

INSECT PHENOLOGY IN A FOREST COCOA-FARM LOCALITY IN WEST AFRICA

BY D. G. GIBBS* AND DENNIS LESTON†

International Capsid Research Team, Cocoa Research Institute of Ghana, Tafo

INTRODUCTION

This paper presents phenological data on a range of insects in a cocoa area. This information is used to characterize the important seasonal periods, and to understand the environmental factors that determine the phenological sequence. The paper attempts to treat seasonality in the insect fauna of this tropical tree crop as a single complex problem.

The statement of Allee *et al.* (1949) that 'We are greatly in need of many seasonal studies in all parts of the world . . .' is confirmed every time a problem in the ecology of tropical forest insects is approached. For example Davis (1945) had to make a detailed examination of seasonality of mosquitoes, of their potential hosts, and of the food of these, as a background to satisfactory study of a single species, *Aedes aegypti* (L.), in Brazilian forests. He defined the succession of seasons in terms of periodicity of biological events. In the few applications of this approach that have been made, notably by Baker and others in the New Hebrides (Baker & Harrison 1936; Baker & Baker 1936), it is shown to have great value in the study of seasons, especially in areas where cyclic fluctuations in the physical factors commonly measured, i.e. rainfall and temperature, are small. The opposite approach is to seek correlations between observed events and seasons defined arbitrarily, for example by rainfall; this frequently leads to wrong conclusions because either enough factors are not considered, or correlations are mistaken for cause and effect relationships.

Most of our data arose from studies of insect pests of cocoa and their potential predators through the year and in different areas. The way in which cocoa is normally grown, as an understorey in thinned high forest, makes it possible to consider the data in a context of forest ecology. The fauna of cocoa farms is much more diverse than that of a pure plantation crop and resembles that of the surrounding natural habitats; several of the species we discuss also occur in primary high forest.

In the following account, notes on the habitats and food of the species considered are given in a Table, and figures of seasonal population data are grouped according to the seasonal patterns shown. A sequence of six seasons, defined by mean monthly rainfall and mean daily sunshine, is put forward as an improved background against which to interpret the various kinds of population curve. These curves are then related to the kind of food resource that the species concerned exploit, and to botanic and climatic events.

The locality

Our observations were made at the Cocoa Research Institute of Ghana, Tafo, Eastern

* Present address: Department of Entomology, Rothamsted Experimental Station, Harpenden, Herts.

† Present address: Department of Zoology, University of Ghana, Legon, Accra.

Region, 6° 14' N and 67 miles from Accra on the Accra–Kumasi road. The Institute's grounds comprise cocoa plots, open areas, compounds, and patches of farm-bush and secondary forest. The surrounding area includes cocoa farms, farms producing local food, farm-bush, an urban block and some secondary forest with primary relicts. A map and notes on the vegetation and vertebrate fauna appear elsewhere (Leston & Hughs 1968). Some of the cocoa grows in plantation plots with shade trees removed, but most is under 'Ghana farm' conditions with many forest trees left to give shade; the term 'cocoa forest' best describes the latter type. In many cocoa plots daylight under the canopy is less than 1% of outside light and is comparable with that in primary forest (Richards 1952).

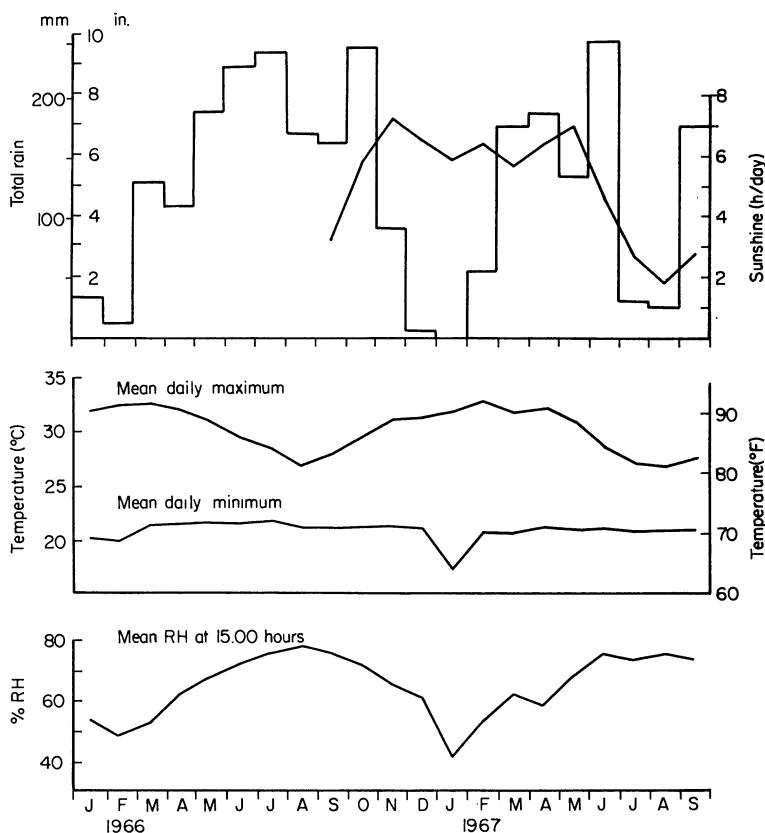


FIG. 1. Weather data for Tafo during the period of sampling. Upper: rainfall (histogram) and sunshine (line); middle: temperature; lower: humidity.

The climax vegetation belongs to the *Celtis-Triplochiton* subdivision of the moist semi-deciduous high forest (Taylor 1952), while on a broader view the locality is at the eastern end of the Ghana–Guinea bloc of 'moist forest at low and medium altitudes' (Keay 1959).

The weather

Tafo is within the zone of equatorial climates, with 'rain in every month, with two

maxima' (Church 1957). Wills (1962) has analysed Ghana rainfall in detail: Tafo comes into his class 2b(ii) with wet seasons from March to July and from September to early November and with two equal maxima (May–June, September–October).

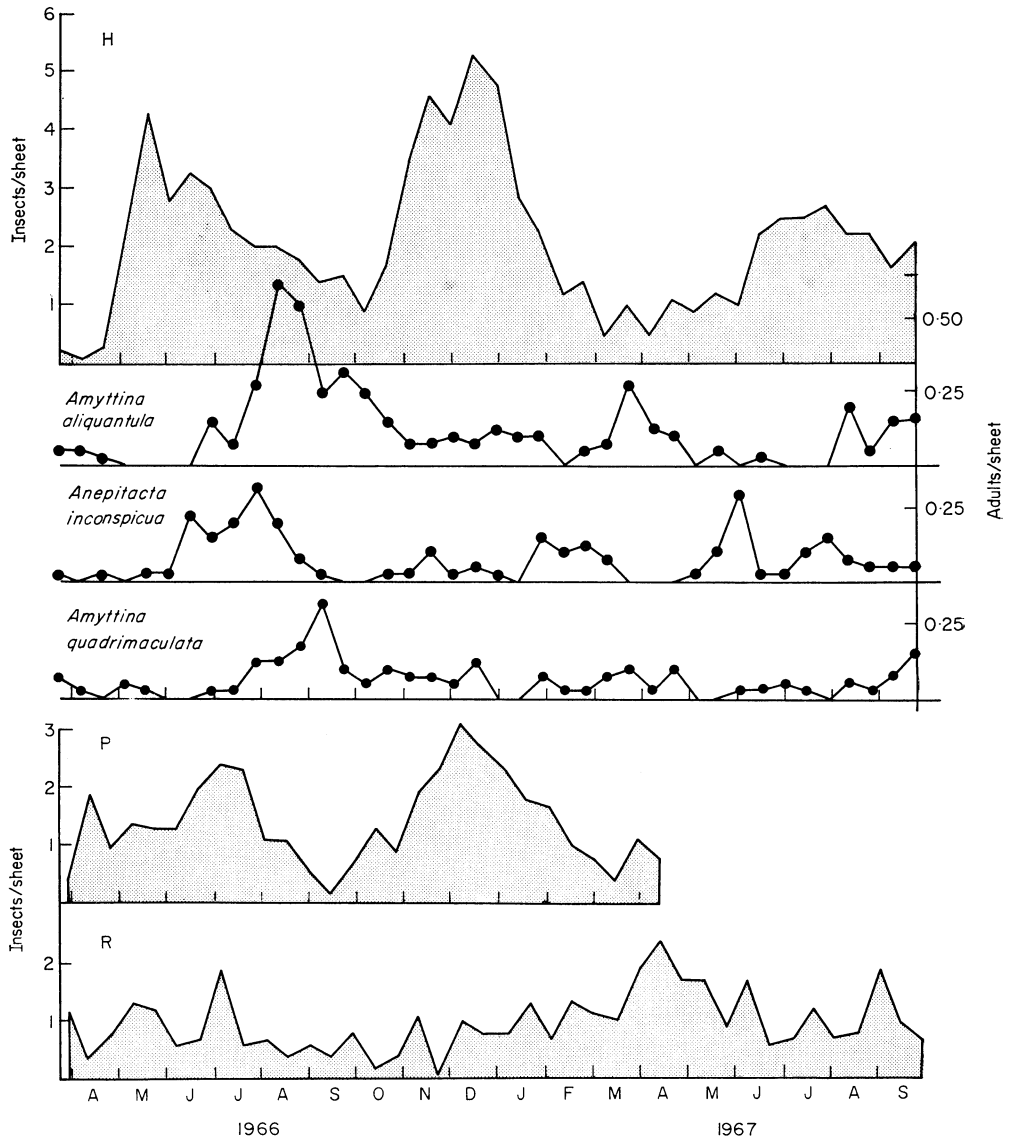


FIG. 2. Predators in foliage. Meconeminae (Tettigonoidea) from knockdown samples in three blocks. Total Meconeminae (stippled area) and adults of the commonest species in block H (●).

Fig. 1 gives weather data for the period of our sampling. In both years harmattan was exceptionally severe: in the December–February period, afternoon relative humidity fell below 40% on 12 and 18 days respectively, compared with only 2 or 3 days in each of the preceding 3 years. Dry conditions were most severe in February in 1966 and in January in

1967; cumulative rain by the end of March was 6.8 in. (173 mm) and 9.2 in. (235 mm) respectively. The August interruption in the rains was slight in 1966 and exceptionally marked in 1967 when July also had little rain.

