OIKOS 24: 42–57. Copenhagen 1973

Spatial and seasonal distribution of Diptera, Homoptera, and Hymenoptera in a moist shrub savanna

Ecological behaviour of winged insect populations in the savannas of Ivory Coast. I

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Duviard, D. and Pollet, A. 1973. Spatial and seasonal distribution of Diptera, Homoptera, and Hymenoptera in a moist shrub savanna. Ecological behaviour of winged insect populations in the savannas of Ivory Coast I. – Oikos 24: 42–57.

During a two-year period insects were trapped by the means of yellow water traps placed at 9 different levels (from 0 to 12 m) inside and above the grass layer of a shrub savanna in the Ivory Coast. Seasonal fluctuations of the insect populations are described and the influence of climate is discussed. Bush fire is an important ecological factor. The importance of sampling more than the grass layer to obtain a complete idea of insect ecology in savanna environment is emphasized.

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В течение двух лет проводили сборы насекомых с помощью ловушек, расположенных на девяти уровнях – от 0 до 20 м высоты в пределах травянистого яруса и над ним в кустарниковой саванне Берега Слоновой Кости. Описаны сезонные колебания численности насекомых, обсуждается роль климатических факторов. Важным экологическим фактором являются пожары в кустарнике. Подчеркивается значение сборов не только в травянистом ярусе, но и за его пределами для получения полной картины особенностей экологии насекомых в условиях саванны.

Manuscript accepted 1 April 1972. This paper was presented to the first IBP Symposium for African Grassland Ecosystem, Lamto, Ivory Coast, 30 December 1971 – 3 January 1972

1. Introduction

For several years D. and Y. Gillon (1963 f.) have studied the ecology of insect populations of the grass layer in an Ivory Coast savanna. They have used the "quadrat" sampling technique (bottomless wiremesh cages of known area, dropped on the vegetation), and their quantitative results deal mostly with the "macro-fauna". But this method does not allow the capture of small winged insects and the powerful fliers. These insects play a notable ecological part in the dynamics of insect communities; for instance many are hyperparasites.

Quantitative techniques are mostly confined to ground level and they often have drastic effects on the environment. After the passage of ecologists the investigated biotope, if not completely destroyed is often badly damaged.

Since Moericke's work (1955) and their extension, by Chauvin and Roth (1966) to general entomological sampling, the use of coloured water traps has become widespread in insect ecology. Several authors using these traps, have discovered the existence of a stratified distribution of insects in vegetation (Roth 1963, 1968, 1970, Gaspar et al. 1968).

Our preliminary investigations (Duviard 1968, 1971, Pollet 1969, 1970a and b) have shown that it was possible to apply the concept stratification and superimposition in the moist tropical environment to the insect community of a savanna or a cotton field, as clearly as to a bird population in a forest or to a plankton community in a lake or a sea. Further, Pollet (1969), using water traps and "quadrat" cages simultaneously, showed that the two techniques tend to complement each other.

The present paper deals with insects caught in yellow water traps during a two-year period. Only general results treating three orders of insects are considered. In the studied area, various taxa show marked seasonal fluctuations, in occurrence and vertical distribution. Successions of insects population both spatial and temporal were encountered. In view of these complications the value of many absolute quantitative sampling techniques must be disputed.

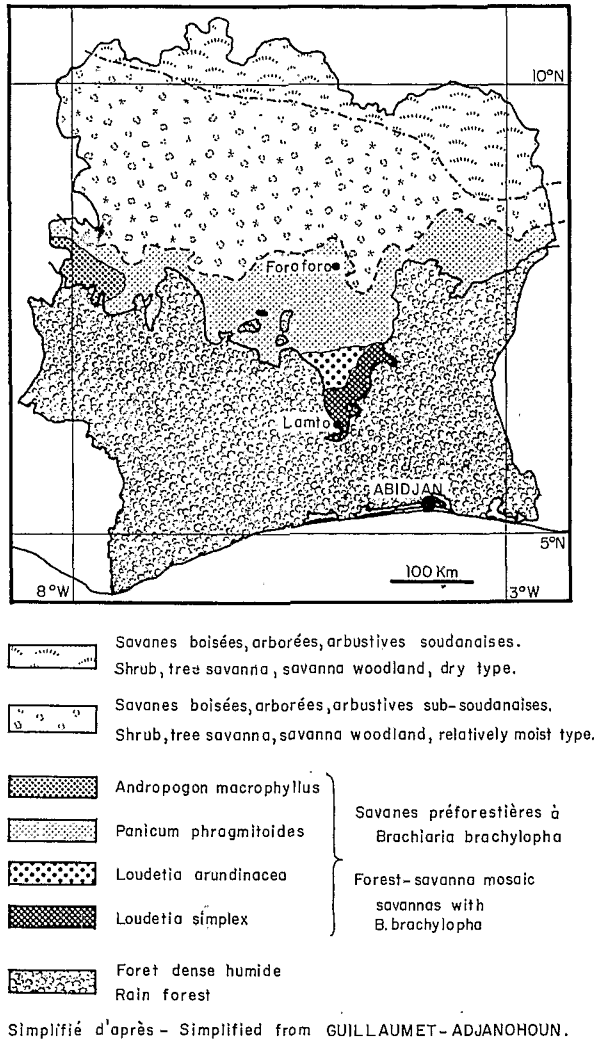


Fig. 1. Situation of the studied savannas in the general phytogeographic prospect of Ivory Coast.

2. Studied area

2.1. General

The field work was conducted at the Tropical Ecology Field Station of Lamto (5°02′W, 6°13′N), with other data having been obtained at Foro-foro (4°55 W, 8°N), in Ivory Coast (West Africa).

The savannas of Lamto belong to the forest-savanna mosaic belt: floristically, they are defined by the presence of the grasses *Brachiaria brachylopha* Stapf., *Loudetia simplex* C. E. Hubbard and the lontar palm, *Borassus aethiopum* Martonne (Adjanohoun 1964, Roland and Heydacker 1963, Roland 1965, Bonvallot et al. 1970, Vuattoux 1970).

The experimental plot was situated in a shrub savanna dominated by Andropogoneae (Bonvallot et al. 1970, belt transect No. 2) typical of well-drained slopes. Although it is one of the dominant savanna types (de la Souchere and Badarello 1969), nevertheless, it is not fully representative of the savanna association as a whole in the Ivory Coast (Fig. 1, Adjanohoun 1964), and it is not permissible on the basis of these results to generalize for all types of savannas.

2.2. Climate

The climate is of a transitional equatorial type, and one of the moistest in the Baoulé savanna. Mean annual rainfall, based on records from 9 years, is 1 297 mm.

During the period of this study (September 1969–July 1971), we observed the following succession, based on water balance estimation (Fig. 2):

