are indicated by different shadings

pogon lucorum and *Forcipomyia nigra* (Ceratopogonidae), however, both these species are also typical inhabitants of moss cushions, so the second peak is probably partially due to the establishment of moss cushions on the logs (see below).

A bi-modal pattern also occurred in the limoniid species *Austrolimnophila ochracea* and *Epiphragma ocellare*. But in both these species, the first peak coincided with dry years. For both species there are probably two phases during which dead wood is attractive: The first occurs, when the decomposing inner bark forms a suitable larval habitat and the second one, when logs have been covered by leaf litter and the moist wood itself becomes a utilizable food resource.

Abundance of Diptera and environmental conditions

Clear temporal patterns could be identified in only a few cases. This is perhaps not surprising in view of the large variability of environmental factors within individual cohorts (Fig. 2). However, ovipositing females are in fact more likely to respond to the environmental properties of a log than to its age per se.

A canonical correspondence analysis (CCA) was performed in order to evaluate relationships between species abundances and environmental factors (Fig. 4). Only species recorded from six or more logs in “year 1” catches were considered. Removing ‘% residual weight’ from the analysis resulted in variance inflation factors <6. Log diameter ($p < 0.025$), precipitation ($p < 0.005$), water content ($p < 0.005$), %C

($p < 0.001$), and %N ($p < 0.01$) contributed significantly to the variance explained by environmental factors (Monte Carlo permutation test; CANOCO 4.02), while the other factors ($P > 0.05$) did not.

Eigenvalues of axes 1 and 2 were 0.222 and 0.161, respectively (Fig. 4) and rather low compared to those obtained from a detrended correspondence analysis of the same species data (axis 1: 0.375, axis 2: 0.269; not shown). Only 14 % of the variance were explained by the first two axes, so there is little need to bother about further axes. Overall, axis 1 appears to reflect a gradient from young (right) to older logs (left), while axis 2 represents a gradient from young (top) to more decomposed logs (bottom) characterized by a variety of different attributes. More specifically, axis 1 represents a %C gradient (intraset correlation: -0,419) but correlations for bark cover and water content are only slightly weaker. Axis 2 represents a density gradient (0.673) but coefficients for diameter, water content, and %C are not much lower. The environmental factors included explain some part of the variation in species composition but cannot provide a full explanation (Jongman et al. 1987).

The resulting joint plot (Fig. 4) should therefore be interpreted tentatively. Instead of including all 62 logs, only the centroids for the nine cohorts are shown (Fig. 4: triangles). The first two cohorts (‘87 and ‘88) are clearly located in quadrant I, while the remaining ones are located more or less close to the origin.

With respect to individual species the emerging patterns are: Quadrant I contains at least two litter-dwelling species (*C. clinochaeta* and *T. saltator*),