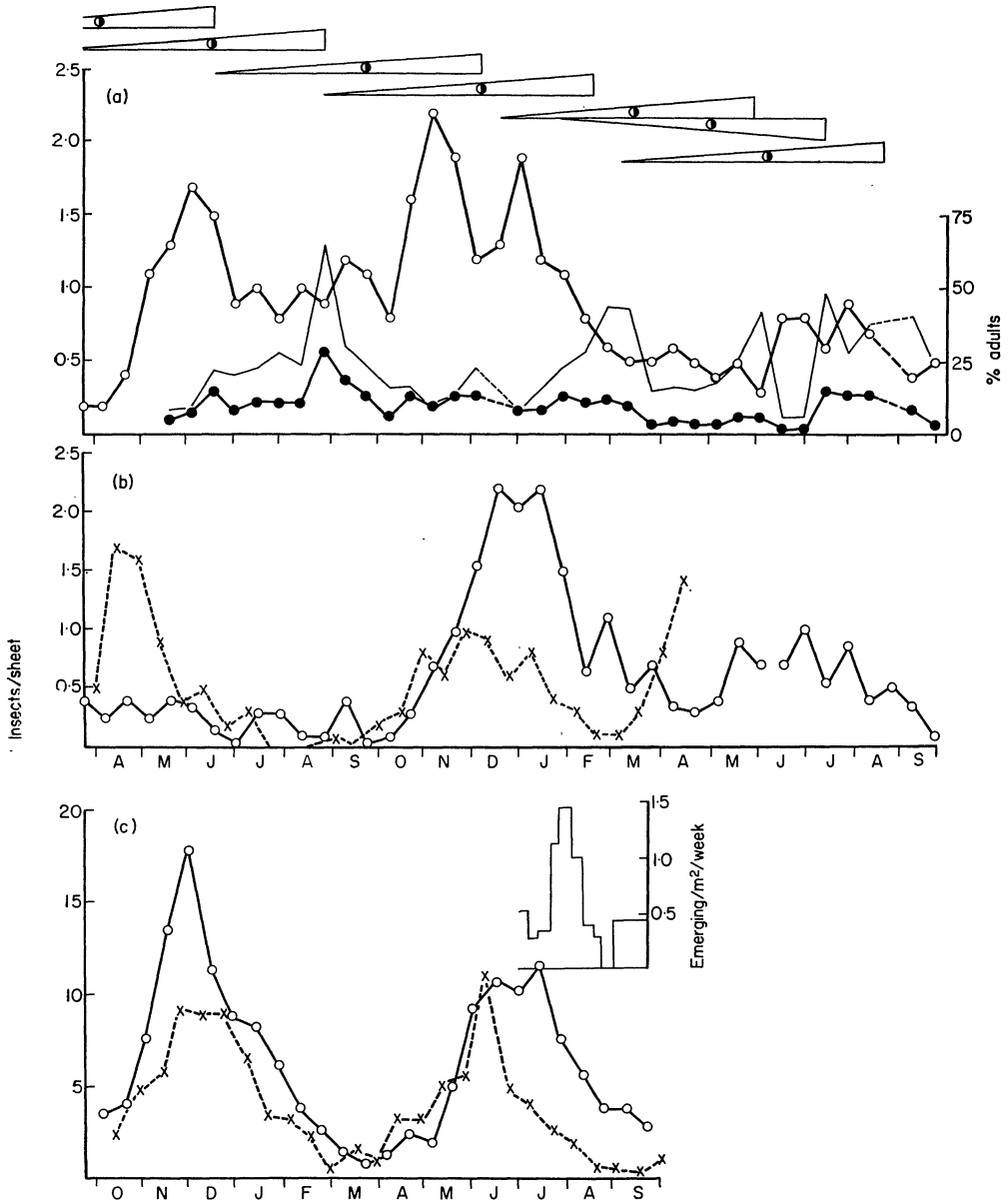


FIG. 3. Predators in foliage (a and b) and leaf feeders (c) from knockdown samples. (a) *Anaxipha longipennis* (Grylloidea) in block H; total (○), adults (●) and percentage of adults (—). Wedges above the curves represent a suggested succession of generations that fits the observed data; (●) time of hatching. (b) *Afrogyllacris africana* (Grylloidea) in blocks H (○) and P (×). (c) *Paraivongius viridiaeneus* (Eumolpidae) in blocks H (○) and R (×); also numbers in emergence cages in block H (histogram).

Sampling sites

A large part of our sampling was done in three contrasting areas of cocoa from March 1966 to September 1967. The largest area, block H, comprised forty plots, each of five \times five cocoa trees, under relatively artificial conditions with forest trees entirely cleared.

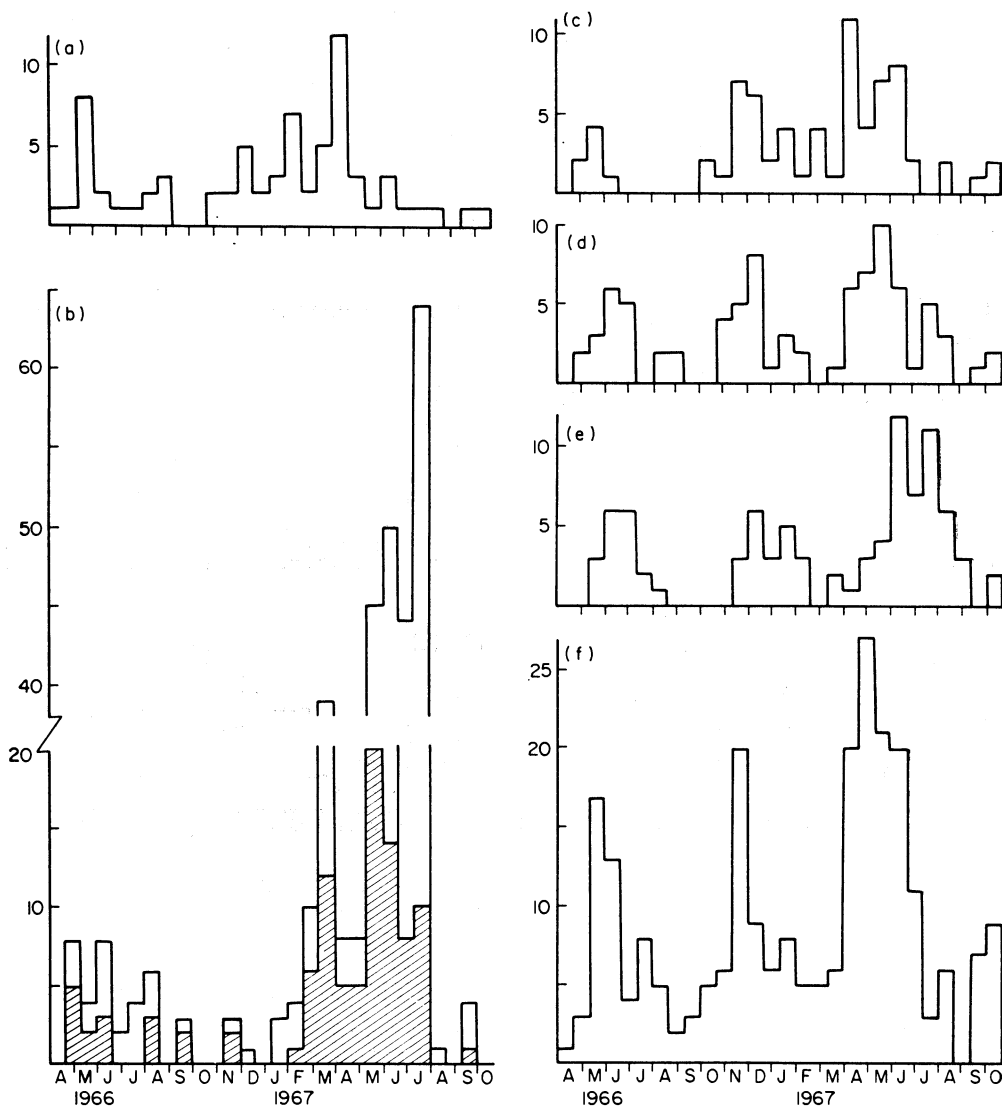


FIG. 4. Mantodea from light trap catches. Totals in 20-day periods; males only except where indicated. (a) *Tarachodes gerstaeckeri*; (b) *Anasigerpes bifasciata*; (c) *Stenopyga ziela*; (d) *Panurgica fratercula*; (e) *P. compressicollis*; (f) *Chloroharpax modesta*.

The cocoa canopy was continuous and intact in some parts, but was badly broken down by the effects of insects and exposure in others. Two smaller areas, each nine plots of six \times six trees, were used for comparison: block R was sheltered from the sides by tall forest trees and except for some breakdown in the dry season had an intact canopy;

block P was healthy, heavily shaded by large trees, and most resembled cocoa grown by the traditional method, as an understorey tree in thinned forest.

Sampling methods

Pyrethrum knockdown in cocoa. At intervals of 2 weeks the canopy in a square between four trees in each of the three plots was sprayed with 0.1% w/v pyrethrum extract from a knapsack mistblower; insects fell onto a cotton sheet of 9 m² spread on the ground beneath the sprayed area. The sixteen (block H) or twenty-five (blocks P,R) available sampling positions in each plot were used in rotation.

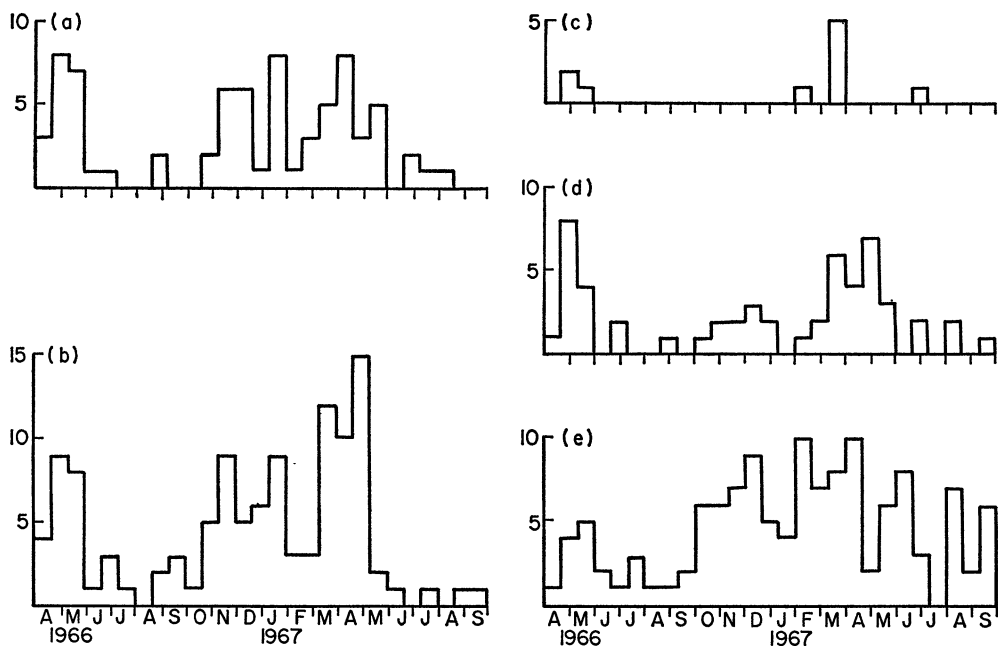


FIG. 5. *Amorphoscelis* spp. (Mantodea) males from light trap catches. Totals in 20-day periods. (a) *A. chopardi*; (b) *A. maculata*; (c) *A. ascalaphoides*; (d) *A. pulchra*; (e) *A. elegans*.