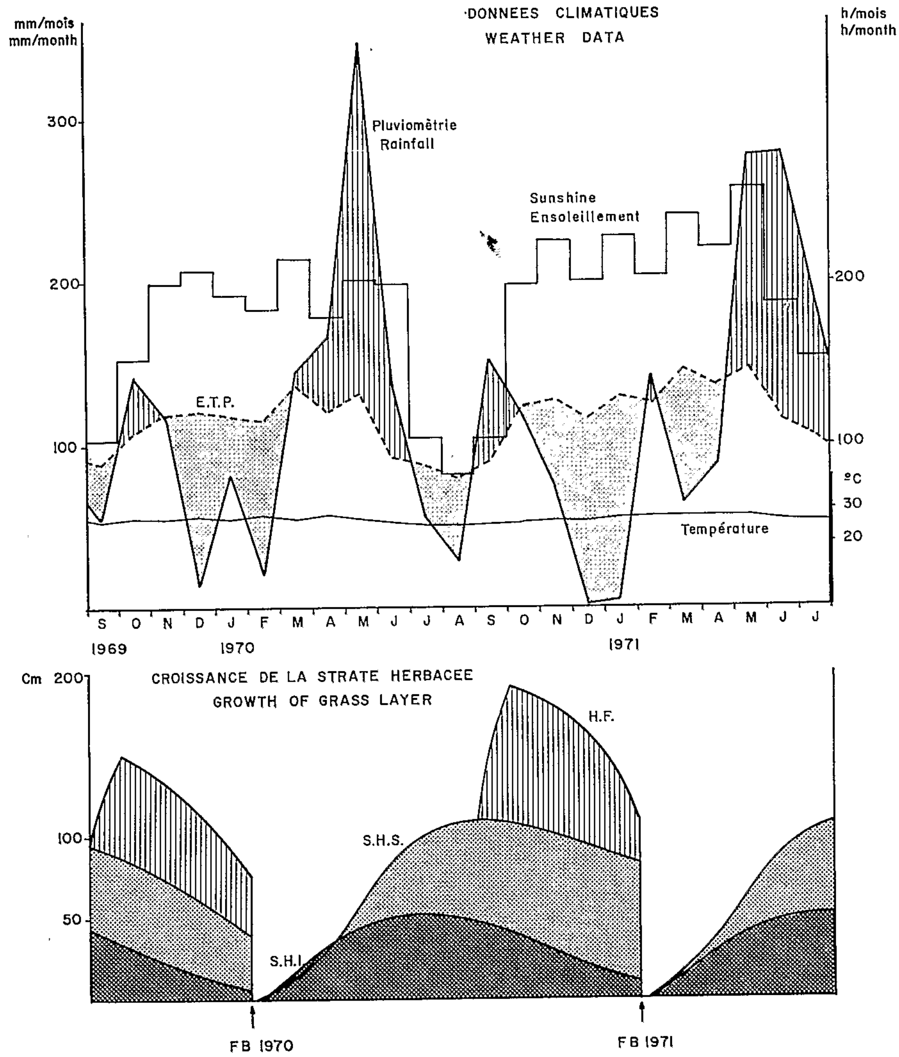


Fig. 2. Lamto weather data (upper part) and vegetation growth of the grass layer (lower part) during the September 1969–July 1971 period. E.T.P.: potential evapo-transpiration; S.H.I.: lower grass layer; S.H.S.: upper grass layer; H.F.: floral stems of Gramineae; F.B.: bush fire.

short dry season: September 1969
second rainy season: mid-September to mid-November 1969
long dry season: mid-November 1969 to mid-March 1970
first rainy season: mid-March to end of June 1970
short dry season: end of June to end of August 1970
second rainy season: end of August to October 1970
long dry season: mid-October 1970 to mid-April 1971; a short rainy period occurred in January–February 1971
first rainy season, from mid-April 1971

However 1969 was a very dry year (rainfall: 902 mm), while 1970 was nearly "normal" (rainfall: 1 188 mm).

2.3. Vegetation

A belt transect (80×40 m, Fig. 3) was established at right angles to the steepest gradient, on the upper part of a well-drained slope. The grass layer consisted mostly of the grasses *Hyparrhenia diplandra* Stapf., *H. chrysargyrea* Stapf., *H. dissoluta* C. E. Hubbard, *H. rufa* Stapf., *Andropogon schirensis* Hochst., *Brachiaria brachylopha* and several Cyperaceae. According to the season, the flowers of *Curculigo pilosa* Engl., *Eulophia eristata* Steud., *Vernonia guineensis* Benth., several *Vigna*, *Tephrosia*, *Indigofera* and *Aloe barteri* Baker could be seen. *Cochlospermum planchonni* Hook. f. is typical of this layer as well as seedlings of *Annona senegalensis* Pers. and *Piliostigma thonningii* Milne-Readhead. The shrub layer, the canopy of which reaches 7–8 m is composed of *Piliostigma thonningii* (Caesalpiniaceae), *Crossopteryx febrifuga* Benth. (Rubiaceae), *Bridelia ferruginea* Benth. (Euphorbiaceae), *Terminalia glaucescens* Planch. (Combretaceae), *Ficus capensis* Thunb. (Moraceae), *Cussonia barteri* Seeman (Araliaceae).

Some lontar palms form a rather high (15–20 m) but scattered tree layer.

The savanna lies on a red tropical ferrugineous soil

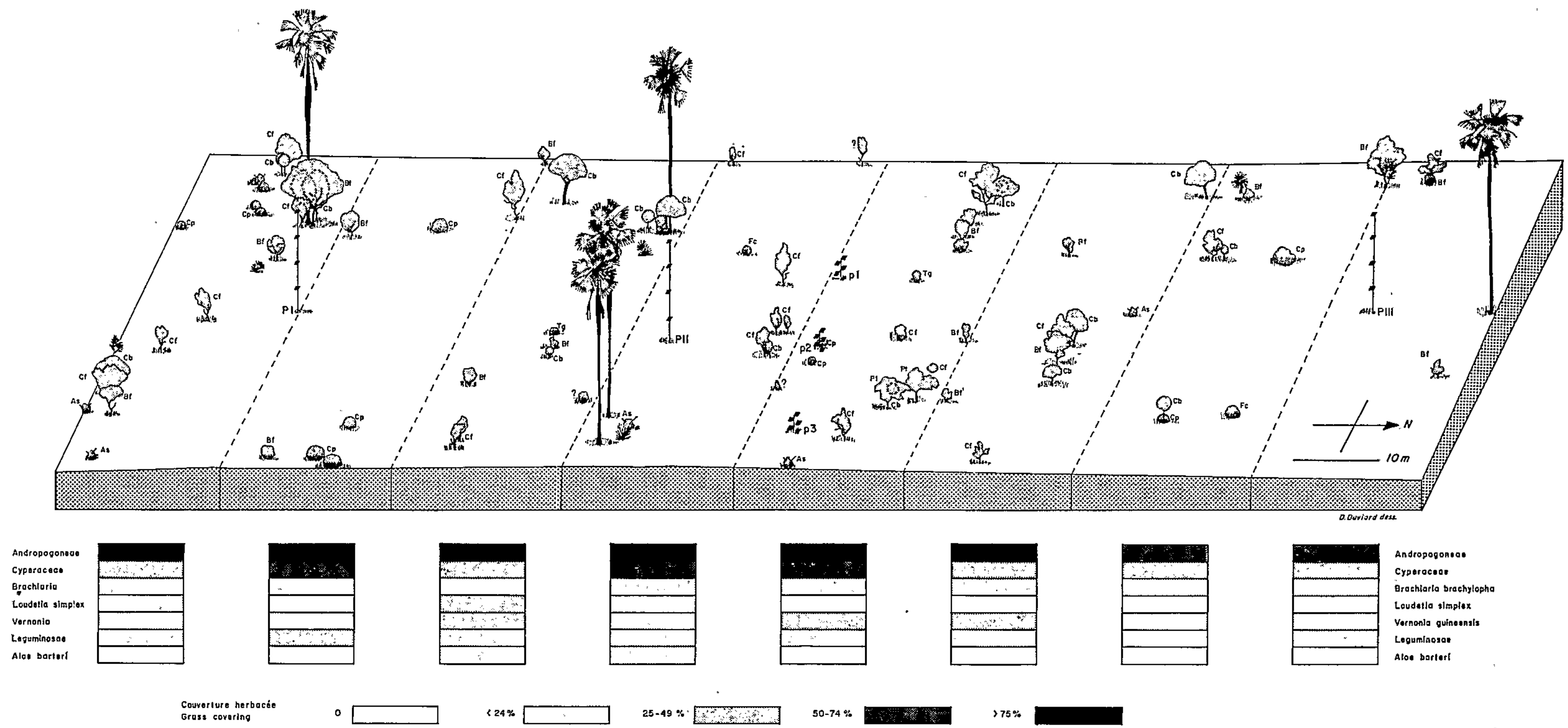


Fig. 3. Diagrammatic representation of the grass, shrub and tree layers on the belt transect where trapping was conducted. The situation of 2.5 and 15 m poles (respectively p1, p2, p3 and PI, PII, PIII) is indicated. Height and length scales are identical. Trees and shrubs bear initials refering to genus and species names, as given in the text. Lontar palms, easily recognizable, have no lettering. The grass layer composition is summarized in the lower part of the diagram. Only approximate ground covering, at maximum growth period (October) has been considered.

through which water readily drains due to a thick gravel layer (at a depth of 40 to 130 cm) (Bonvallot et al. 1970).

Monnier (1968), Roland and Heydacker (1963) have described the vegetation cycle in these savannas as being very largely determined by rainfall, and bush fires in the dry seasons (controlled on the land belonging to the field station). The fire destroys the whole of the grass layer. Fig. 2 illustrates the annual development from bare, ash-covered ground through an open stage of discrete grass tussocks, to completely closed ground covering, 2–3 m high, of maximum vegetation, constituted of the following components:

1. The lower grass layer, a densely entangled stratum, immediately above ground level, composed of dead leaves of Gramineae and a few low forbs.

2. The upper grass layer, a less entangled stratum, comprising a photosynthetically active layer of grass sward and other erect herbs.

3. An erect upper stratum consisting solely of parallel flower stems and inflorescenses of the grasses. As the dry season proceeds, the distinction between these different strata tends to break down, producing a dense and impenetrable biotope. At this time of the year nocturnal dew is common, and the drying, moribund vegetation is soaked with water every morning.