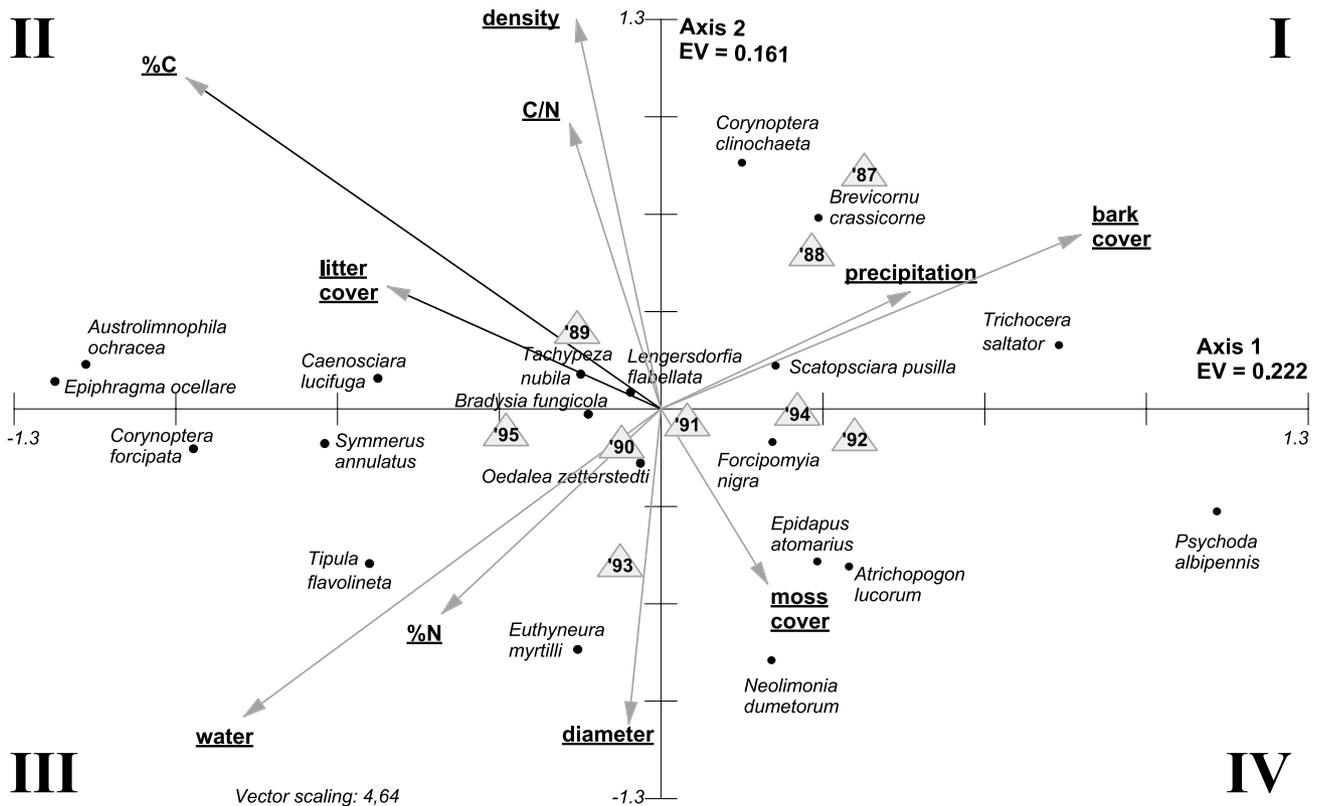


Fig. 4. Joint plot of dipteran species and environmental factors of dead beech wood; triangles indicate the centroid position of the nine cohorts. EV = eigenvalues

which may be favoured by high summer precipitation rates. Quadrant II contains species most abundant on moist logs with little bark cover (*A. ochracea*, *E. ocellare*, *C. lucifuga*). *T. flavolineata* (quadrant III) responded positively to logs with high contents of water and low density. *E. myrtilli* would probably be better placed in quadrant IV, which contains some inhabitants of moss cushions. The position of *N. dumetorum*, however, is certainly not due to a preference for moss cushions but for strongly decayed logs with low density and C:N ratios (see below).

Since it proved difficult to assign a species' distribution unambiguously to a single factor based on this CCA, and since it is implicit to CCA that 'species react to the same composite gradients of environmental factors' (Jongman et al. 1987), which may not apply to all species considered here, we also looked at the species' abundances in response to the ten environmental factors in isolation.

For each species included in the CCA, correlations between abundance and the ten environmental factors were determined using Spearman rank correlation (Table 2). Based on the findings of Hövemeyer (1998), four ecological groups of Diptera were differentiated. Predictions on their responses to individual

environmental factors were formulated, which are indicated in the title row of the respective group (Table 2). These predictions were tested using a one-sided test, while in all other cases two-sided tests were used to identify significant correlations.

Table 2 shows results from 42 one-sided tests and 158 two-sided tests. This implies that two and eight results, respectively, with $p < 0.05$ may have cropped up merely by chance. Therefore only p -values < 0.025 should be considered significant.

Litter-dwelling species: These species were expected to be favoured by high precipitation rates in the previous summer but this prediction only applied to *C. clinochaeta*. Generally, correlations with $p < 0.05$ were rare in this group. The pattern of low p -values in *C. forcipata* was similar to those of the *C. lucifuga* and *T. flavolineata* (see below) suggesting that *C. forcipata* may be a saproxylic species, too.

Moss cushion species: Mean abundances of these species were predicted to increase with moss cover and log diameter, and to decrease with litter cover. The prediction on moss cover was tested using only data from 1990 onwards, i.e., for those years when moss cushions were actually present. All three species appeared to be positively influenced by the presence of moss

Table 2. Relationships between environmental factors and abundances of dipteran species from four ecological groups [Trophic groups are indicated in brackets]. Spearman correlation coefficients ($r_s < 0.10$) are given along with the corresponding p-values. P-values < 0.05 are printed in bold letters. Shaded areas indicate one-sided tests, with the predicted trend (+ or -) indicated in the respective title row

	prec	diam	litt_c	%N	water	moss_c	%C	bark_c	C/N	density
n =	9	62	62	62	62	42	62	62	62	62
Litter dwelling species	+									
<i>Corynoptera clinochaeta</i> [PS]	0.79 0.013									
<i>Corynoptera forcipata</i> [PS]					0.32 0.012			-0.32 0.014		
<i>Epidapus atomarius</i> [PS]		0.25 0.054								
<i>Lengersdorfia flabellata</i> [PS]		0.30 0.018				0.27 0.078				-0.22 0.088
<i>Scatopsiara pusilla</i> [PS]		0.37 0.004						0.24 0.066		
<i>Trichocera saltator</i> [PS]		0.24 0.060								
Moss cushion species		+	-			+				
<i>Atrichopogon lucorum</i> [MI]	0.50 0.079	0.32 0.007				0.29 0.033	-0.27 0.016			-0.26 0.044
<i>Euthyneura myrtilli</i> [Zx]				0.36 0.004	0.25 0.054	0.34 0.016	-0.41 0.001	-0.27 0.036	-0.34 0.008	-0.27 0.038
<i>Forcipomyia nigra</i> [MI]	0.62 0.082	0.28 0.015	-0.32 0.006			0.23 0.073				
Saproxylic species				+	+			-	-	-
<i>Austrolimnophila ochracea</i> [X]					0.24 0.032		0.25 0.054			
<i>Caenosciara lucifuga</i> [PSx]					0.30 0.009			-0.24 0.032		
<i>Epiphragma ocellare</i> [X]										
<i>Neolimonia dumetorum</i> [PSx]		0.24 0.062		0.27 0.019	0.38 0.002		-0.35 0.006	-0.20 0.058	-0.27 0.016	-0.42 0.0006
<i>Oedalea zetterstedti</i> [Zx]					0.25 0.026			-0.18 0.076		
<i>Tipula flavolineata</i> [X]		0.33 0.010			0.37 0.002			-0.29 0.013		-0.26 0.019
unplaced species										
<i>Bradysia fungicola</i> [PS]		0.25 0.052								
<i>Brevicornu crassipes</i> [MAMY]				-0.27 0.034	-0.27 0.034				0.27 0.032	0.29 0.024
<i>Psychoda albipennis</i> [MI]							-0.30 0.020			
<i>Symmerus annulatus</i> [MAMY]	-0.84 0.018									
<i>Tachypeza nubila</i> [Z]				0.25 0.046	0.35 0.006	0.29 0.066			-0.24 0.056	-0.025 0.050
		+			+	+		-	-	-
mean species number per log		0.30 0.010		0.22 0.092	0.49 0.0001	0.43 0.0004	-0.23 0.072	-0.24 0.032	-0.23 0.036	-0.30 0.010