Light trapping. A 125 W white ultraviolet lamp with Robinson trap was operated daily from 17.30 to 06.30 hours. It was situated in cocoa under high forest shade about 200 m from block R. In our figures light trap catches have been grouped in 20-day periods.

Emergence traps in cocoa. Fourteen gauze-topped wooden boxes each covering 0.5 m² were used in block H from June to September 1967; they sampled eumolpid beetles emerging from the soil.

General collecting. Background information on habitats and prey or host plants of the species sampled by these methods was obtained by searching, sweeping, beating, etc. If a species was searched for often enough throughout the year, seasonal data based only on this method have been included.

Plant names follow Hutchinson & Dalziel (1954 *et seq.*).

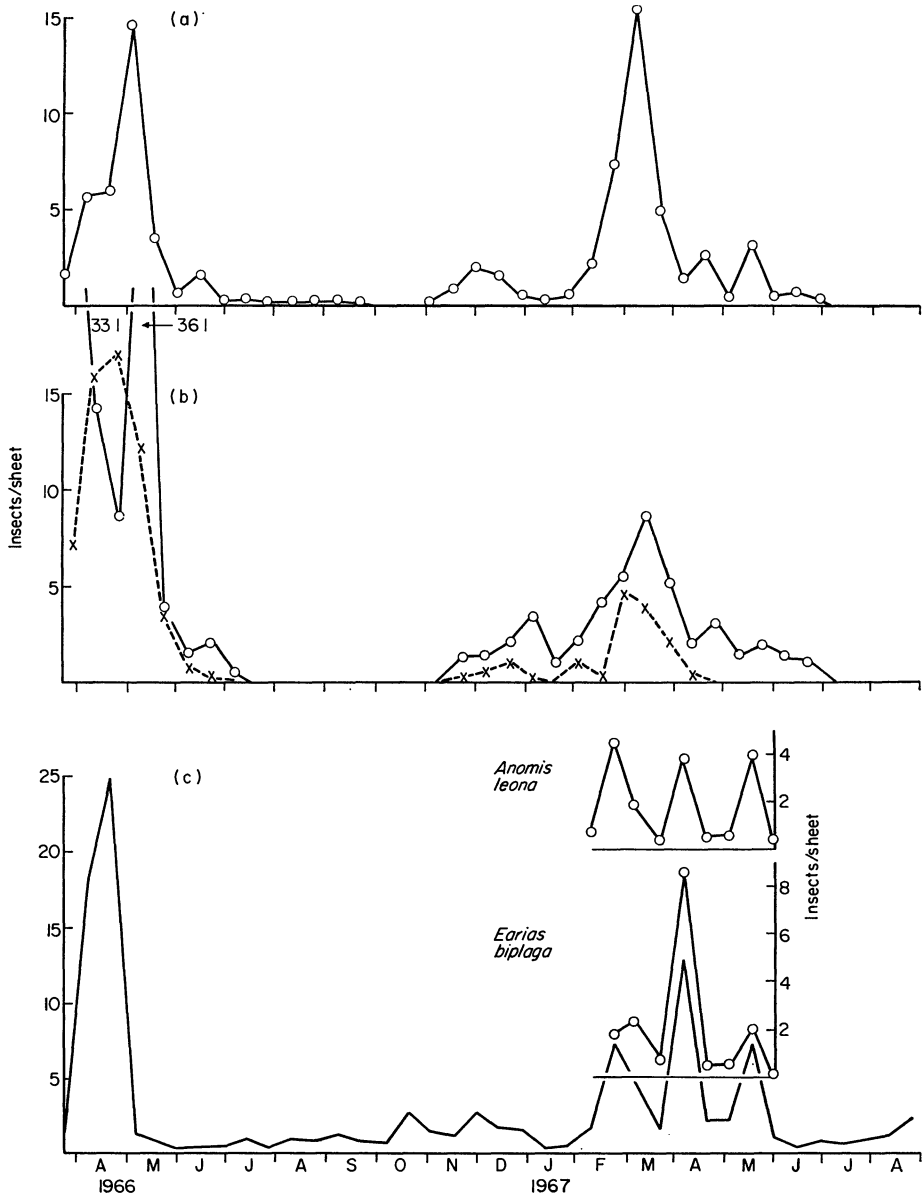


FIG. 6. Shoot meristem feeders from knockdown samples. (a) *Tyora tessmanni* (Psyllidae) in block H. (b) *T. tessmanni* in blocks R (○) and P (×). (c) Caterpillars in block H. Total numbers, and separate curves for two species in the 1967 peak period.

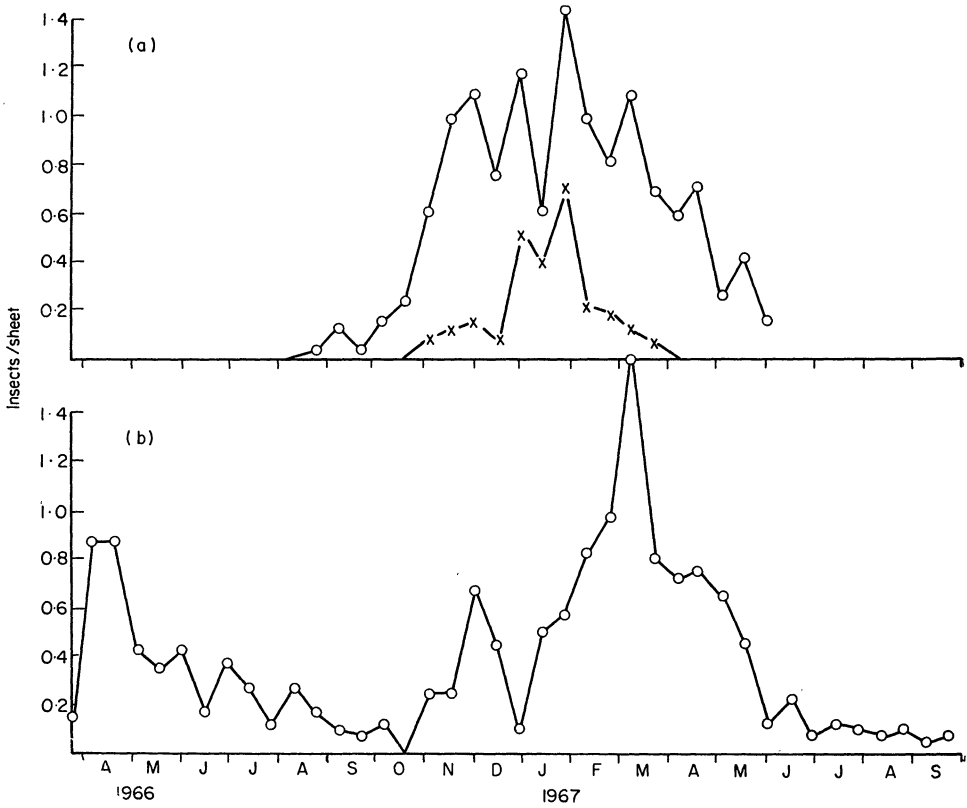


FIG. 7. Regenerative tissue feeders from knockdown samples in block H. (a) *Sahlbergella singularis* (○, up to June 1967 only) and *Euscyrtes bivittatus* (Grylloidea) (×). (b) *Halyomorpha reflexa* (Pentatomidae).

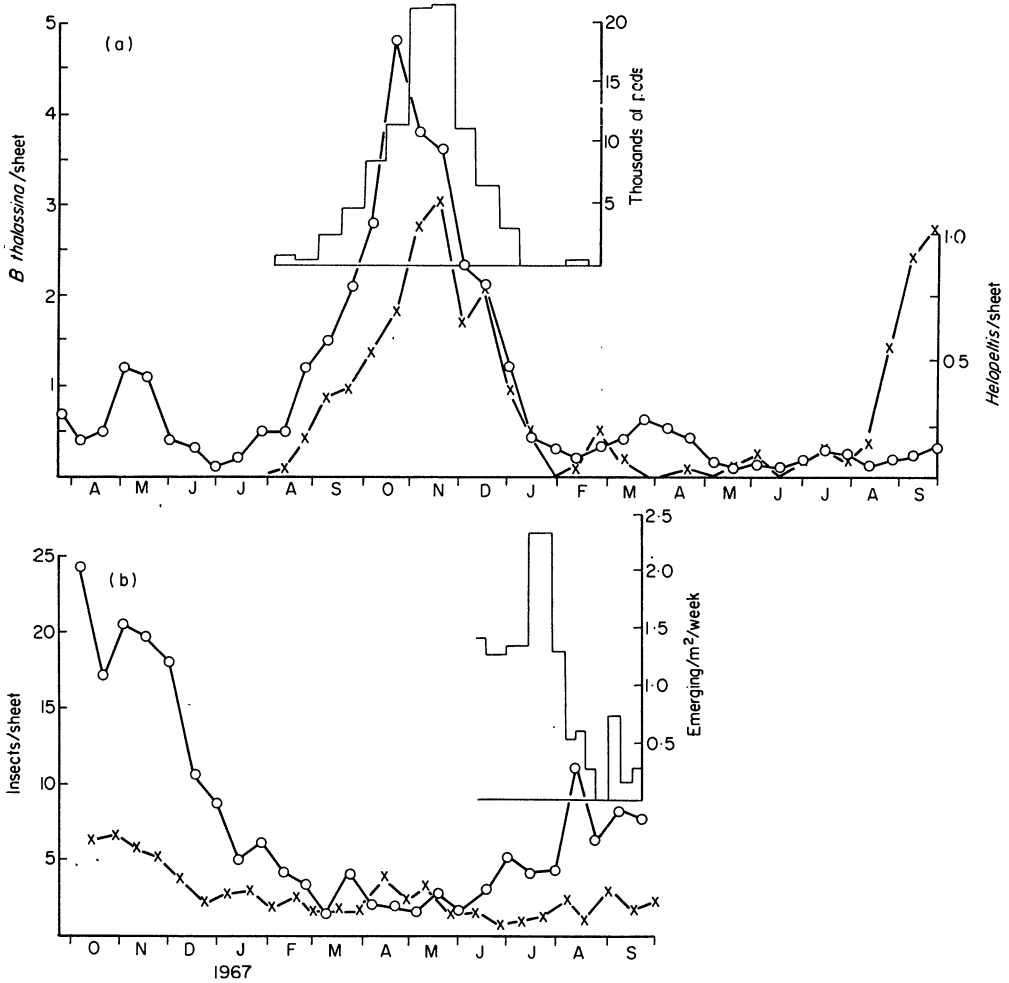


FIG. 8. Cocoa-pod feeders from knockdown samples. (a) *Bathycolia thalassina* (Pentatomidae) (O) and *Helopeltis* spp. (Miridae) (x) in block H; also number of pods harvested at 2-week intervals during the main harvest (histogram). (b) *Paraivongius semipiceus* (Eumolpidae) in blocks H (O) and R (x); also numbers in emergence cages in block H (histogram).