Concerning the shrub and tree layers, the dry season is marked by the falling of the leaves, a process that is completed drastically by the bush fire, which moreover damages the woody parts of these layers. Shortly after the first rains new leaves are produced.

3. Methods

The choice of a sampling technique must correspond to the purpose of the study. Our problem was to determine how the different flying components of the insect community are distributed in the vegetation in the various stages of its normal seasonal development. It was necessary to sample without destruction or alteration of the vegetation structure, and consequently all the normal quantitative techniques were precluded.

The method chosen would have to be adapted to the structural heterogeneity of the biotope, and equally applicable to the various layers. Moreover, the side-effects of sampling on the vegetation must be minimal. For these reasons we chose Moericke's yellow water traps.

Although the insects taken represent a biased sample, the data so obtained are reproducible and give a satisfactory idea of the insect community dynamics. Outbursts, migrations, and dispersal flights have been studied this way.

The yellow water traps were of very simple construction: yellow bowls were filled with water together with a few drops of liquid detergent (3 per cent teepol). Placed at different heights in the environment, they are periodically visited and the trapped insects removed and preserved in 70 per cent ethanol. Yet although very simple, the phenomena involved are much more complex. According to Roth (1970), "water" and "yellow" factors are indistinguishable and act simultaneously under influence of direct or diffuse solar radiation. He showed that water acted either as a source of humidity or as a reflecting surface. The wavelength of the radiation emitted by the trap is of primary importance; the best results are obtained with a wavelength of 5 450 Å, which is reflected by a bright lemon yellow. He obtains the best results in direct sunlight, but as Pollet (1970a, b) pointed out, direct illumination is not so important under tropical conditions.

We chose square zinc tanks (25 × 25 × 10 cm) (as used by Gaspar et al. 1968), to the original plastic plates which are too light and shallow for tropical heavy rains and winds. The inner surface of the trap was painted bright yellow, grounding with lead oxide. The outer surface was not painted.

One of the difficulties met with was in the choice of apparatus to support the traps. For financial reasons, and also to avoid disturbance in the biotope, it was impossible to use high scaffolding such as those used by Cachan & Duval (1963) and Paulian (1947) in the rain forest of Banco, Ivory Coast. Instead we used two types of poles (15 m and 2.5 m long, Pollet 1970a and b, Duviard 1971) (Fig. 4, 5) that were good answers to our necessities. These cheap structures were easy to erect and allowed us to trap at the following heights: 0, 50, 100, 150, 200, 300, 600, 900 and 1 200 cm above ground level. To obtain a satisfactorily representative sample, we ran simultaneously 3 short and 3 long poles (see Fig. 3, for position on the transect). Trapping was conducted as regularly as possible over 48-hr periods (from 0800 hr to 0800 hr two days later) once or twice a month. The 2.5 m poles were used from 17 September 1969 to 20 July 1971, and the 15 m poles were used only from 25 June 1970 to 20 July 1971.

4. Seasonal fluctuations of the insect fauna

Only the active individuals of an insect community are caught, as these alone are likely to be attracted by the traps. They constitute what Roth (1968) calls the "operating population" (*population opérationelle*), in opposition to the "instant population" (*population actuelle*), "mass of insects present in a given place, at a given instant".

In the studied savanna, the operating population consists of numerous taxonomical entities; but Diptera, Homoptera and Hymenoptera were by far the most numerous in our samples. Because of the taxonomic diversity, and the difficulty of working at species level, we determined our insects at family or super-family level. The study at species level of particular groups will be done later.

We have plotted the catch against total rainfall during the 30 days prior to trapping. In the resultant graphs,

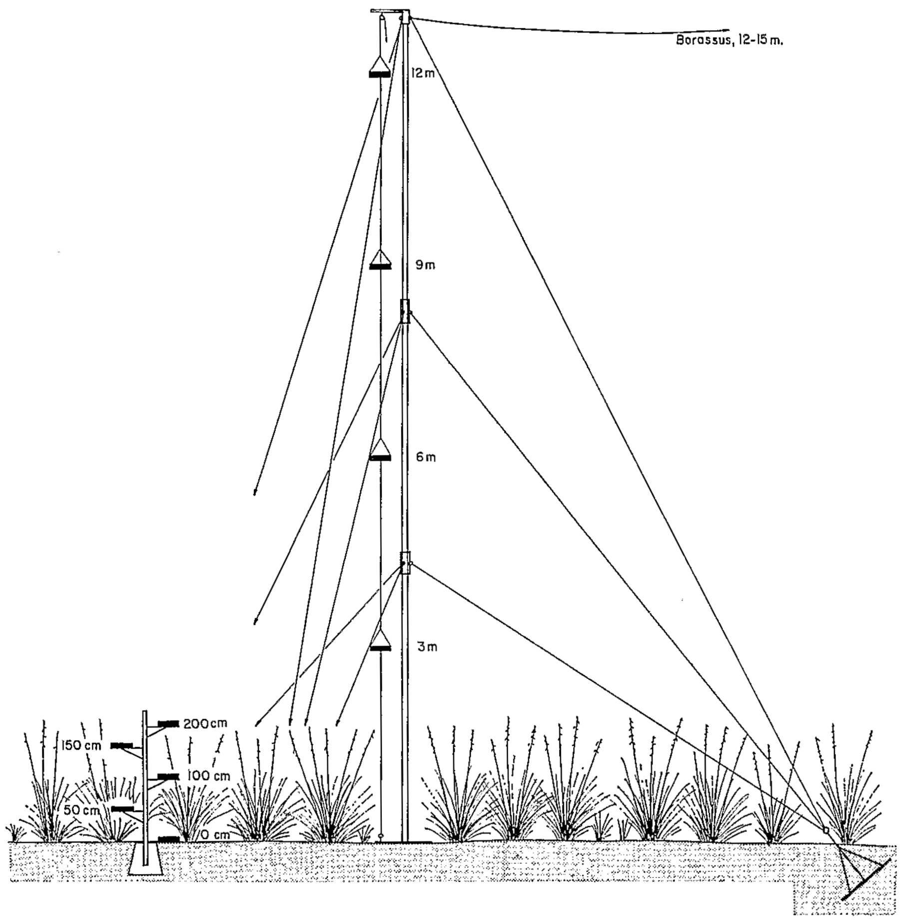


Fig. 4. Trapping apparatus in the savanna at maximum grass development. Small poles are held by a buried concrete block. Cross bars hold removable tanks at different heights. 15 m poles are made of 3 portions of aluminium tubes, maintained by collars. The pole rests on a large metal plate and is sustained by a three-level rigging system, anchored in the ground by large tripods welded to iron plates. A series of four tanks is hauled by a steel cable and a pulley at definite levels. A cable joins the head of the pole to the nearest palm tree, which is a necessary help to erect the pole. Water traps are 25 × 25 × 10 cm tanks, painted bright yellow inside, and filled to 1/3 with clear water + 3 per cent teepol.

the points obtained were always distributed in two swarms lying on either side of 60 mm rainfall. Thus when calculating the correlation coefficient, r, the two groups of values have been treated separately. We denote as "dry" periods those in which total rainfall was less than 60 mm; and as "moist" those in which total rainfall exceeded 60 mm. Three families of insects have been studied in this way. Primary data and calculated correlation coefficients are presented in Tab. 1.

4.1. Diptera

The following groups of Diptera were present in our material: Anthomyiidae, Asilidae, Calliphoridae, Cecidomyiidae, Dolichopodidae, Haplostomata, Empididae, Mycetophilidae, Phoridae, Sciaridae, Syrphidae, Tachinidae. Hematophagous Diptera, although present in the savanna and very abundant during certain seasons, were not attracted to our traps, except for a few Simuliidae,

Fig. 5. Part of our apparatus as it appears in the savanna. The grass layer is at its maximum, culminating at 1–1.2 m, while floral stems are nearly 2 m high.