cushions. The two ceratopogonids, *A. lucorum* and *F. nigra*, also tended to be more abundant in years preceded by moist summers. In the zoophagous *E. myrtilli* many correlations with $p < 0.05$ to factors reflecting nutritive quality were found, which probably rather reflect preferences of its prey species.

Saproxyllic species: In this group mean abundances were predicted to increase with water content and %N and to decrease with density, % bark cover, and C:N ratio. Almost all species were positively affected by high water content. Abundance of *E. ocellare*, however, was not correlated to any environmental factor, while abundance of *N. dumetorum* was correlated to a large number of environmental factors. *T. flavolineata* appeared to prefer thick low-density logs. All environmental factors related to food quality were only rarely correlated with abundances in this group.

Unplaced species: *T. nubila* and *B. crassipes* appear to respond to environmental factors in a way similar to saproxyllic species. In the other species of this

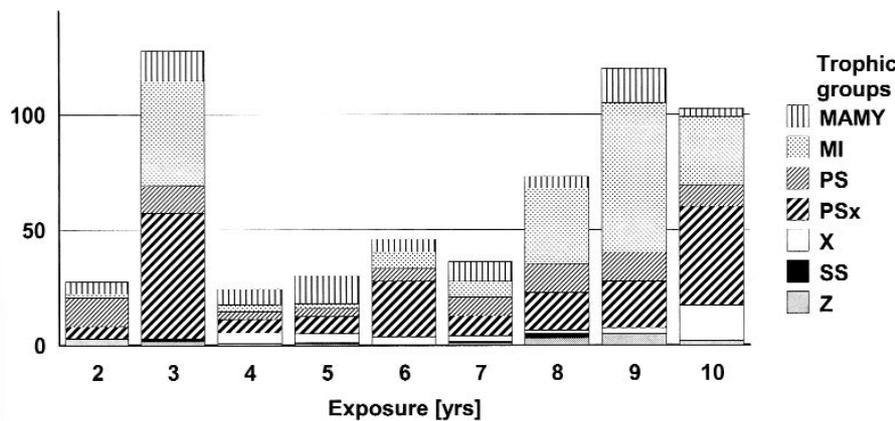
group correlations with $p < 0.05$ are rare. The negative correlation between precipitation and abundance of *S. annulatus* is due to the species' emergence pattern which is restricted to dry years (Fig. 3). It is unknown, whether this correlation reflects a cause-and-effect relationship.

Abundance and diversity in the course of succession

Dead wood can mean different things to different dipteran species and catches may also contain species which are not directly involved in the decomposition of dead wood. So only trophic groups linked more or less closely to wood decay as primary or higher order consumers will be considered here.

Abundance and diversity of emerged Diptera were measured in terms of mean number of individuals per log and mean number of species per log, respectively (Fig. 5). Results presented here are based on the

Mean # individuals per log



Mean # species per log

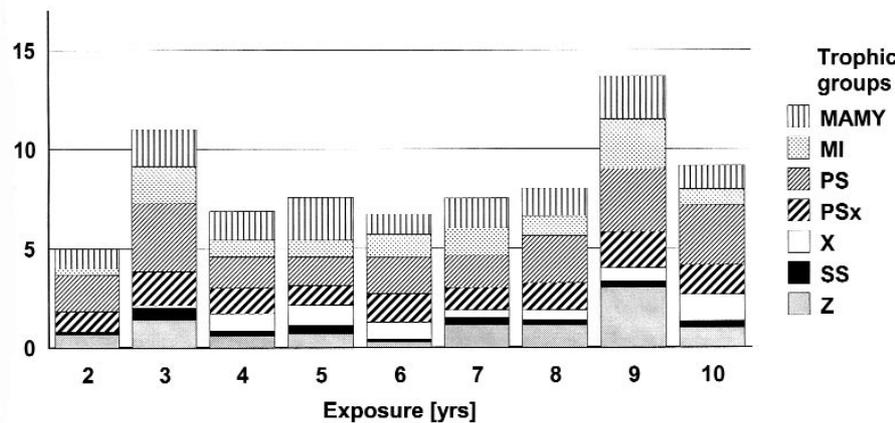


Fig. 5. Changes in mean abundances (upper panel) and mean species densities of Diptera (lower panel) with log age. See Materials and Methods for abbreviations of trophic groups