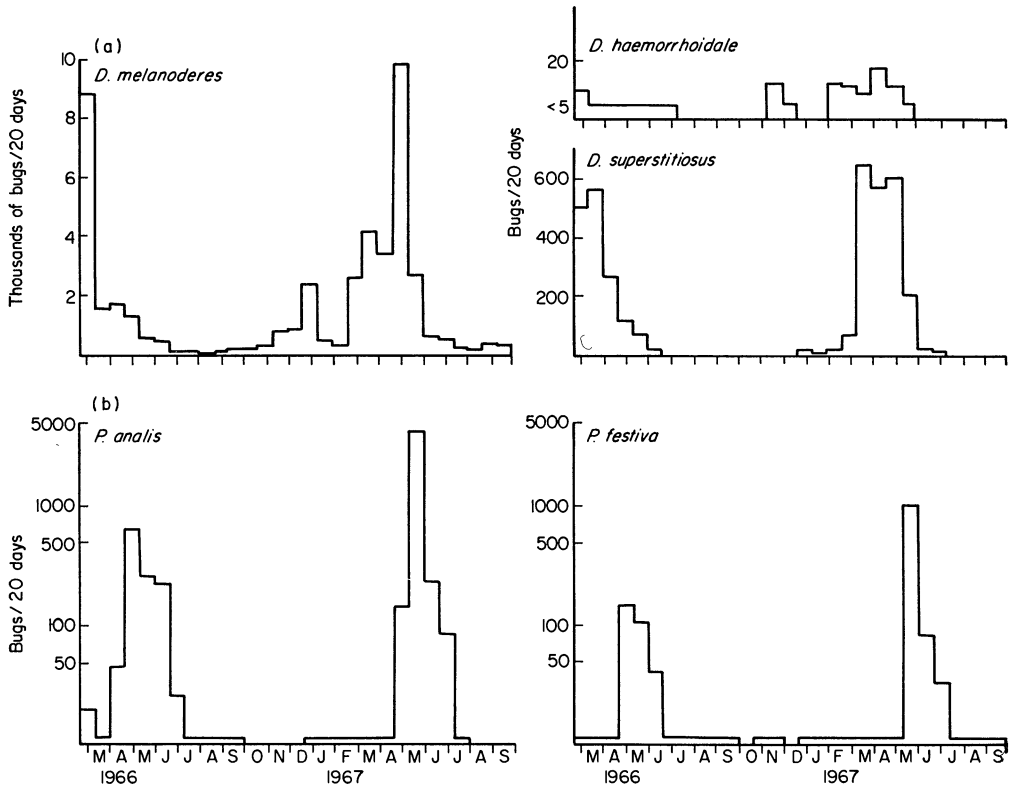


FIG. 9. Fruit-feeding Heteroptera from light trap catches. Totals in 20-day periods. (a) *Dysdercus* spp. (Pyrrhocoridae); (b) *Physopelta* spp. (Largidae).

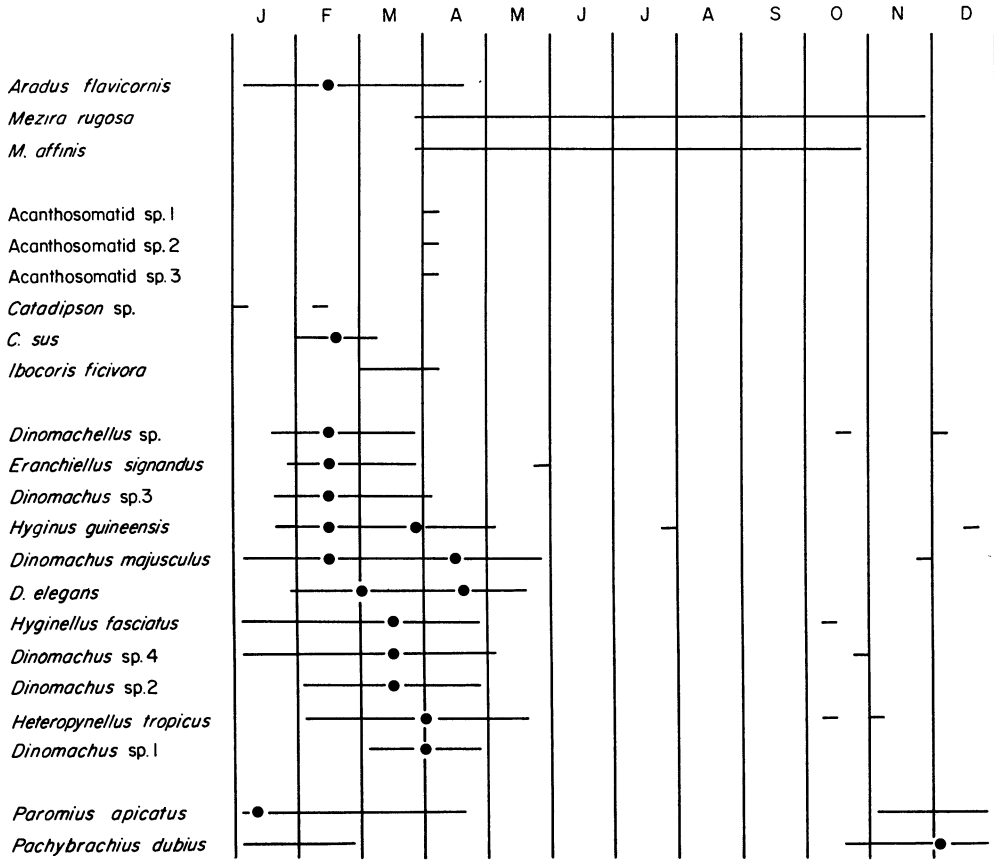


FIG. 10. Various Heteroptera from light trap catches and knockdown samples in both years combined. Continuous bars show main period of occurrence with peaks indicated (●); short bars show single weeks in which a species occurred outside the main period.

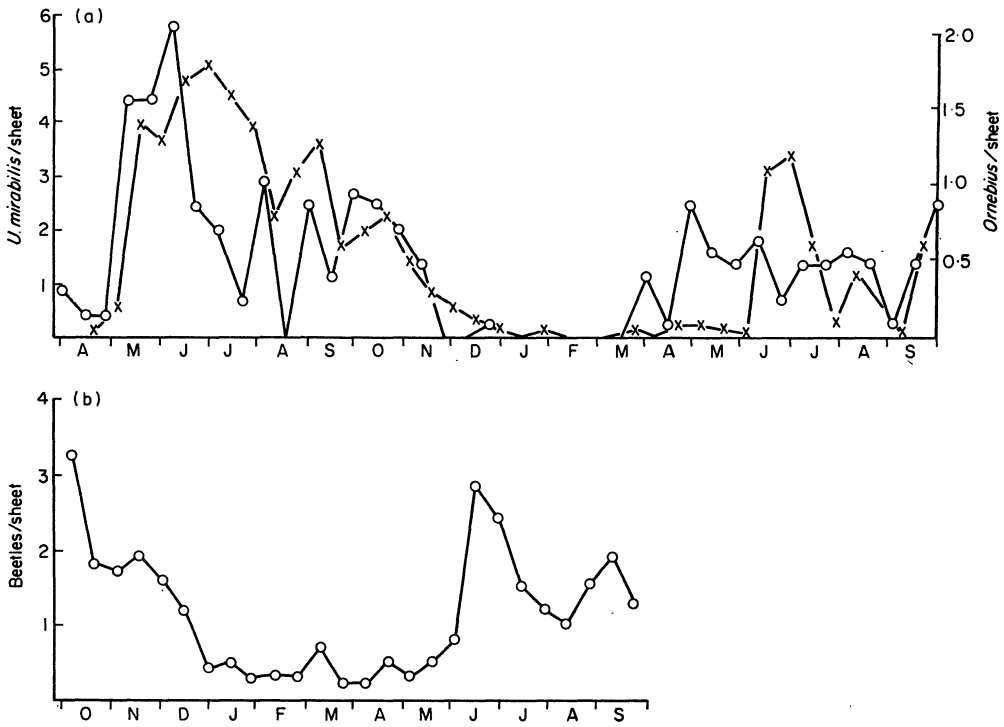


FIG. 11. Various species from knockdown samples. (a) A small predator in litter, *Ornebius* sp. (Grylloidea) (×) in block H and a fungus feeder, *Ussingeria mirabilis* (Aradidae) (○) in block R. (b) A leaf feeder with larvae probably wood-boring, *Proictes schachi* (Curculionidae) in block H.

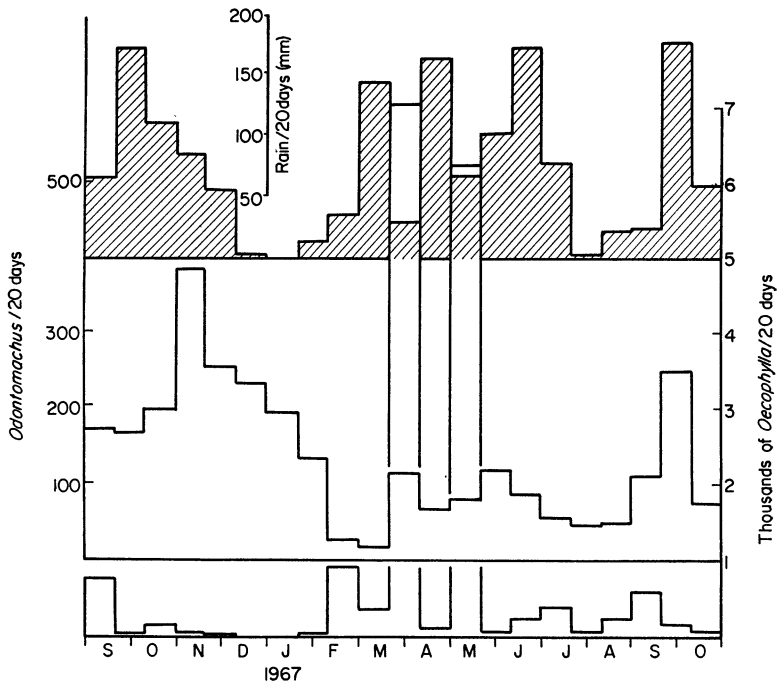


FIG. 12. Ants (alate females) from light trap catches. Totals in 20-day periods. Rain in 20-day periods (hatched), *Odontomachus haematodus* (upper histogram), *Oecophylla longinoda* (lower histogram).