Tab. 1. Number of Dolichopodidae, Phoridae and Jassidae caught on specific trapping occasions and corresponding rainfall data. The correlation coefficient, r was calculated according to the formula: $r = \frac{\text{covariance (x,y)}}{\sqrt{\text{var (x), var (y)}}}$

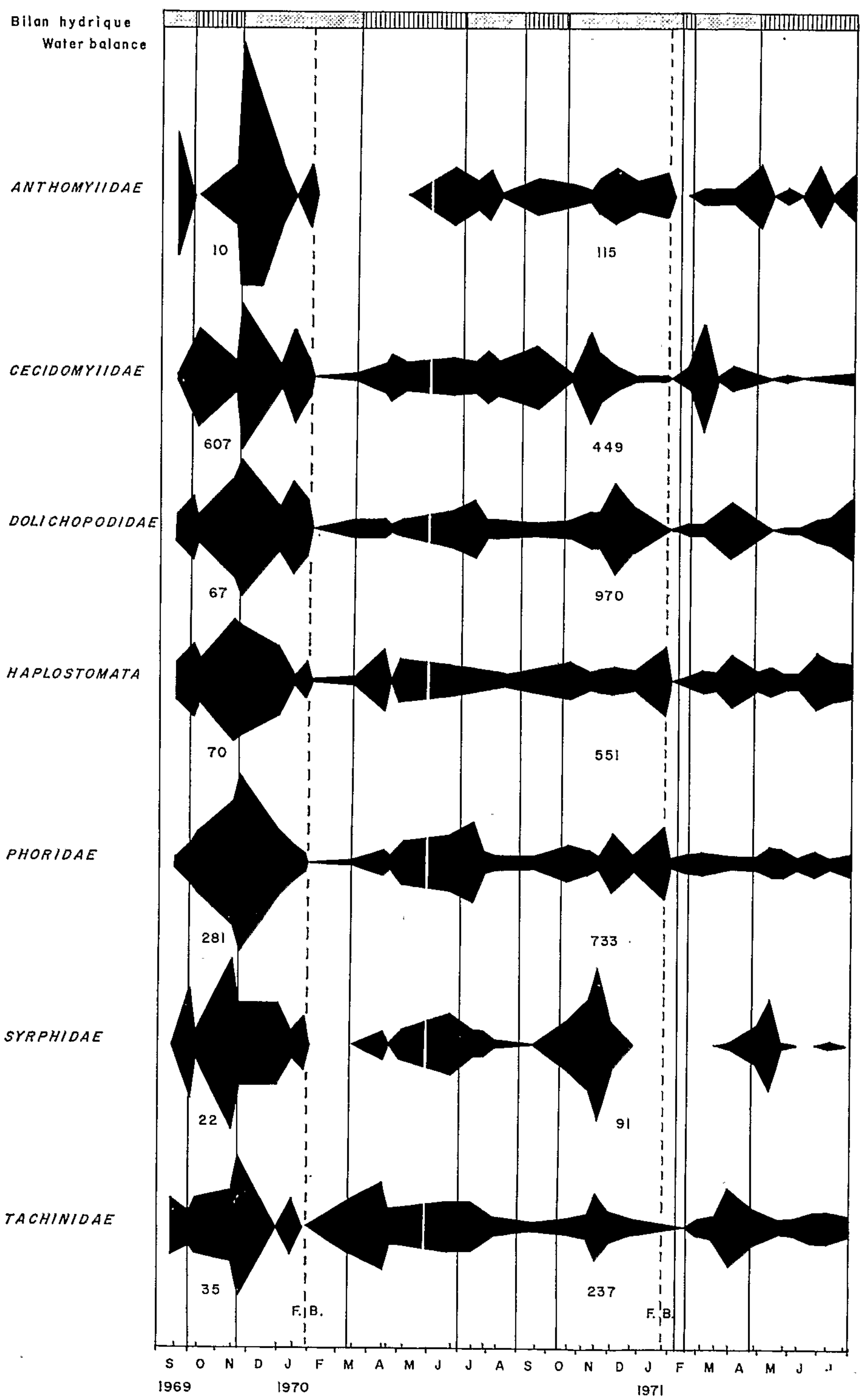
Date of trapping	amount of rainfall during 30 days prior to trapping	numbers caught Dolichopodidae (Diptera)	Phoridae (Diptera)	Jassidae (Homoptera)
17.09.69	26.8 mm	3	4	22
17.10.	93.8	7	19	43
22.10.	99.3	3	27	55
15.11.	116.6	11	55	32
19.11.	96.8	15	80	33
31.12.	5.0	5	31	50
15.01.70	34.9	10	17	86
24.01	39.0	6	9	40
14.03	46.6	2	2	14
16.04	90.2	2	12	45
18.04	84.5	1	6	46
6.05	115.2	2	19	34
25.06	37.0	53	56	37
16.07	18.0	74	86	58
28.07	7.1	27	23	42
11.08	39.2	25	7	44
17.09	78.1	13	14	44
20.10	21.0	28	29	56
4.11	104.2	50	15	85
17.11	34.0	48	12	89
2.12	6.1	123	56	134
22.12	0.0	52	14	62
26.01.71	0.0	7	62	200
17.02	46.8	19	24	58
1.02	94.7	15	21	28
16.03	35.5	32	18	17
30.03	31.5	69	6	97
28.04	33.5	21	12	50
11.05	37.9	2	20	43
25.05	108.1	9	21	40
9.06	87.9	6	12	34
22.06	125.6	30	6	32
7.07	61.8	36	10	22
20.07	12.3	83	15	58

	amount of rainfall < 60 mm (n = 20)	amount of rainfall > 60 mm (n = 14)
Dolichopodidae	r = −0,36 negative correlation slightly significant	r = −0,04 negative correlation not significant
Phoridae	r = −0,43 negative correlation significant	r = +0,20 positive correlation not significant
Jassidae	r = −0,49 negative correlation significant	r = +0,20 positive correlation not significant

Tabanidae, Ceratopogonidae. This confirms Roth's (1970) observations.

The Cecidomyiidae (1056 individuals), Dolichopodidae (1037 individuals), Phoridae (1015 individuals) were the most important families in our catches. Seasonal fluctuations of the different groups (Fig. 6) possess some features in common: the same general shape of the curves, with numerous peaks of abundance; troughs in the latter part of the dry season in relation to savanna burning; increase of population level during the rainy season (May–June). These phenomena are similar to those discussed by Gillon and Pernes (1968) for other

Fig. 6. Seasonal fluctuations of the main groups of trapped Diptera. At the top of the graph, dotted areas represent ecologically dry periods, while striped areas represent periods with a positive water balance (see also Fig. 2). The annual bush fire is indicated (F.B.). The population curves are given in percentage for two consecutive periods, separated by a white stripe: first period with 2.5 m poles only, second period with both 2.5 m and 15 m poles (see text). For each period, actual numbers of trapped insects are indicated below the curves.



arthropods of the savanna. Diptera may be classified in two groups: a) population increasing with the rains; Dolichopodidae, Syrphidae, Tachinidae; b) population decreasing with increasing rains: Anthomyiidae, Cecidomyiidae, Haplostomata.

For the Phoridae, we observed a different behaviour related to high or low rainfall. During "dry" period, lower rainfall values are correlated with higher number of trapped flies (negative correlation, very significant). In "moist" period the inverse phenomena seems to occur (positive correlation, slightly significant).

For the Dolichopodidae, in the two cases (rainfall over and under 60 mm during the 30 previous days) the correlation is feebly negative: higher rainfall values are correlated with a lower number of captures.

4.2. Homoptera

Three groups of Homoptera were trapped in fair numbers: Aphidoidea, Jassidae, Psyllidae. Other groups (Aleyrodidae, Membracidae, Delphacidae, Cercopidae) were encountered, but in small numbers, and they will not be discussed here. The general aspect of the seasonal fluctuation curves were very different for each group (Fig. 7).

Aphidoidea show outbreak peaks that can be related to marked vegetative growth of the grass layer, i.e. during rainy periods. But maximum numbers of captures occur during ecologically dry periods. Furthermore, it is necessary to compare fluctuations in numbers of aphids and Dolichopodidae, their main supposed predators in this environment. As one of us (Duviard 1971) has observed in a cotton field, the outbreaks of aphids precede and initiate those of dolichopodids; these flies, in return, reduce their preys' populations, in a classical prey-predator balance. The same remark can be made concerning the Syrphidae which are, however, less abundant than the dolichopodids.

Jassidae are very abundant in our samples (2177 individuals) but the number of species is apparently high (more than 80) which explains the fairly constant population level throughout the trapping period. An increase occurred, however, during the dry season, which was interpreted as a result of intense activity of these insects, searching for food. The incidence of bush fire exerts a long-term depressive effect on the numbers of Jassidae because of the disappearance of suitable foodplants. These observations are very similar to those of Pollet (1970a and b), who suggested an inactive phase of the jassids during this difficult period.