catches of “year 1” (however, both results for catches from “year 2” and the total catch exhibit similar patterns). Mean total abundance tended to increase with the age of the logs (Fig. 5). But this pattern is disturbed by the high value for cohort 3, which corresponds to 1988, a year preceded by a very moist summer (Fig. 1). Nevertheless, the positive relationship between emergence abundance and exposure is almost significant (Spearman rank correlation: $r_s=0.467$; $p=0.093$; $n=9$; one-sided test). If cohorts 3 and 9, i.e. the cohorts following moist summers, are omitted as outliers, the positive trend is highly significant ($r_s=0.929$; $p=0.011$; $n=7$; one-sided test). As to individual trophic groups, microhumiphages (MI) and phytosaprophages associated with dead wood (PSx) increased in numbers with log age ($r_s=0.893$; $p=0.014$ in both cases).

One might predict that abundance of Diptera should increase with high summer precipitation rates in the previous year, however, there was no significant trend of this kind (all cohorts: $r_s=0.57$; $p=0.054$; $n=9$; one-sided test; cohorts 3 and 9 omitted: $r_s=0.11$; $p=0.396$; $n=7$; one-sided test).

Mean number of species per log, i.e. species density, tended to increase with log age but the distorting effect of cohort 3 is again visible (Fig. 4). Correlation between total species density and log age was almost significant ($r_s=0.533$; $p=0.066$) for the whole data set and highly significant after cohorts 3 and 9 had been omitted as outliers ($r_s=0.821$; $p=0.022$). Phytosaprophages associated with dead wood (PSx) are the only trophic group species density of which was significantly correlated with log age ($r_s=0.750$; $p<0.05$). Mean species density was not correlated to summer precipitation rates in the previous year ($p>0.35$) but to some other environmental factors (Table 2; bottom line). It tended to increase with log diameter, which is not surprising since big logs should be inhabited by more species than small ones. More importantly, species density increased with moss cover and water content; the negative correlations to bark cover, relative density, and C:N ratio were as expected but much weaker (Table 2).

Discussion

Only few studies have looked at Diptera emerging from dead wood, hence, there are few data to which the findings of the present study can be compared. Previous studies (Kleinevoss et al. 1996; Haase et al. 1998; Hövemeyer 1998) reported abundance values ranging from 8 to 54 individuals per litre of dead wood for branches similar in size to those studied here; the respective value for the present study calculated across all cohorts is 76 individuals per litre (catches from year

1 only), so the trapping method employed appears very efficient.

The present study is unique in sampling flies emerging from individual logs for two years. This idea originated from previous findings (Swift et al. 1984; pers. observation) on *Tipula flavolineata* suggesting that some saproxylic species may take more than one year to complete larval development. This is probably true for some large species (Tipulidae, Limoniidae) and perhaps also for some predators (e.g., *X. compeditus*; Fig. 3). But high abundance values in “year 2” of small saprophagous species can be interpreted only with difficulty. It was both surprising and interesting to find so many individuals and species occurring in the catches from “year 2” (Appendix 1), but whether this was due to successful reproduction inside the traps, retarded larval development, and/or delayed emergence is unknown.

As to the temporal patterns of dipteran emergence abundances, Derksen (1941) found that *Neolimonia dumetorum* and *Euthyneura* spp. occurred on old (10 years) and *Tipula flavolineata* on medium-aged (4–6 years) beech stumps. This is in rough accordance with the findings of the present study. Activity of *T. flavolineata* was highest in but not restricted to logs with relative densities between 0.1–0.3 g/cm³ (Swift et al. 1984). This is in full accordance with the results of the present study. While relative density is usually measured as a property of the entire log, decomposition may proceed faster in some parts of it than in others, and this may account for the occurrence of *T. flavolineata* in logs with high overall relative density.

More generally, it proved very difficult to identify relationships between abundance of dipteran species and environmental factors. This is due to several reasons: While there is probably environmental heterogeneity within individual logs, there is certainly high variability within cohorts (Fig. 2), since every log undergoes a very special decomposition process (Derksen 1941). Furthermore, most species are highly aggregated: for example, *Scatopsiara pusilla* was recorded from 32 logs but 19% of the individuals were reared from a single log, and many other species exhibited similar distributional patterns. Another problem is that many potentially suitable logs were left uncolonized: for example, *Euthyneura myrtilli* was recorded from three logs with moss cover >85% but was absent from the remaining four logs in the same cover class. Similar patterns hold for *Atrichopogon lucorum*, *Forcipomyia nigra* and several other species. The combined effects of distributional inconsistencies of this kind result in severe difficulties in identifying statistically significant relationships between environmental factors and fly abundances even in the more common species.

In view of these difficulties, it was surprising to find that – on the community level – abundance and diversity of xylobiont Diptera tended to increase with log age as predicted, even if the patterns were somewhat obscured by the effect of high precipitation rates in some years. Water content and moss cover were strongly correlated with species density and are probably the strongest driving forces promoting diversity of xylobiont Diptera in logs of this size. Towards the end of the decomposition process species diversity might be expected to decline, because the remaining material will become more and more homogeneous again. A decline of this kind, however, did not become obvious in the course of this 10-year study.