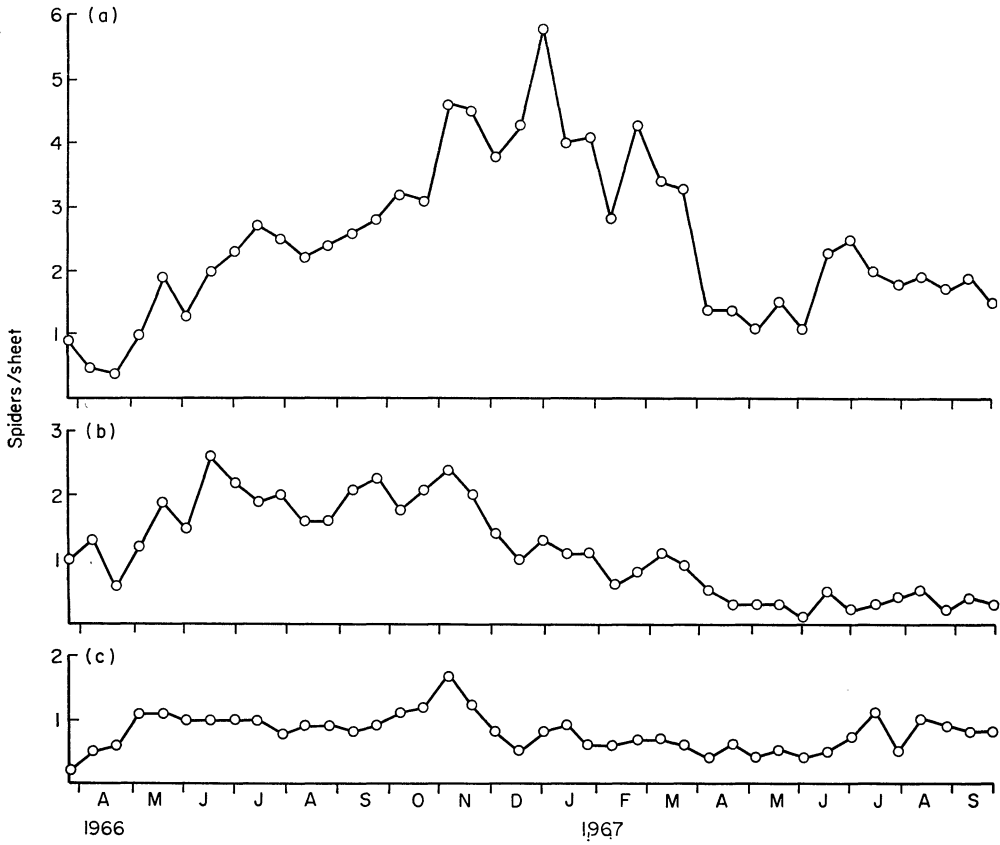


Fig. 13. Salticid spiders from knockdown samples in block H. (a) *Viciria* spp.; (b) *Telamonia* sp. (1230); (c) *Telamonia* sp. (1237).

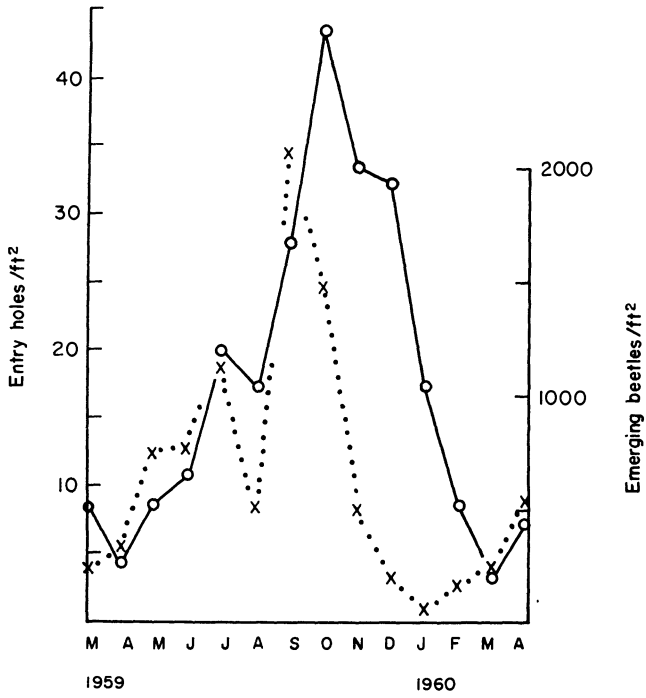


FIG. 14. Invasion and emergence by wood-boring Platypodidae and Scolytidae (from data of Roberts 1961). ○, Entry holes in billets of wood left in the open for 3 weeks in each month; ×, monthly totals of five common species emerging from samples of the same billets kept for 10 weeks after exposure.

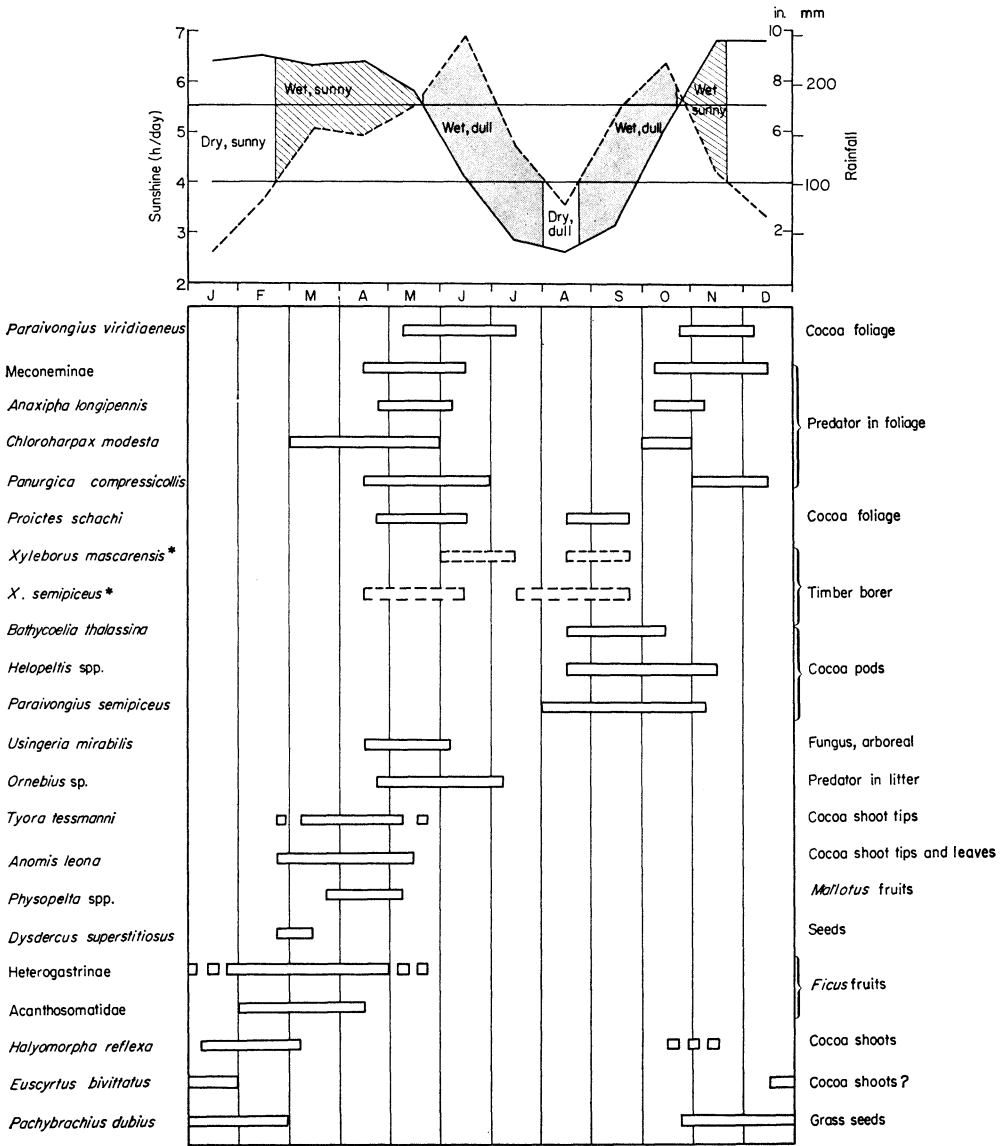


FIG. 15. Periods of insect population increase in relation to seasons. Upper: diagram of six seasons based on rainfall (-----) and sunshine (——); limits are drawn where these lines cross horizontal lines at mean $5\frac{1}{2}$ h sun/day and 4 in. rain/month. Rainfall based on 30 year means (Walker 1962), sunshine on 20–22 year means (Walker 1962 and new data) at Tafo. Lower: diagram showing main periods of increase in numbers of a range of the species sampled. The food source of each species is indicated. * From data of Roberts (1961) on rate of emergence from experimental blocks of woods (cf. Fig. 14).

THE SPECIES SAMPLED

Table 1. *Annotated table giving species sampled, method of sampling, habitat and food*

Taxon	Sampling method	Habitat where sampled and food
ORTHOPTERA		
<i>Amyttina aliquantula</i> (Karsch)	} Knockdown	Cocoa foliage; carnivorous (Paulian 1947), but young larvae may also eat leaves
<i>A. quadrimaculata</i> (Karny)		
<i>Anepitacta inconspicua</i> Brunner (Tettigonoidea: Meconeminae); Fig. 2		
<i>Afrogyllacris africana</i> (Brunner) (Tettigonoidea: Gryllacrididae); Fig. 3(b)	Knockdown	Branches of cocoa trees; from gut contents, eats small insects and mites
<i>Anaxipha longipennis</i> Serville (Grylloidea: Trigonidiidae); Fig. 3(a)	Knockdown	Cocoa foliage; from gut contents, carnivorous
<i>Ornebius</i> sp. (Grylloidea: Mogoplistidae); Fig. 11(a)	Accidental in knockdown samples	Leaf litter under cocoa; from gut contents, probably eats small arthropods in litter
<i>Euscyrtus bivittatus</i> Guerin (Grylloidea: Eneopteridae); Fig. 7(a)	Knockdown	Gut contents shredded bark; probably eats regenerative shoots of cocoa. Widespread away from cocoa
MANTODEA		
<i>Amorphoscelis</i> spp.* (Amorphoscelidae); Fig. 5	Light trap	Runs after prey on tree trunks; one or two species seen low down on cocoa trunks, others probably live in cocoa canopy
<i>Tarachodes gerstaeckeri</i> Werner (Mantidae: Tarachodinae); Fig. 4 (males)	Light trap	Collected in cocoa canopy Females brachypterous, occasional in knockdown samples
<i>Stenopyga ziela</i> Roy (Mantidae: Angelinae); Fig. 4	Light trap (males)	Arboreal. Females brachypterous, occasional in knockdown samples
<i>Chloroharpax modesta</i> (Gerstaecker) (Hymenopodidae: Hymenopodinae); Fig. 4	Light trap (males)	Probably in canopy of upper-storey trees, since rare in knockdown samples. Females macrop- terous, but never at light
<i>Panurgica compressicollis</i> (Saussure) (Hymenopodidae: Hymenopodinae); Fig. 4	Light trap (males)	As last species
<i>P. fratercula</i> Rehn (Hymenopodidae: Hymeno- podinae); Fig. 4	Light trap (males)	Habitat probably as last two species. Females never sampled
<i>Anasigerpes bifasciata</i> Giglio-Tos (Hymenopodidae: Acromatinae); Fig. 4	Light trap (both sexes)	Habitat probably as last three species
HOMOPTERA		
<i>Tyora tessmanni</i> (Aulmann)† (Psyllidae); Fig. 6(a and b)	Knockdown (adults only)	Early instars within newly active cocoa shoot tips, later ones and adults on expanded but un- hardened flush leaves
HETEROPTERA		
<i>Aradus flavicornis</i> Dalman (Aradidae: Aradinae); Fig. 10	Light trap	Food not known