Correlation studies between number of trapped jassids and rainfall during the 30 previous days show a

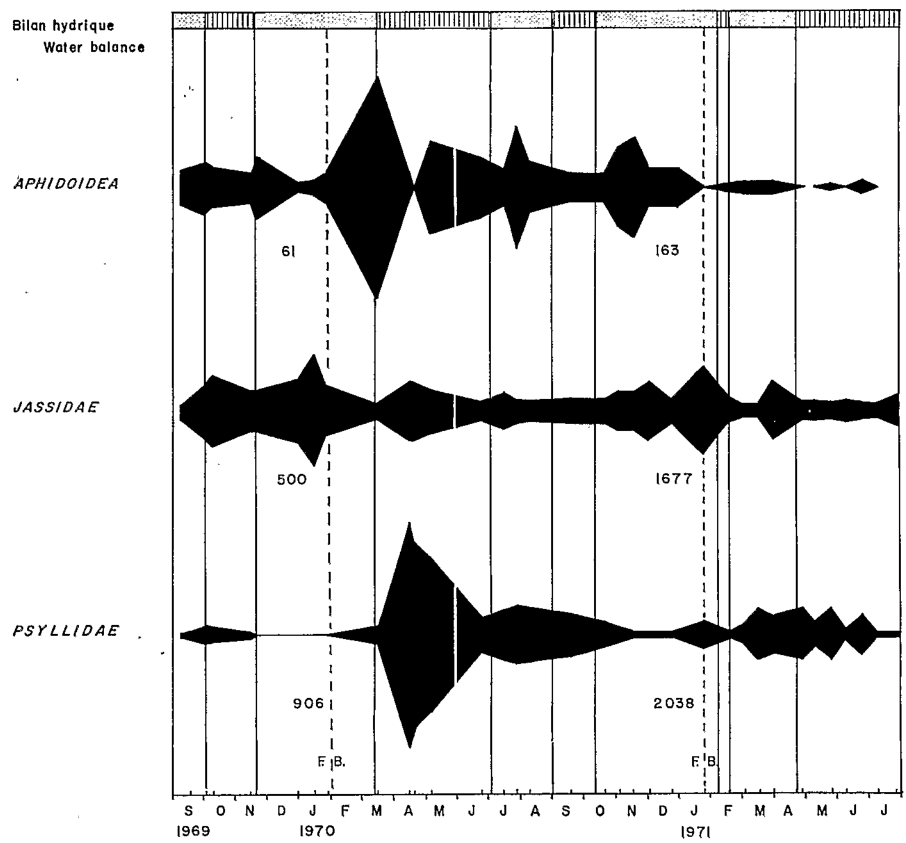


Fig. 7. Seasonal fluctuations of the main groups of trapped Homoptera. Explanations see Fig. 6.

negative correlation, highly significant, during "dry" period; during "moist" period, this correlation is positive, feebly significant, showing the complete indifference toward climatic conditions, and the big dependence of Jassidae on fresh vegetation.

Psyllidae (2944 individuals taken) seem closely dependent on a healthy vegetative substratum. Shortly after the savanna fires, when the grass was sprouting, the psyllid population increased rapidly to a level that was maintained until the onset of dry season.

4.3. Hymenoptera

The Hymenoptera present in our samples belong to taxa that are not easily determined below the super-family level. Best represented groups are Apoidea, Bethyloidea, Chalcidoidea, Proctotrypoidea, Sphecoidea and winged Formicoidea, but Vespoidea, Pompiloidea, Cynipidea, and Ichneumonoidea are also present (Fig. 8).

Apoidea present very particular seasonal fluctuations. Outburst peaks are of two types:

Rainy season outbreaks (April–May, October) correspond exactly to the flowering periods of the lower field layer (Cyperaceae, *Vernonia guineensis*), during the first rainy season Duviard (1971); and of the upper field layer (Gramineae, Leguminoseae) during the second rainy season.

Dry season outbreaks are probably correlated with active research for water, already observed by Roth and Couturier (1966). African ecologists know well the exasperating flights of the "sweat bees". They disappear temporarily after the savanna fire.

The case of Formicoidea, of which only winged imagines are caught during mass flights of dispersion, is an exception. Apart from the December 1970 peak, all the take-off periods are closely associated with large increases in rainfall during the 30 days previous to trapping.

The last four groups Bethyloidea, Chalcidoidea, Proctotrypoidea, and Sphecoidea are parasites or predators. Therefore, correlations between population dynamics and climatic factors are far less evident. The fluctuations of Bethyloidea alone seem closely related to rainfall. For the other taxa, diversity of species is probably responsible for the numerous peaks. Heavy rainfall and bush fire seem, anyhow, to have a depressant effect.

5. Spatial structure of the insect community

For each considered level, the catches for the June 1970–August 1971 period have been summed. During this period the 2.5 and the 15 m poles worked together. Thus, we obtain curves representing the cumulative spatial distribution for each considered group (Fig. 9). This procedure makes no allowance of the annual variations of the grass layer, but gives an overall view of the average situation of the altitudinal distribution of insects.

Except for Asilidae (a single, very large species) and Mycetophilidae, all the groups of insects are caught at every level of trapping. But each taxonomic entity has its own preferred activity level. Several groups have, however, two or more activity levels, each one presumably corresponding to one or a few ecologically closely related species. Taking in account the structure of the environment the altitudinal distribution can be described as follows:

Insects active in the grass layer.
- Commonly close to ground level: Sphecoidea, Membracidae, Cecidomyiidae, Anthomyiidae, Tachinidae.
- Commonly in the grass layer: Chalcidoidea, Dolichopodidae, Psyllidae, Vespoidea, Aphidoidea, Proctotrypoidea, Dryinidae, Syrphidae, Phoridae.
- Commonly at the top of the grass layer: Empididae, Sciaridae.

Insects above (but in close contact with) the grass layer:
- Jassidae, Mycetophilidae.

Insects active in the shrub layer.
- Commonly at its lower level: Cecidomyiidae, Tachinidae, Psyllidae, Procotrypodea, Syrphidae, winged Formicoidea, Calliphoridae, Mycetophilidae, Haplostomata.
- Commonly at it upper level: Sphecoidea, Chalcidoidea, Aphidoidea, Proctotrypoidea, winged Formicoidea, Haplostomata, Apoidea.

Insects active above the shrub layer:
- Cecidomyiidae, Chalcidoidea, Psyllidae, Aphidoidea, Proctotrypoidea, Dryinidae, Haplostomata, Apoidea, Asilidae.

This spatial distribution of insects requires some comment. First, we observe for most of the groups a constriction of the curves between field layer and shrub layer populations; at which level a gap exists in the vegetation almost throughout the year (above grass layer, beneath shrub crowns). The low numbers from this height reflect this discontinuity in the vegetation across which passage of small insects is quite restricted.

On the other hand, the fauna in the shrub layer moves in a very open horizontally discontinous environment (Fig. 3). Movements and exchanges between clumps or stands must be particularly intense at this level to account for the relative abundance of the captures. The operating population is certainly not relatively more numerous in the shrub layer than in the grass layer, but more active, and thus, more likely to be caught.

Higher up, above the general level of shrub crowns, the number of trapped insects naturally decreases. Only a few groups such as the Apoidea and Asilidae, are really numerous, at this height (9–12 m). These are good flyers and travel unimpeded over long distances, frequently cruising at this level.

But, as a whole, these interpretations are too schematic, and take no account of the changes in the layer structure. We shall therefore examine the phenology of three of the most numerous insect groups in relation to the different vegetational layers.

Sphecoidea

Vertical displacements occur in the sphecoid populations according to the state of the vegetation (Figs. 10, 11). They are prevalent at ground level in February–March when the vegetation is low; but later in the year, particularly from August onwards when the grass layer is fully developed, they are more numerous at 50 cm. The numbers also vary with the season, being depressed by heavy rains. However, according to Gillon and Gillon (1967), the rainy season is also the period of least abundance of their preferred prey, lepidoptera caterpillars; whereas, during the dry season, both sphecoids