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Appendix 1. Species list of Diptera reared from dead beech wood. TG = trophic group (see Materials and methods for abbreviations); Freq = frequency; mExp = mean year of emergence in terms of log age; SD = standard deviation; b = bimodal distribution

	TG	Freq (n)	#ind. year1	#ind. year2	#ind. total	mExp years	SD
Trichoceridae							
<i>Trichocera hiemalis</i> (DEGEER, 1776)	PS	2	2	3	5	3	
<i>Trichocera major</i> EDWARDS, 1921	PS	1	1		1	8	
<i>Trichocera parva</i> MEIGEN, 1804	PS	1		1	1	6	
<i>Trichocera saltator</i> (HARRIS, 1776)	PS	11	19	14	33	6,3	2
Tipulidae							
<i>Tipula flavolineata</i> MEIGEN, 1830	X	19	64	24	88	7,1	1,5
<i>Tipula irrorata</i> MACQUART, 1826	PS	1	1		1	10	
Limoniidae							
<i>Austrolimnophila ochracea</i> (MEIGEN, 1804)	X	11	143	4	147	7,9	2,6b
<i>Cheilotrichia cinerascens</i> (MEIGEN, 1804)	PS	3	8	1	9	3,2	0,6
<i>Chionea belgica</i> (BECKER, 1912)	PS	4	4	2	6	4,6	1,7
<i>Epiphragma ocellare</i> (LINNAEUS, 1761)	X	7	24		24	7	2,6b
<i>Neolimonia dumetorum</i> (MEIGEN, 1804)	PS	17	99	131	230	7,6	1,4
<i>Molophilus appendiculatus</i> STAEGER, 1840	PS	2	2		2	6,4	1,5
<i>Ormosia lineata</i> (MEIGEN, 1804)	PS	6	5	1	6	5,6	2,8
<i>Tasiocera fuscescens</i> (LACKSCHEWITZ, 1940)	PS	1	1		1	6	
<i>Tasiocera murina</i> (MEIGEN, 1818)	PS	3	5		5	4,6	0,8
Pediciidae							
<i>Ula sylvatica</i> (MEIGEN, 1818)	PS	1	1		1	9	
Psychodidae							
<i>Pericoma spec.</i>	MI	1		1	1	6	
<i>Psychoda albipennis</i> ZETTERSTEDT, 1850	MI	15	50	47	97	6,9	2,2
<i>Philosepedon humeralis</i> (MEIGEN, 1818)	MI	1	2		2	9	
<i>Psychoda gemina</i> (EATON, 1904)	MI	4	6	148	154	7,9	0,7
<i>Psychoda parthenogenetica</i> TONNOIR, 1940	MI	2	2	4	6	4	1
<i>Psychoda severini</i> TONNOIR, 1922	MI	7	31	15	46	8	2,2
<i>Trichomyia urbica</i> HALIDAY IN CURTIS, 1839	MI	2	1	1	2	8,1	1
Chironomidae							
Ceratopogonidae							
<i>Atrichopogon lucorum</i> (MEIGEN, 1818)	MI	18	558	70	628	6,7	2,7b
<i>Forcipomyia nigra</i> (WINNERTZ, 1852)	MI	40	652	417	1069	6,8	2,7b
Bolitophilidae							
<i>Bolitophila hybrida</i> (MEIGEN, 1804)	MAMY	1	1		1	5	
Ditomyiidae							
<i>Symmerus annulatus</i> (MEIGEN, 1830)	MAMY	7	30	5	35	5,8	0,7
Keroplastidae							
<i>Isoneuromyia semirufa</i> (MEIGEN, 1830)	MAMY	1		1	1	3	
<i>Macrocera pusilla</i> (MEIGEN, 1830)	Z	1		1	1	3	
<i>Macrocera vittata</i> (MEIGEN, 1830)	Z	1	1		1	10	
<i>Macrocera</i> indet. females	Z	1	1		1	8	
<i>Neoplatyura modesta</i> (WINNERTZ, 1863)	MAMY	2	3		3	8,7	1
<i>Orfelia fasciata</i> (MEIGEN, 1804)	MAMY	3	1	3	4	5,8	2,8
<i>Rutylapa ruficornis</i> (ZETTERSTEDT, 1851)	MAMY	1		1	1	10	
<i>Urytalpa ochracea</i> (MEIGEN, 1818)	MAMY	1		1	1	4	
Mycetophilidae							
<i>Acnemia amoena</i> WINNERTZ, 1863	MAMY	1		2	2	3	
<i>Allodia lugens</i> (WIEDEMANN, 1817)	MAMY	1		1	1	7	
<i>Allodia spec.</i>	MAMY	1		1	1	6	
<i>Anatella setigera</i> EDWARDS, 1921	MAMY	1		7	7	3	
<i>Anatella</i> indet. females	MAMY	1		1	1	7	
<i>Boletina gripha</i> DZIEDZICKI, 1885	MAMY	1		1	1	7	
<i>Boletina moravica</i> LANDROCK, 1912	MAMY	1	1		1	5	
<i>Boletina</i> indet. females	MAMY	9	11	4	15	4,3	0,8