* In addition to the species in Fig. 5, *A. simulans* Giglio-Tos, *A. lagrecai* Roy, *A. lamottei* Roy, *A. nigriventer* Beir and *A. laxeretic* Karsch occurred in smaller numbers; their seasonal pattern did not differ from that of the commoner species.

† A fairly important pest of cocoa (Cotterell 1927; Alibert 1951). Population changes may be influenced by the mirid predator, *Deraeocoris crigi* (Leston & Gibbs 1968).

<i>Usingeria mirabilis</i> Schouteden (Aradidae: Mezirinae); Fig. 11(a)	Knockdown	Cocoa canopy (common only in block R); probably feeds on mycelia of white-thread blight fungus, <i>Marasmius scandens</i> Masee
<i>Mezira rugosa</i> (Signoret) (Aradidae: Mezirinae); Fig. 10	Sweeping and searching	Rotten logs, under bark; probably fungivorous
<i>M. affinis</i> Schouteden (Aradidae: Mezirinae); Fig. 10	Knockdown	Cocoa canopy; fungivorous
Acanthosomatidae;* Fig. 10	Light trap, regular searching	Young shoots, perhaps sometimes fruits, of <i>Ficus</i> trees
<i>Halyomorpha reflexa</i> (Signoret)† (Pentatomidae); Fig. 7(b)	Knockdown	Stylets apparently enter pith of young regenerative shoots of cocoa
<i>Bathycoelia thalassina</i> (Herrich-Schaffer)‡ (Pentatomidae); Fig. 8(a)	Knockdown	Stylets enter beans in developing cocoa pod (Lodos 1967)
<i>Physopelta</i> spp. (Largidae); Fig. 9(b)	Light trap	Three species, all feeding on developing fruits of <i>Mallotus oppositifolius</i> (Euphorbiaceae), a common shrub or small tree (Leston 1968)
<i>Dysdercus supersticiosus</i> (F.) (Pyrrhocoridae); Fig. 9(a)	Light trap	Ripe seeds of Bombacaceae and Sterculiaceae§
<i>D. melanoderes</i> Karsch (Pyrrhocoridae); Fig. 9(a)	Light trap	As last species
<i>D. haemorrhoidale</i> Signoret (Pyrrhocoridae); Fig. 9(a)	Light trap	Hosts not known, probably similar to last two species
Heterogastrinae (Lygaeidae);¶ Fig. 10	Light trap	Seeds of ripe <i>Ficus</i> fruits, reached from outside fruit by very long rostrum
<i>Paromius apicatus</i> (Stal) (Lygaeidae: Rhyparachrominae); Fig. 10	In knockdown during seasonal dispersal	Seeds of grasses in derived savanna areas and clearings in forest
<i>Pachybrachius dubius</i> (Reuter) (Lygaeidae: Rhyparachrominae); Fig. 10	In knockdown during seasonal dispersal	As last species
<i>Helopeltis</i> spp.** (Miridae: Bryocorinae); Fig. 8(a)	Knockdown	Parenchyma just under epidermis of cocoa pods
<i>Sahlbergella singularis</i> Haglund†† (Miridae: Bryocorinae); Fig. 7(a)	Knockdown	Parenchyma just under epidermis of cocoa pods and shoots, particularly regenerative shoots

* Species sampled were *Catadipson sus* Breddin, *Catadipson* sp., *Ibocoris ficivora* Roche and three undescribed species.

† This bug occurs, sometimes abundantly, on the common shrub *Solanum verbascifolium*, which was present near the sampling area.

‡ This species, which has a large number of shrubby and arboreal host plants, has been a local pest of cocoa in the last few years. A high normal rate of parasitism may have been reduced by trials of certain insecticides, and one suspect material was used in block H before sampling began. Numbers remained low in the second year of sampling, by which time natural controls have presumably recovered.

§ Two common hosts, *Sterculia rhinopelta* and *Ceiba pentandra*, have ripe seeds from November to January and from February to April respectively (Taylor 1962).

¶ The species sampled were *Dinomachus elegans* Scudder, *D. majusculus* Scudder, *Eranchiellus signandus* Scudder, *Heteropynellus tropicus* Scudder, *Hyginellus fasciatus* Scudder, *Hyginus guineensis* Scudder and five new species. Host plants include *Ficus kamerunensis*, *F. praticola*, *F. capensis*, *F. vogeliana* and *F. vallis-choudae*, all forest trees some of which start as stranglers.

** *Helopeltis bergrothi* Reuter and *H. sanguineus* Poppus are the species usually said to occur on cocoa in Ghana, but Dr G. Schmitz is revising the genus and informs us that neither name is correct.

†† Seasonal changes in numbers of the economically important cocoa capsids, *Sahlbergella singularis* and *Distantiella theobroma* (Distant) are discussed by Gibbs *et al.* (1968). Maximum numbers on mature cocoa can occur at any time from September to February and there are often two peaks in this period. Early increase, at the same time as that of *Helopeltis* spp., coincides with cocoa pod development, although large populations may occur on vegetative tissues locally. Later, in the dry season, feeding in vegetative tissues, particularly vertical regenerative shoots (chupons), is widespread but still shows great local variation. Large numbers may occur on seedling cocoa at almost any time.

LEPIDOPTERA

<i>Earias biplaga</i> Walker and <i>Anomis leona</i> (Schaus) (Noctuidae); Fig. 6(c)	Knockdown (larvae)	Young larvae inside newly active cocoa shoot tips, older ones on flush leaves
--	--------------------	---

HYMENOPTERA

<i>Odontomachus haematodus</i> Auctt (Formicidae: Ponerinae); Fig. 12	Light trap (females)	Nests in ground or rotten wood under heavy shade; common under cocoa. Food probably mainly termites
<i>Oecophylla longinoda</i> (Latreille) (Formicidae: Formicinae); Fig. 12	Light trap	Nests of folded leaves are common in cocoa trees. Large range of prey; tend coccids

COLEOPTERA

<i>Paraivongius semipiceus</i> (Jacquemart) (Eumolpidae); Fig. 8(b)	Knockdown, emergence cages	Mainly surface tissues of cocoa pods, sometimes leaves or shoots
<i>P. viridiaeneus</i> (Jacquemart) (Eumolpidae); Fig. 3(c)	Knockdown, emergence cages	Flush or recently mature cocoa leaves, also on bark and leaf petioles
<i>Proictes schachi</i> Hoffman (Curculionidae); Fig. 11(b)	Knockdown	Adults on cocoa leaves. Most curculionid larvae either live in soil or bore in plant tissues; <i>P. schachi</i> probably does the latter as never occurred in emergence cages

ARANEIDA

Salticidae*	Knockdown	Predators on cocoa
-------------	-----------	--------------------

* Species of *Viciria* hunt mainly in foliage; they include *V. equestris* Simon, *V. ocellata* (Thorell), *V. chabanaudi* Fage and *V. niveimana*. An undescribed species of *Telamonia* (sp. 1230) hunts on the trunk and larger branches; it appears to prey mainly on ants, including species as aggressive as *Oecophylla longinoda*. Another species (sp. 1237), in an undescribed genus hunts mainly on the smaller branches and on basal shoots.

THE SEASONS

The main periods of population increase in a range of the species treated in the previous section are summarized in Fig. 15, together with a diagram showing the seasons we recognize. Population increase of many species occurs in a period from the latter part of the dry season in February through the build-up of the rains to May and June. In some species with two main periods of increase in the year, the second peak is in the period during which rainfall lessens in late October and November. The diagram shows that these periods form two out of six seasons defined by a combination of mean monthly rainfall and mean daily sunshine. Because sunshine figures were not available for the earlier part of our sampling period, the diagram is based on long-term means. Months with more or less than 4 in. (102 mm) of rain and with more or less than 5½ h mean daily sunshine are separated; 4 in. of rain per month is often quoted as the lower limit of effective rainfall in the tropics (Charter 1941; Beard 1944), and the sunshine line was put at the level that best fitted the insect data. The seasons have the following limits:

(1) Dry sunny season: late November–mid-February. This includes the harmattan period, late December–mid-February, during which, some days (0 to about 18) have RH at 15.00 hours $\leq 40\%$ (Gibbs, Pickett & Leston 1968).

(2) First wet sunny season (first transitional): late February–late May. Although hours of sunshine are rather less than in the dry sunny season the absence of harmattan dust haze gives brighter skies.

(3) First wet dull season: June and July.

(4) Dry dull season: August. Low rainfall does not imply dry season conditions because humidities remain high. Cloud cover is maximal: Foggie (1947) records 0 h sunshine in August for four consecutive years at Kumasi.

(5) Second wet dull season: late August–mid-October.

(6) Second wet sunny season (second transitional): late October–mid-November. The two transitional seasons are marked by an increased frequency of line squalls (Walker 1962).

The limits given vary between years because there is wide scatter in the distribution of both rainfall and sunshine. Annual rainfall at Tafo varied from 48 to 85 in. (1219 to 2159 mm) during the 30 years for which figures are available; January rainfall varied from 0 to 5 in. (0 to 127 mm), October from 4 to 17 in. (102 to 432 mm) and so on. Such variability is normal for all equatorial climates, for example in southern Malaya (Corner 1952) and in Java where Schimper (1903) recorded a spell of 14 dry-days in the middle of the rainy season and commented on its effect on plants. Wet months can simultaneously be bright because of the diurnal cloud pattern: many days during the rains have sunny mornings. Bernard (1945) gives figures for Bambesa (Congo-Kinshasa, 3°N), which apparently has a climate similar to that of Tafo, showing that in the wet months March–April–May and October–November 70–81% of rain falls between 17.00 and 08.00 hours, but less than 70% within these times in other months. Chamney (1930) found that about 77% of the annual rainfall at Kumasi is between 16.00 and 04.00 hours.