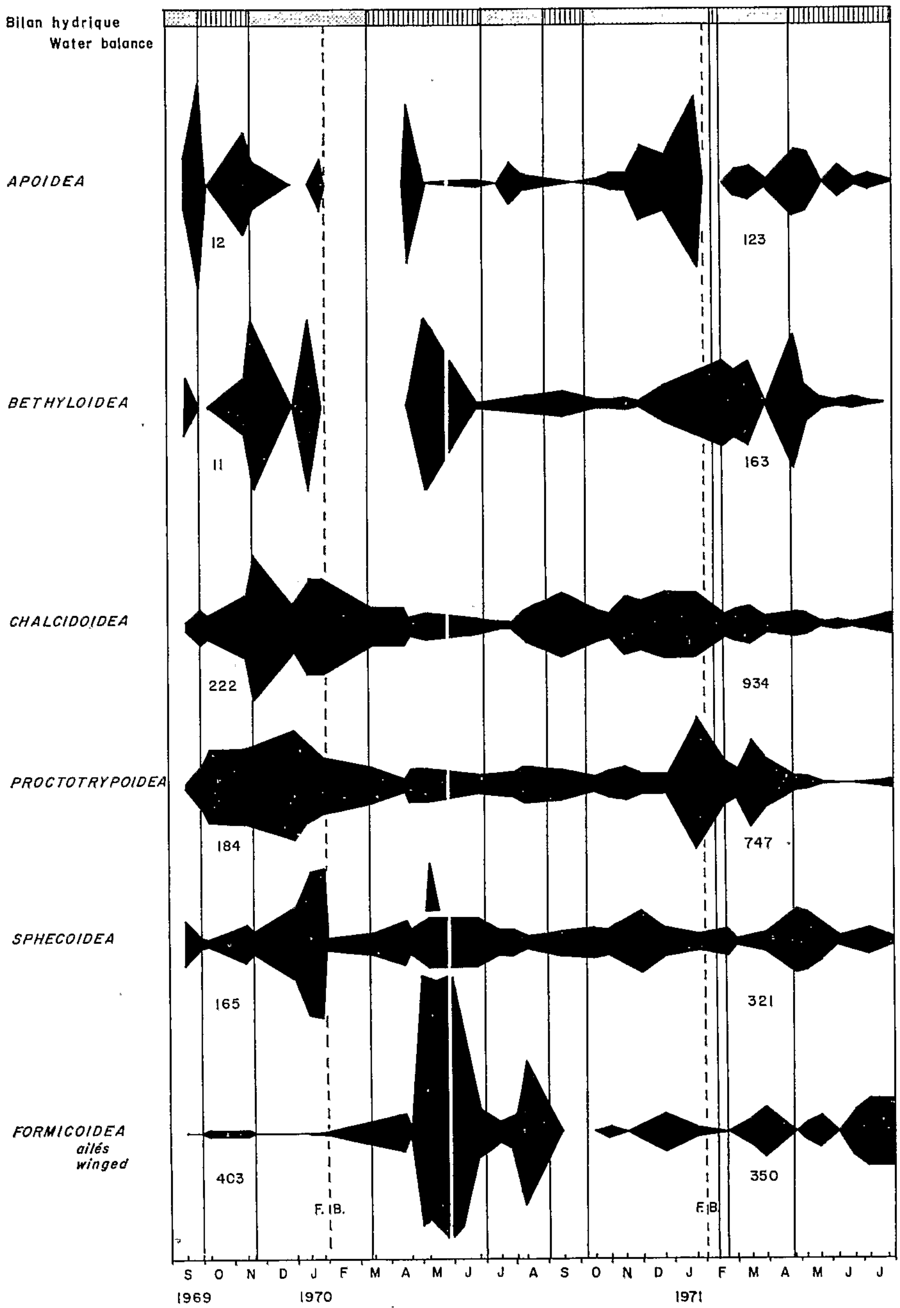


Fig. 8. Seasonal fluctuations of the main groups of trapped Hymenoptera. Explanations see Fig. 6.

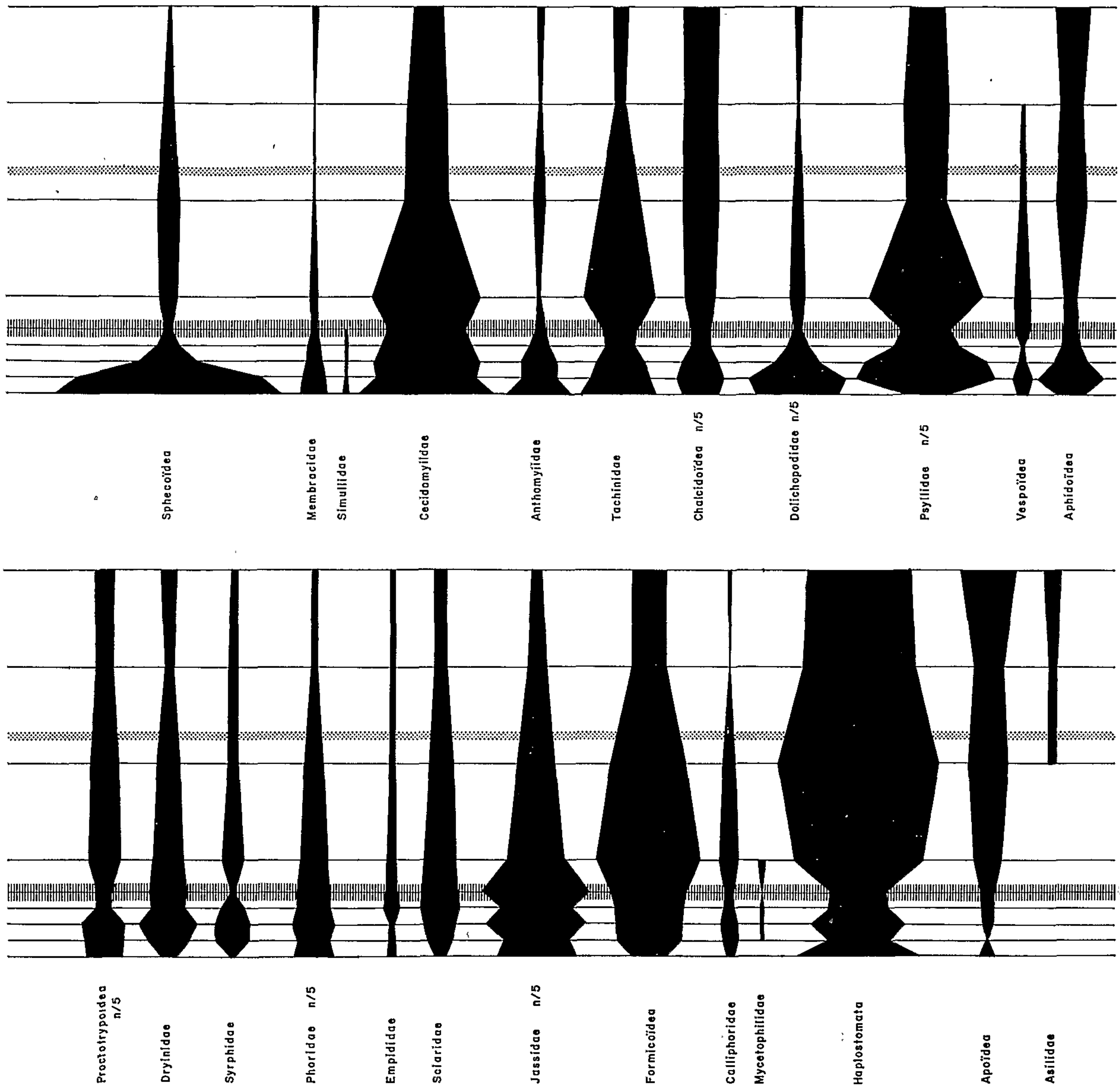


Fig. 9. Vertical distribution of the main trapped groups of insects in the shrub savanna. Horizontal lines represent the different levels of trapping: 0, 50, 100, 150, 200, 300, 600, 900 and 1200 cm above ground level (see Fig. 3). Striped zone indicates the upper surface of grass layer at maximum growth; dotted zone represents the upper surface of the shrub crowns. Curves are constructed from actual catches numbers; for some groups, the number is divided by 5 (n/5) to facilitate graphical representation.

and caterpillars are numerous. These observations exemplify the way in which quadrat-cage and water-trapping complement each other.

Dolichopodidae

These flies as adults inhabit the grass layer (Figs. 10 and 12) and display, like the sphecoids, vertical displacements, related to the vegetation cycle. This is most apparent during the flowering of the Gramineae. A similar situation exists in the dolichopodid population inhabiting the shrub layer. These results are very similar to those reported by Duviard (1971), from a cotton field in central Ivory Coast (Foro-foro, Fig. 1), and seem to be characteristic for savanna dolichopodids. Further, behavioural variations, closely dependent on the environmental conditions have been observed in different species of these flies (Couturier 1970). These will probably become apparent when the present material (consisting of more than 20 spp.) is treated at the species level.

Year-to-year variations in numbers were also noted. Thus, in the dry year of 1969, the dolichopodids were rather scarce, while in 1970 and 1971 (with "normal" rainfall), they were more numerous.

Jassidae

As stated earlier, this group consists of more than 80 spp. For this reason several species or species groups, each dominating a particular level, are superimposed on each other at any one time in the material. Generally, jassids are very active and quite numerous at the higher levels. A first maximum was observed at the top of the grass layer (indicating vertical migrations correlated to grass growth) and a second inside the shrub layer. They were very abundant in the layer formed by parallel flower stems of the grasses.