	TG	Freq (n)	#ind. year1	#ind. year2	#ind. total	mExp years	SD
<i>Brachypeza spec.</i>	MAMY	1	1		1	8	
<i>Brevicornu crassicorne</i> (STANNIUS, 1831)	MAMY	45	263	178	441	5,6	2,5
<i>Brevicornu griseicolle</i> (STAEGER, 1840)	MAMY	1	1		1	9	
<i>Brevicornu sericoma</i> (MEIGEN, 1830)	MAMY	1	3		3	8	
<i>Cordyla brevicornis</i> (STAEGER, 1840)	MAMY	1	2		2	7	
<i>Cordyla crassicornis</i> MEIGEN, 1818	MAMY	1	1		1	5	
<i>Cordyla fissa</i> EDWARDS, 1925	MAMY	13	25	70	95	8,2	1,5
<i>Cordyla flaviceps</i> (STAEGER, 1840)	MAMY	1		1	1	8	
<i>Cordyla</i> indet. females	MAMY	3	2	1	3	4,4	2,1
<i>Docosia gilvipes</i> (WALKER, 1856)	MAMY	1	1		1	8	
<i>Ectrepesthoneura hirta</i> (WINNERTZ, 1846)	MAMY	12	19	40	59	7,4	2,1
<i>Ectrepesthoneura colyeri?</i> CHANDLER, 1980	MAMY	1	1		1	9	
<i>Exechia lundstroemi</i> LANDROCK, 1923	MAMY	1	4	7	11	10	
<i>Exechia</i> indet. females	MAMY	2	2	1	3	5,5	1,9
<i>Exechiopsis leptura</i> (MEIGEN, 1830)	MAMY	2	2	1	3	5,6	0,9
<i>Leia spec.</i>	MAMY	1		2	2	7	
<i>Mycetophila fungorum</i> (DEGEER, 1776)	MAMY	3	3	2	5	8,9	1,4
<i>Mycetophila mikii</i> DZIEDZICKI, 1884	MAMY	1	1		1	5	
<i>Mycetophila ocellus</i> WALKER, 1848	MAMY	1	23		23	5	
<i>Mycetophila</i> indet. females	MAMY	1		1	1	3	
<i>Mycomya punctata</i> (MEIGEN, 1804)	MAMY	1		1	1	3	
<i>Mycomya sigma</i> JOHANNSEN, 1910	MAMY	1	1		1	8	
<i>Mycomya</i> indet. females	MAMY	6	11	4	15	7	1,6
<i>Palaeodocosia spec. female</i>	MAMY	1	1		1	5	
<i>Phronia exigua</i> (ZETTERSTEDT, 1852)	MAMY	1		7	7	8	
<i>Phronia strenua</i> WINNERTZ, 1863	MAMY	1	1		1	9	
<i>Phronia</i> indet. females	MAMY	1	1		1	7	
<i>Rymosia affinis</i> WINNERTZ, 1863	MAMY	2	18	1	19	8,8	0,8
<i>Rymosia</i> indet. females	MAMY	4	1	6	7	6,9	2,6
<i>Sciophila fenestrella</i> CURTIS, 1837	MAMY	1	1		1	6	
<i>Sciophila</i> indet. females	MAMY	1	1		1	5	
<i>Trichonta spec.</i> (female)	MAMY	1	1		1	8	
<i>Zygomyia humeralis</i> (WIEDEMANN, 1817)	MAMY	3	4	2	6	6,1	0,7
<i>Zygomyia pictipennis</i> (STAEGER, 1840)	MAMY	3	20	1	21	7	0,2
<i>Zygomyia</i> indet. females	MAMY	4	2	4	6	4,9	2,2
Sciaridae							
<i>Bradysia amoena</i> (WINNERTZ, 1867)	PS	1	4		4	7	
<i>Bradysia aprica</i> (WINNERTZ, 1867)	PS	1	7		7	7	
<i>Bradysia fimbriata</i> TUOMIKOSKI, 1960	PS	4	16	53	69	8,6	0,9
<i>Bradysia fungicola</i> (WINNERTZ, 1867)	PSx	14	444	281	725	3,9	1,8
<i>Bradysia spec.</i>	MAMY	1	2		2	3	
<i>Bradysia</i> indet. females	PS	5	8	2	10	7,3	2,1
<i>Caenosciara alnicola</i> (TUOMIKOSKI, 1957)	PSx	2	3	8	11	6,8	0,4
<i>Caenosciara lucifuga</i> MOHRIG, 1970	PSx	29	548	1201	1749	7,5	2
<i>Corynoptera bistrispina</i> (BUKOWSKI & LENGERSDORF, 1936)	PS	1		13	13	3	
<i>Corynoptera clinochaeta</i> TUOMIKOSKI, 1960	PS	16	116	74	190	4,4	3,1b
<i>Corynoptera flavicauda</i> (ZETTERSTEDT, 1855)	PS	1		30	30	3	
<i>Corynoptera forcipata</i> (WINNERTZ, 1867)	PS	13	40	54	94	6,9	2,1
<i>Corynoptera longicornis</i> (BUKOWSKI & LENGERSDORF, 1936)	PS	1	3		3	8	
<i>Corynoptera luteofusca</i> (BUKOWSKI & LENGERSDORF, 1936)	PS	1	3		3	10	
<i>Corynoptera parvula</i> (WINNERTZ, 1867)	PS	1	1		1	10	
<i>Ctenosciara hyalipennis</i> (MEIGEN, 1804)	PS	1		1	1	5	
<i>Epidapus atomarius</i> (DEGEER, 1778)	PS	26	48	269	317	6,1	1,2