Seasons in western Europe were first defined by biological and agricultural events and only later by physical ones, but tropical climatology has followed the reverse and tends to recognize seasons defined by rainfall alone. Kendrew (1961) says 'the seasons are distinguished in part by temperature but mainly by humidity and rainfall', and Miller (1961) 'by the absence of any marked temperature changes in this zone, rainfall becomes the determinant of season'. Boateng (1959), writing of Ghana, states 'the only significant division of the year here is into rainy seasons and dry seasons'. In attempts to classify climates for analysis of crop potentials two kinds of formula have been used. The first evaluates effective rainfall by using mean monthly rain and number of rainy days; for cocoa growing in West Africa Chamney (1928) presents two such measures of 'degree of wetness' and 'effective rainfall'. The second kind of formulation combines rainfall measurements with estimates of evapotranspiration, which themselves include temperature components. Such formulae are criticised by Church (1957) and by Papadakis (1966) who uses his own formula; Wills (1962) discusses their validity for Ghana.

Signs that a system of seasons defined only by rainfall is found inadequate are few, but Davis (1945) needed a six-season system to interpret phenology in a Brazilian forest. Earlier it was shown in the New Hebrides (15°S) that a locality generally regarded as non-seasonal had a hot wet season followed by a hotter and wetter one which encompassed the main reproductive period for ten selected plant species (Baker & Harrison 1936; Baker & Baker 1936). Corner (1952) found seasonality of similar events in Southern Malaya (1–3°N) and associated it largely with changes from wet to dry seasons.

PATTERNS OF SEASONAL POPULATION CHANGE

Most of the patterns of seasonal change in numbers given in Figs. 2–14 and summarized in Fig. 15 can be classified according to the kind of food resource that the species concerned exploit. The botanic and climatic events with which these patterns are associated are discussed in the following sections.

Periodicity of leaf production in cocoa and other trees

The phenology of insects that feed on cocoa leaves can be considered only after the periodicity of cocoa-leaf production has been discussed, because existing accounts of the latter in West Africa are difficult to interpret. Cocoa has flushes of vegetative growth in which new shoots elongate and young leaves fully expand in quick succession, then gradually harden. Greenwood & Posnette (1950) found that flushing occurred at intervals of roughly 2 months except during the season of main rains when there was no flushing. Their data for 7 years indicate that there is a major flush in March–April and two others in the period October–December, as stated also by McKelvie (1962). The extent to which trees flushed at other times varied greatly between years and between trees; unshaded cocoa flushed outside the main periods more often than shaded. Two years' data of Hurd & Cunningham (1961) show the same pattern. Both sets of results were considered by the authors to confirm the earlier observation of Humphries (1944) in Trinidad that cocoa flushes only while maximum daily temperatures exceed about 28° C and it was concluded that flushing has an endogenous rhythm, but is triggered only above this critical temperature.

All the above data on flushing periodicity are based on means of a few arbitrary categories of flush on many trees; they conceal the fact that an individual cocoa tree does not normally flush more than twice in a year. Alvim (1967) concludes that there are two main peaks of flushing by cocoa at Bahia, Brazil (13°S), in September–October and in February–March or March–April. He interprets the figures from most cocoa growing areas in both hemispheres as showing roughly the same peaks. We suggest the most likely explanation of results that have been obtained is the following. Times when cocoa may flush occur at roughly 2-month intervals. These times are probably determined cyclically by the interval between bud-burst and a critical stage of leaf development, and this interval might be affected by temperature and other factors. A large flush in March–April, after the dry season, is likely because the decreased leaf complement caused by drought stimulates replacement and because weather conditions, rain alternating with long periods of bright sun, are very suitable for growth at this time. If production of new foliage in March–April is sub-normal on some trees because of bad soil conditions, insect attack, or debilitation caused by excessive exposure, these trees may flush again 2 months later, if growing conditions permit. Later than this, during the wet dull and dry dull weather from June to September, flushing is much less common. The life of a cocoa leaf is normally of the order of 8 or 9 months (McKelvie 1962), so the foliage produced in March–April will be senescing when the return of long sunny periods during wet weather brings about the second period of maximum flush in October–November.

Many patterns of seasonal leaf production have been observed in trees of the tropical high forest (Richards 1952; Corner 1952), although quantitative studies of these patterns have not yet been attempted. Some trees in Ghana forests shed and renew their leaves three or four times a year, others in the March–April and late September–November periods. Cocoa, with a short-term aseasonal periodicity of facultative flush and a longer-term seasonal periodicity of maximum flush, shows elements of both these flushing patterns.

Flushing in March–April frequently follows a period of dry season deciduousness. Of ten species of forest trees observed by Njoku (1963) in the botanic garden at Ibadan, Nigeria, nine flushed some time in the period February–April, the tenth in this period and in November; seven of these species were deciduous in the dry season. The onset of dry

weather is earlier at Ibadan than at Tafo, so more dry season deciduousness and less flushing in the shorter second wet sunny season might be expected there, but there are insufficient data for comparison. An analysis of the extensive data of Taylor (1962) shows the distribution of leaflessness through the year in 158 forest-tree species in Ghana (Fig. 16): between thirty-five and forty-two of these were deciduous in each of the three driest months, December–February.

To summarize the data that are available: in West African semi-deciduous forest a large proportion of tree species, whether deciduous or not, have a major flushing period in the first wet sunny season; another flush in the second wet sunny season appears to vary in importance between areas.

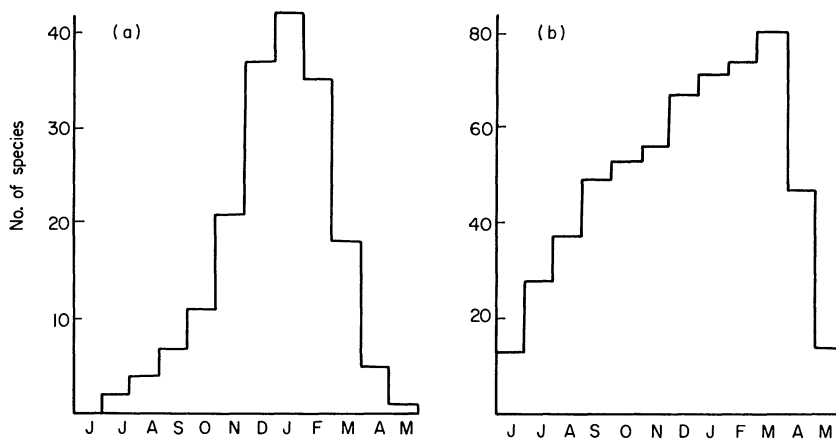


FIG. 16. Seasonal distribution of (a) leaflessness, (b) fruiting in 158 tree species in forests of southern Ghana (from data of Taylor 1962).

Leaf feeders

Adults of the eumolpid *Paraivongius viridiaeneus* (Fig. 3c) feed on cocoa leaves. The two main periods of population increase (from late wet sunny to early wet dull season, and from wet sunny to early dry sunny season) correspond with times that leaves produced in the two peak flushing periods approach maturity. It is not known if emergence from the soil continued when adults of *P. viridiaeneus* were scarce because emergence cages were not used during this period. A pause in reproductive activity may have occurred but this seems unlikely because seasonal changes in food amounts are not extreme. The succession of generations was therefore, probably uninterrupted.

Adults of the curculionid *Proictes schachi* (Fig. 11b) also feed on leaves, but their seasonal occurrence differs from that of *Paraivongius viridiaeneus*. They are most numerous in June and in September or October, with a decline in between, and are scarce for the rest of the year. This population curve, which shows positive correlation with rainfall during the wet and dry dull seasons, resembles that of some wood-boring beetles and will be discussed with these later (p. 543).

Another bimodal periodicity of numbers that is positively correlated with bimodality of leaf production is found in the giant land snails (Achatinidae). Owen (1966) found marked breeding peaks of an achatinid at Kampala, Uganda (0°20'N) in January–February and in July, and thought these stemmed from the newly hatched snails meeting

maximum food and minimum risk of desiccation. Owen associates this periodicity only with rainfall, but the relationship is not close and the peaks of abundance indicate anticipation of rainfall rather than a response to wetness. In the Ghana forest zone two species of Achatinidae are collected for food, mainly from mid-February to April and from early September to the end of October (Martinson 1929); observations at Tafo confirm these peaks. Achatinid snails feed on leaves and are most abundant in the two wet sunny seasons. It would be instructive to relate the figures from Kampala to sunshine as well as to rain.

Shoot meristem feeders

The psyllid *Tyora tessmanni* (Fig. 6a and b) and the noctuid caterpillars *Earias biplaga* and *Anomis leona* (Fig. 6c) have closely similar seasonal population curves. Their main period of increase in numbers was in the first wet sunny season, in April in 1966, at the end of February in 1967, although it is possible that a separate generation of caterpillars produced large numbers just before sampling began. The times when numbers increased were the same in all three knockdown blocks, but peaks in blocks P and R in 1967 were much smaller than in 1966. The data suggest a similarity in requirements that is at first unexpected in a fluid-feeding psyllid and chewing caterpillars. On the other hand, some caterpillars that feed on fast-growing tissue probably depend more on fluids in translocation than on cell tissue since they produce only small amounts of digestive enzymes (Hocking & Depner 1961).

Entwistle (1962–63, 1964, 1965) gives numbers of *Earias biplaga* and *Anomis leona* and the percentage of plants infested by *Tyora tessmanni* on cocoa seedlings at Ibadan, Nigeria. Numbers of *Earias biplaga* fluctuated irregularly with a marked peak in March 1962, but numbers in the same period of 1963 little exceeded those reached at several other times of the year. *Anomis leona* had marked maxima in May–June 1962 and March–April 1963 and much smaller but well-defined ones in December–January in both years. This curve for *A. leona* strikingly resembles that for *Tyora tessmanni* at Tafo, but the Ibadan curve for *T. tessmanni* is quite different, with a sharp peak in January 1961, then a gradual increase from March to a peak in September–October. By contrast, 13 months' sampling of adult *T. tessmanni* by Eastop (1958) at Ibadan using water-filled yellow trays showed an abrupt peak in April 1957 and a smaller one in the previous August.

The data for Tafo and Ibadan together show that all three species occur throughout the year. On mature trees, increase in numbers coincides with the period of maximum leaf production in the first wet sunny season, but on seedlings, which flush more often than mature trees (Greenwood & Posnette 1950), there may be increase at almost any time, at least in *T. tessmanni* and *Earias biplaga*. We cannot suggest why the second major flush period on mature trees is not exploited.