6. Discussion

Yellow water traps are not the perfect means of sampling insect communities. First, this technique is only semi-quantitative, and it is impossible to determine absolute abundance as the "drained area" is unknown, and the size of the catch is related to activity. Furthermore, as Roth (1970) stated, the attractiveness of the trap is different from one insect group to another (see also Moericke's work on aphids); and Duviard and Roth (unpubl.) have shown seasonal fluctuations of the trap's attractiveness in the studied savanna.

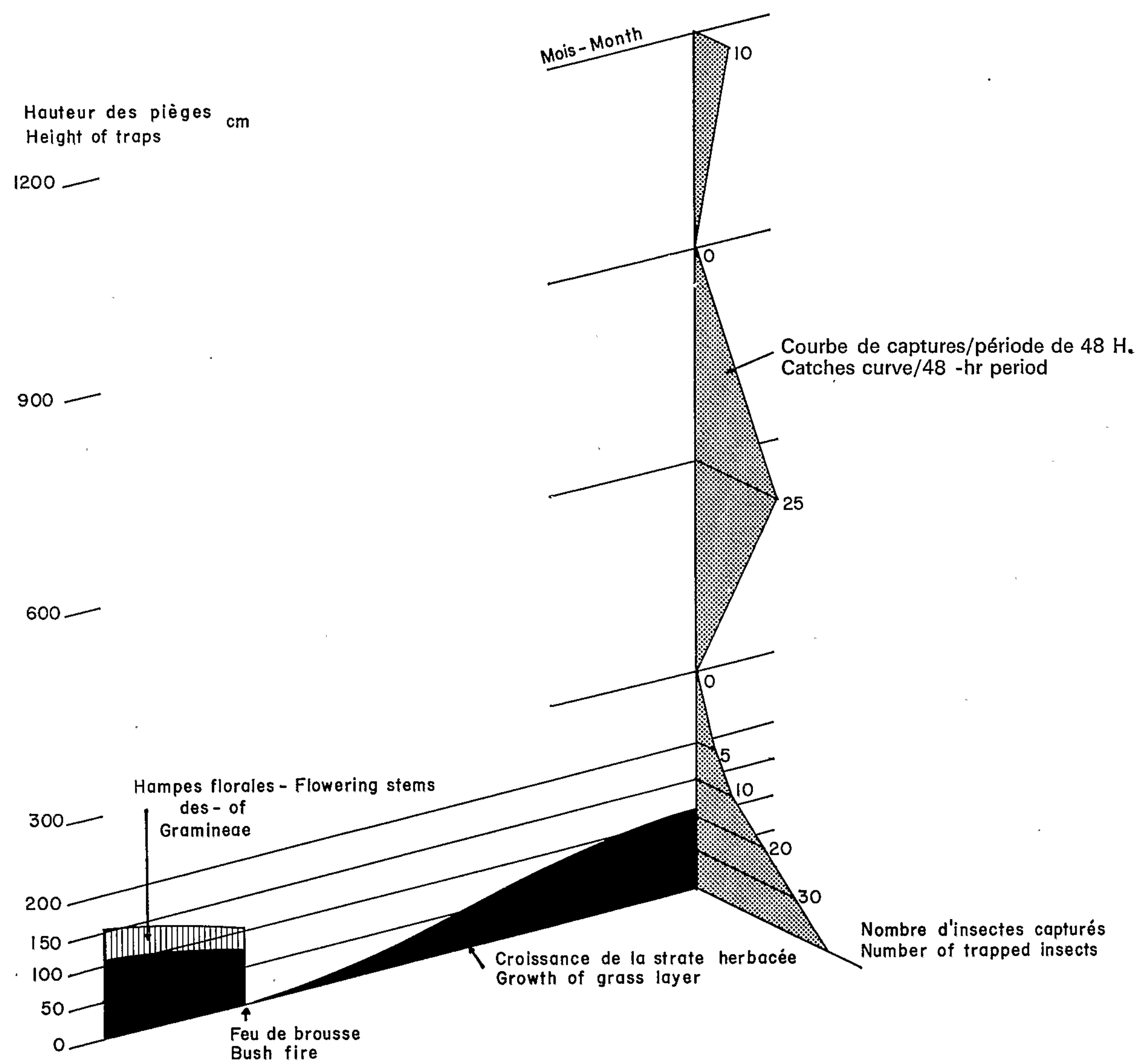


Fig. 10. Explanation of Figs 11, 12 and 13.

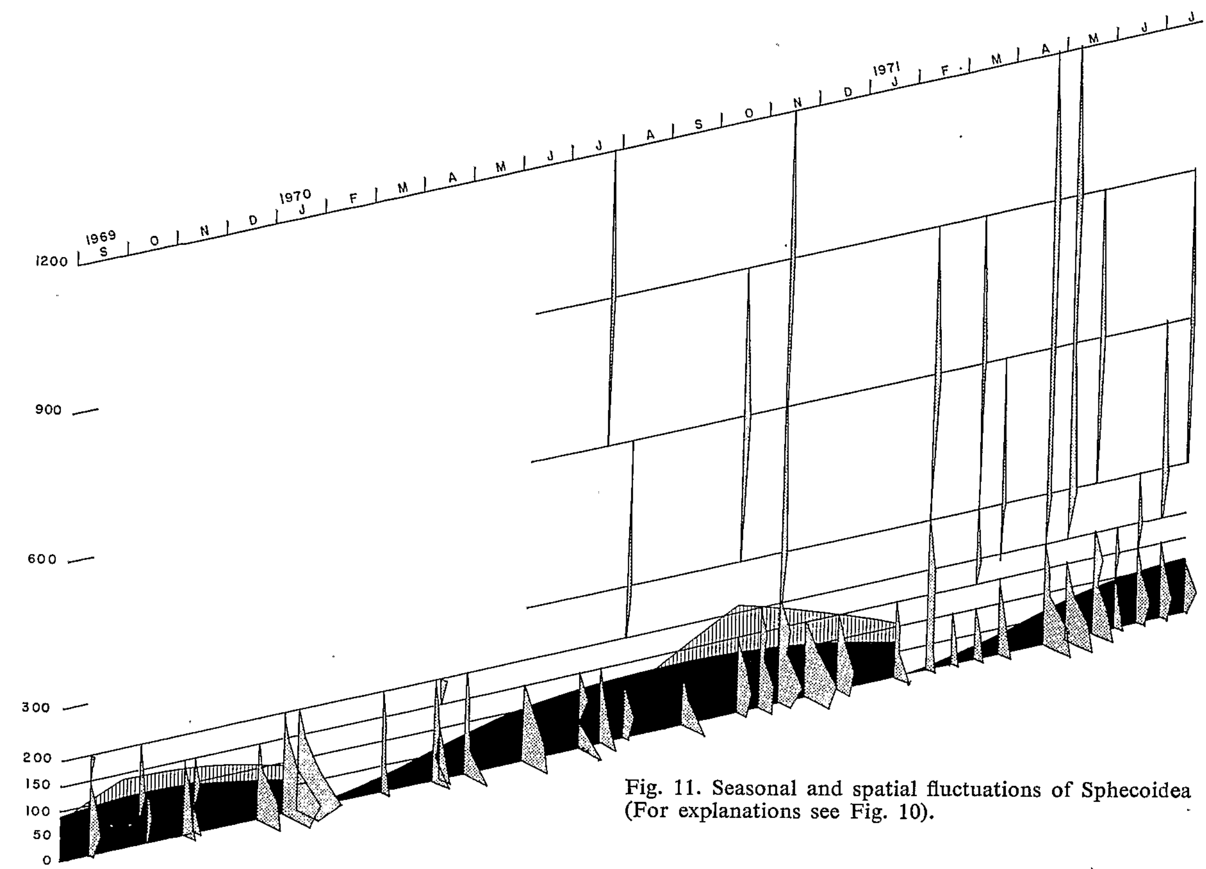


Fig. 11. Seasonal and spatial fluctuations of Sphecoidea (For explanations see Fig. 10).