	TG	Freq (n)	#ind. year1	#ind. year2	#ind. total	mExp years	SD
<i>Epidapus gracilis</i> (WALKER, 1840)	PS	1		1	1	2	
<i>Epidapus schillei</i> FREY, 1948	PS	1		3	3	2	
<i>Lengersdorfia flabellata</i> (LENGERSDORF, 1942)	PS	32	84	59	143	6,5	2,3
<i>Peyerimhoffia vagabunda</i> (KIEFFER, 1903)	PS	1		1	1	3	
<i>Scatopsciara pusilla</i> (MEIGEN, 1818)	PSx	40	245	188	433	5,8	2,6
<i>Sciara spec.</i> (females)	PS	1	3		3	6	
<i>Trichosia pilosa</i> (STAEGER, 1840)	PSx	4	29	4	33	7,3	0,9
<i>Trichosia scutellata</i> (STAEGER, 1840)	PSx	5	42	4	46	8,8	1,7
<i>Trichosia subpilosa</i> (EDWARDS, 1925)	PSx	4	9	1	10	5,5	1,4
<i>Trichosia viatica</i> (WINNERTZ, 1867)	PSx	5	6	1	7	9,6	0,7
<i>Trichosia</i> indet. females	PS	5	9	1	10	5,8	0,7
<i>Xylosciara heptacantha</i> TUOMIKOSKI, 1957	PSx	1	5		5	8	
Cecidomyiidae							
<i>Heteropeza pygmaea</i> WINNERTZ, 1846	HYPH	1	74		74	2	
Lestremiinae	HYPH	46	212	167	379	7,2	2,6
other Cecidomyiidae	PH	60	533	273	806	6,4	2,5
Scatopsidae							
<i>Apiloscatopse picea</i> (MEIGEN, 1818)	PS	3	5		5	4,6	0,8
<i>Apiloscatopse scutellata</i> (LOEW, 1846)	PS	9	7	11	18	4,9	2,4
Bibionidae							
<i>Bibio lepidus</i> LOEW, 1871	PS	2		2	2	6,5	0,5
Anisopodidae							
<i>Sylvicola cincta</i> (FABRICIUS, 1787)	PS	4	4	1	5	5,1	3,5
<i>Sylvicola fenestralis</i> (SCOPOLI, 1763)	PS	13	35	3	38	3,8	2,3
Xylophagidae							
<i>Xylophagus compeditus</i> MEIGEN, 1820	Z	5	3	3	6	3,9	1,2
Hybotidae							
<i>Drapetis ephippiata</i> (FALLÉN, 1815)	Z	1		1	1	3	
<i>Drapetis parilis</i> COLLIN, 1926	Z	1		1	1	9	
<i>Euthyneura gyllenhalli</i> (ZETTERSTEDT, 1838)	Z	2	3		3	8,7	1
<i>Euthyneura myrtilli</i> MACQUART, 1836	Z	7	18	2	20	8	1,7
<i>Leptozepe flavipes</i> (MEIGEN, 1820)	Z	1	3		3	8	
<i>Oedalea zetterstedti</i> COLLIN, 1926	Z	16	17	11	28	7	2,2
<i>Oropezella sphenoptera</i> (LOEW, 1873)	Z	2		2	2	8,1	1
<i>Platypalpus luteus</i> (MEIGEN, 1804)	Z	2	1	1	2	6,5	3,5
<i>Platypalpus major</i> (ZETTERSTEDT, 1842)	Z	1		1	1	7	
<i>Platypalpus mikii</i> (BECKER, 1890)	Z	1	1		1	7	
<i>Platypalpus nigricoxa</i> (MIK, 1884)	Z	1		1	1	5	
<i>Platypalpus pectoralis</i> (FALLÉN, 1815)	Z	3	1	3	4	6,4	2,1
<i>Platypalpus unicus</i> (COLLIN, 1961)	Z	5	1	4	5	6	2,2
<i>Tachypeza nubila</i> (MEIGEN, 1804)	Z	27	26	38	64	6,7	2,5
Empididae							
<i>Dryodromia testacea</i> RONDANI, 1856	Z	1	1		1	7	
<i>Empis grisea</i> FALLÉN, 1816	Z	1		1	1	9	
<i>Hilara galactoptera</i> STROBL, 1910	Z	5	4	3	7	5,6	2,4
<i>Xanthempis lutea</i> MEIGEN, 1804	Z	1	1		1	6	
Dolichopodidae							
<i>Medetera cuspidata</i> COLLIN, 1941	Z	2	4		4	3,3	0,4
<i>Medetera impigra</i> COLLIN, 1941	Z	2	10	1	11	2	
<i>Medetera muralis</i> MEIGEN, 1824	Z	7	10	2	12	4,2	3,2
Lonchopteridae							
<i>Lonchoptera lutea</i> PANZER, 1809	SS	6	5	2	7	5,1	2,9
<i>Lonchoptera nitidifrons</i> STROBL, 1898	SS	1	1		1	3	
<i>Lonchoptera tristis</i> MEIGEN, 1824	SS	2	1	1	2	3,4	1,5
Phoridae							
	ZS	63	783	1105	1888	6,4	2,4