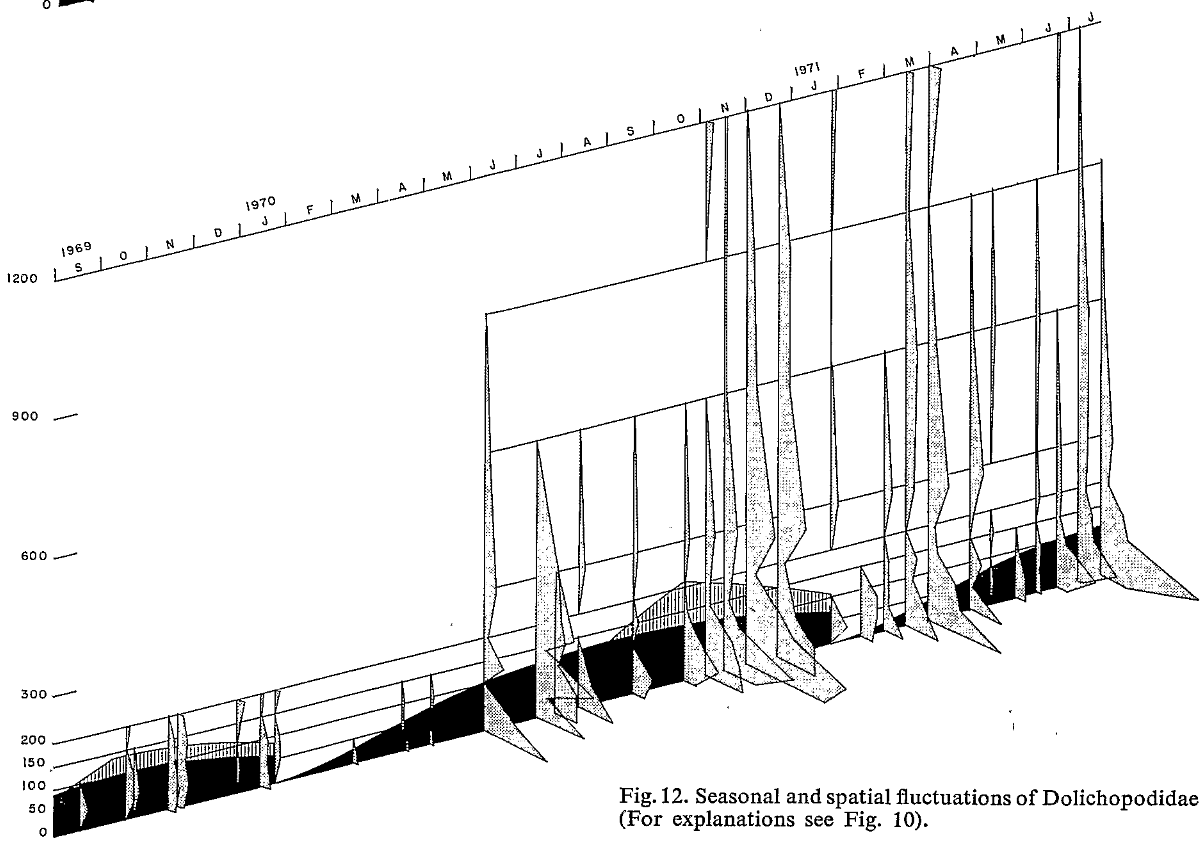


Fig. 12. Seasonal and spatial fluctuations of Dolichopodidae (For explanations see Fig. 10).

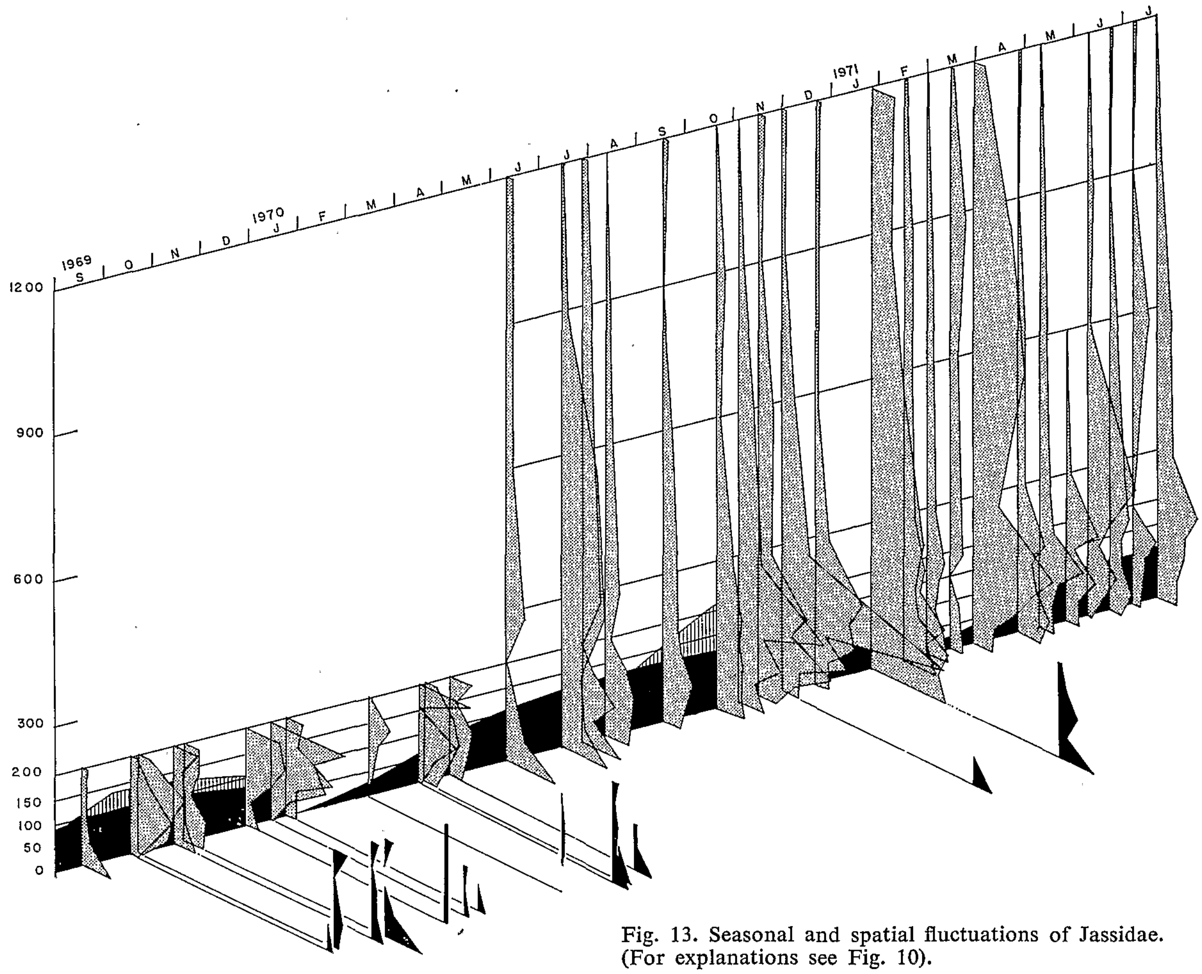


Fig. 13. Seasonal and spatial fluctuations of Jassidae. (For explanations see Fig. 10).

Nevertheless, this technique is indispensable for the study of the winged fauna's distribution within a given environment; the fact that data are similar from one year to another bears witness to the reliability of the technique. Although based on different taxa, our results are very similar to those obtained from quadrat sampling techniques (Gillon and Gillon, 1967) in the same savanna system. Some general phenomena seem characteristic of insect ecology in savanna environment: rain-dependent seasonal fluctuations, depressant effect of the dry season, influence of bush fires, etc.

The lack of taxonomic precision of this preliminary paper precludes a detailed analysis of the data. It is intended to extend this study to the species level in order to obtain a better understanding of the ecology of the winged insect community in the savanna.

The insect ecologist ultimately faces a dilemma: either to study intensively the ecology of a few species (for which purpose he will choose an effective quantitative sampling method, often damaging to the biotope), or to investigate selected phenomena affecting the entire insect community in order to comprehend its seasonal behaviour, spatial distribution, interspecific relationships, etc.

The so-called "quantitative" sampling techniques are generally inadequate with regard to micro-parasites and predators, and even to primary consumers such as many Diptera and the entire Homoptera. The biomass involved is admittedly small, but their influence on the ecosystem may be of major importance.

Water-trap sampling, although simple and inexpensive, and non-destructive, frequently needs to be complemented by "quadrat" cages as proposed by Chazeau (1970) for sampling of the lower vegetation levels. This is the only way to make a reliable distinction between operating and instant populations and thus affording a better idea of the insect community.

7. Acknowledgements

The authors wish to thank Professor Lamotte, who allowed them to work at the Lamto Field Station; Mr Chefson, ORSTOM, whose help was essential in the design and construction of the 15-m poles; Mr J. L. Tournier, Station de Géophysique de Lamto, for providing weather data, various members of the Laboratoire d'Entomologie, ORSTOM, for help in trapping and sorting insects. Professor Bergerard kindly read the manuscript.

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