	TG	Freq (n)	#ind. year1	#ind. year2	#ind. total	mExp years	SD
Syrphidae							
<i>Cheilosia fasciata</i> SCHINER&EGGER, 1853	PH	8	3	8	11	6,5	2,2
<i>Xylota segnis</i> (LINNAEUS, 1758)	PSx	1	1		1	3	
Pipunculidae							
<i>Chalarus spec.</i>	PaPh	4	1	5	6	5,9	2,3
Asteiidae							
<i>Leiomyza scatophagina</i> (FALLÉN, 1823)	PH	1		4	4	3	
Clusiidae							
<i>Clusiodes albimanus</i> (MEIGEN, 1830)	X	2	2		2	9,1	1
<i>Clusiodes verticalis</i> (COLLIN, 1912)	?	2	6		6	8,4	1,4
<i>Clusia flava</i> (MEIGEN, 1830)	X	2	2		2	9	
Drosophilidae							
<i>Drosophila phalerata</i> MEIGEN, 1830	?	3	3	6	9	7,1	1,8
<i>Drosophila transversa</i> FALLÉN, 1823	PS	1	1		1	9	
<i>Drosophilidae spec.</i>	?	1	2		2	8	
<i>Stegana coleoptrata</i> (SCOPOLI, 1763)	KO	1	1		1	2	
Heleomyzidae							
<i>Heteromyza rotundicornis</i> (ZETTERSTEDT, 1846)	KO	6	2	12	14	8,2	2,1
<i>Oecothea praecox</i> LOEW, 1862	KO	1	1		1	9	
<i>Suillia fuscicornis</i> (ZETTERSTEDT, 1847)	MAMY	1		3	3	8	
<i>Suillia pallida</i> (FALLÉN, 1820)	MAMY	2	1	1	2	2,5	0,5
<i>Suillia vaginata?</i> (LOEW, 1862)	MAMY	1	38		38	3	
<i>Tephrochlamys flavipes</i> (ZETTERSTEDT, 1838)	KO	5	4	3	7	6,2	2,2
Lauxaniidae							
<i>Lyciella platycephala</i> (LOEW, 1847)	SS	6	3	5	8	5,1	2,4
<i>Lyciella rorida</i> (FALLÉN, 1820)	SS	1	1		1	5	
<i>Minettia longipennis</i> (FABRICIUS, 1794)	SS	1	1		1	8	
<i>Sapromyza basalis</i> ZETTERSTEDT, 1847	SS	1		1	1	10	
Sciomyzidae							
<i>Coremacera fabricii</i> ROZKOSNY, 1981	Z	1	1		1	8	
<i>Pherbellia annulipes</i> (ZETTERSTEDT, 1846)	Z	4	6	5	11	9,1	0,3
Sphaeroceridae							
	ZS	55	197	193	390	5,8	2,6
Fanniidae							
<i>Fannia ornata</i> (MEIGEN, 1826)	SS	8	4	6	10	5,8	3,2
<i>Fannia parva</i> (STEIN, 1895)	SS	1	2		2	7	
<i>Fannia polychaeta</i> (STEIN, 1895)	SS	4	2	5	7	8,7	1,9
<i>Fannia postica</i> (STEIN, 1895)	SS	1		1	1	8	
<i>Fannia speciosa</i> (VILLENEUVE, 1898)	SS	2	1	1	2	8	2
<i>Fannia umbrosa</i> (STEIN, 1895)	SS	1	16		16	8	
Muscidae							
<i>Helina lasiophthalmus</i> (MACQUART, 1835)	Z	1	1		1	9	
<i>Phaonia pallida</i> (FABRICIUS, 1787)	Z	1		1	1	3	
<i>Potamia setifemur</i> (STEIN, 1916)	Z	1	2		2	9	
Calliphoridae							
<i>Cynomyia mortuorum</i> (LINNAEUS, 1761)	ZS	2		4	4	6,5	3,5
Sarcophagidae							
<i>Sarcophaga spec.</i>	PaPs	1		1	1	7	
Anthomyiidae							
<i>Mycophaga testacea</i> (GIMMERTHAL, 1834)	MAMY	3	3	5	8	9	2,3
<i>Pegohylemyia fugax</i> (MEIGEN, 1826)	PH	1		1	1	6	
<i>Phorbia atrogrisea?</i> TIENSUU, 1936	Z	1	1		1	9	
<i>Anthomyiidae spec.</i>	?	1		1	1	7	
Tachinidae							
<i>Eloceria delecta</i> (MEIGEN, 1824)	PaPs	2	1	1	2	10	
<i>Hebia flavipes</i> ROBINEAU-DESVOIDY, 1930	PAPH	1		1	1	3	
DIPTERA total			6108	5508	11616		