Regenerative tissue feeders

In the cocoa capsids, *Distantiella theobroma* and *Sahlbergella singularis*, the large populations that may occur in January and February (Fig. 7a) feed mainly on the vegetative tissues of cocoa, especially fast-growing regenerative shoots. Gibbs *et al.* (1968) suggested that capsid numbers on these tissues increase independently of those that build up the pods in August–December or, under some local conditions, on normal branches

(fans), and that they depend on seasonal change in some aspect of the nutrition that regenerating shoots provide. The nature of this change is obscure, but it may involve mobilization of reserves when regeneration is stimulated after various setbacks to growth, especially drought.

Other insects show population changes that may have a similar cause. For example the pentatomid *Halyomorpha reflexa* (Fig. 7b) feeds from the pith of regenerating shoots, tissue that is probably physiologically similar to the superficial parenchyma used by cocoa capsids. Numbers of *H. reflexa* increase from January to early March. The grylloid *Euscyrthus bivittatus* (Fig. 7a) probably chews the bark of regenerating shoots and is present on cocoa for a limited period in the dry season, numbers increasing in late December and January. Population changes of both *Halyomorpha reflexa* and *Euscyrthus bivittatus* on cocoa are difficult to interpret but the similarity of their periodicity to that of cocoa capsids on the same feeding site suggests that they exploit the same seasonal change in food.

Fruit and seed feeders

The bugs *Bathycoelia thalassina* and *Helopeltis* spp. and the beetle *Paraivongius semipiceus* feed on cocoa pods, and their main period of population increase is from the dry dull season to the beginning of the wet sunny season (Fig. 8). This is the period in which the main crop of cocoa pods develops. Data on seasonal development of the food source of many other arboreal fruit and seed feeders (Figs. 9 and 10) are sparse, but maximum numbers of these species in the light trap occur in the latter part of the period in which Taylor (1962) found the largest number of forest trees fruiting, i.e. January–April (Fig. 16). The times at which peaks of *Dysdercus* spp. occur agree closely with the known periods of ripe seed production by their hosts. It is likely too that populations of the heterogastrine lygaeids, which feed on *Ficus* fruits, are associated closely with a February–April period of maximum fruiting. A range of host species may have a sequence of ripening which the bugs can exploit because of their mobility. Maximum light trap catches probably occur at population peaks that are supported by maximum food availability and accompanied by dispersal.

Little is known about the periodicity of grass-seed production, but most grasses in clearings seem to have ripe seeds in the early or middle dry season just before being burnt. The explosive dispersal of grass-seed feeding rhyparochromines that results in their occurrence in knockdown samples from cocoa trees is largely restricted to the dry season. Three grass-feeding mirids, *Trigonotylus ? tenuis* Reuter, *Stenotus gestroi* Poppius and *S. transvaalensis* (Distant) also have peak numbers from late November to January. The last two species are seed-feeders and the first is possibly a stem-feeder.

Litter and fungus feeders

Hopkins (1966), working in a forest in Western Nigeria where the climate resembles that of Tafo, found that leaf litter accumulated on the forest floor during the dry season, then decomposed at a maximum rate when alternately wetted and dried as rains increased in April and May. The quantity of litter was greatly reduced by June, and by August was less than 10% of that present in March.

The cricket *Ornebius* (Fig. 11a) probably preys on some of the small arthropods directly involved in litter breakdown. Its main period of increase in numbers in May and

June, followed by gradual decline over several months, is probably directly related to the amount of litter breakdown taking place.

A similar seasonal population curve is shown by the aradid *Usingeria mirabilis*, a species with an entirely different feeding behaviour (Fig. 11a). On cocoa this bug probably feeds on mycelia of white-thread blight fungus infecting the foliage. Conditions that favour maximum breakdown (largely fungal) of leaf litter are likely to also affect fungal activity in dying leaves still on the tree. Data for other fungus feeders, *Mezira affinis* and *M. rugosa* (Fig. 10), suggest that they may have the same curve. Another aradid, *Aradus flavicornis*, is most numerous in the dry season and so may not be dependent on fungi.

Predators

Predatory orthopteroids and mantids together reach maximum numbers in April–May and again, less clearly, in October–November (Figs. 2–5). The second peak tends to decline less sharply than the first and large numbers may also occur in December–January. It is impossible to overlook the fact that annual population peaks in both groups tend towards a bimodality that coincides with the two wet sunny seasons. In other words foliage-inhabiting predators have a major period of population increase when leaf-feeding prey are most numerous. Unpublished observations (D.L.) suggest that common Reduviidae (Heteroptera) on cocoa show a similar pattern, except for species that prey on ants.

Clear seasonal population changes were not detected in salticid spiders (Fig. 13) in the 18 months' sampling. If they occur they are less marked, and more variable, than in most of the other insect groups. If, as is likely, the common salticids on cocoa prey mainly on ants, lack of marked seasonal changes may reflect relatively constant numbers of prey.

Light trap catches of ants (Fig. 12) show much greater night to night variation than those of other groups, but large flights are more frequent at certain times which are likely to follow periods of maximum larval development. In 1966–67 maximum light trap catches of *Odontomachus haematodus* were within the period from late second wet dull season to early dry sunny season, and probably followed increase in numbers during successive generations through the wet seasons from April to September. A steady decrease from November 1966 to March 1967 lagged 6–8 weeks behind decreasing rainfall and may indicate a reduction in numbers of developing larvae in dry weather, when nests in soil or wood are liable to desiccate. *Oecophylla longinoda* has a different nesting habit, which is adapted to exposure, and its main flight period in the first wet sunny season indicates that the numbers of developing larvae do not decline in dry weather. Development may even be accelerated by high temperatures in the dry sunny season.

Population curves correlated with rainfall

The only insect we found in which numbers in samples were closely associated with rainfall is the curculionid *Proictes schachi* (Fig. 11b), but the literature contains examples of such correlation in groups we have not considered. Roberts (1961) gives data for wood-boring scolytid and platypodid beetles in the Bobiri Forest Reserve, Ghana. In each month, he counted the number of holes that appeared in experimental blocks of timber left in the open for 3 weeks, and also of the number of adult beetles that emerged when

some of the blocks were kept in the laboratory for 10 weeks after the period of exposure. The results are reproduced graphically in Fig. 14. The rate of attack increased from a minimum in March–April to a peak in October, was still high in November–December, then quickly decreased. Figures for emergence suggest that the success of infestation varied between months and corresponded closely with rain during the wet and dull part of the year (an interpretation slightly different from that of Roberts). Infestation as late as November–December had little success, as did that in August. The results suggest that the beetle larvae developed successfully only in moist wood. It is likely that the larva of *P. schachi* bores in cocoa shoots; if this is so, its requirements may be similar to those of other wood-borers.

DISCUSSION

Sampling methods

Records from the two main sampling methods, light trapping and knockdown, present some problems of interpretation, particularly as data on any one species were not usually obtained by both methods. Sometimes the two kinds of data give similar population curves in groups that have habits in common. For example Mantodea and Meconeminae, two groups of predators in foliage, showed similar bimodal population curves from light trap catches and knockdown samples respectively. In other examples, the size of light trap catches did not vary in proportion to population size through the year; light trap maxima were apparently restricted in varying degree to periods of dispersal that occurred when maximum population size had been reached. In the cocoa capsid *Sahlbergella singularis*, data from both light traps and knockdowns (Gibbs *et al.* 1968) showed initial increase in numbers at the same time (September–October); numbers from knockdowns then stopped increasing, but those from the light trap reached a larger peak in January, just before a final decrease that was shown by both methods. The curve for largids (Fig. 9b) may reflect a more restricted dispersal period, and an extreme is shown by *Oecophylla longinoda* (Fig. 12) where large light-trap catches were not only confined to a limited period, probably following maximum larval development, but occurred only on a few nights in this period. Most of our curves derived from light trap data, however, probably indicate the time of maximum population increase, and where field observations are available, as for many Heteroptera, they support this conclusion. In ants, however, which always require separate attention, interpretation of the data must be more tentative because of the apparent dependence of flights on temperature and humidity.

In population curves derived from knockdown samples the size of peaks in different places and different years must be compared with caution because sampling at the fairly long interval of 2 weeks might, in a species with a short generation time, miss the real population peak. Light-trap samples, taken nightly, do not have this defect and sometimes show large differences between the two years sampled. Such variation appears to be characteristic of many of the species we have considered.

Seasonal distribution of population increases

Seasonal change was usual in populations of the species sampled, but almost all species were taken throughout the year and it often appeared that the succession of generations was uninterrupted. In every month some species were in a spell of major increase, but

Fig. 15 shows that, among the species sampled, the periods in which numbers increased were not evenly distributed over the six seasons. In particular the first wet sunny season covered the period of increase of a large range of insects, including chewing and fluid-feeding, phytophagous and predatory forms. This increase was associated with maximum availability of new leaves and meristematic tissue. A bimodal population curve with peaks in the first and second wet sunny seasons also occurred repeatedly; with the exception of *Paraivongius viridiaeneus* (Fig. 3c) our samples were of predators that live in foliage (Figs. 3–5), but a bimodal periodicity is likely to be widespread in leaf-feeding forms. The species in our samples that feed on young leaves (Fig. 6) had maximum numbers in the first wet sunny season only, but some of the caterpillars sampled by Entwistle (1962–63, 1964) apparently increased in the second wet sunny season instead. The dry sunny season is a time for ripening of fruits (Fig. 16), especially of the drier kinds, and populations of fruit- and seed-feeding species increase either in this season (Fig. 10) or in the first wet sunny season (Fig. 9).

The above patterns of seasonal population increase have a positive correlation with some aspect of primary plant production that the species concerned exploit for food. The frequency with which this simple relationship, direct in plant feeders or indirect in predators, was encountered in our sampling suggests it is a widespread one. Danilevskii (1965) concludes that, because day-length at the equator varies little, 'this provides for an even flow of energy throughout the year'. Data on production of leaves and fruits and on populations of insects associated with these, indicate that the flow of energy is far from even. The large observed variation in production is accompanied by substantial seasonal variation in hours of sunshine, and it can be predicted that sunshine will be found at least as important as rainfall in tropical forest phenology.

Phenology and life cycles

Our data serve only to provide correlations between population events and seasons, but some predictions about the mechanisms by which life cycles of some of the species we have considered are geared to seasonal environmental changes can be attempted. In particular, the large year-to-year variability in physical environmental factors, illustrated by the weather at Tafo in 1966 and 1967 (Fig. 1), is likely to be important.

A pattern of successive generations that we have postulated for the cricket *Anaxipha* attempts to show how times of population increase might be adjusted if the time when optimum conditions occur varies. In Fig. 3(a) changes in the larva–adult ratio have been used to derive a hypothetical succession of overlapping generations with 3 months' egg development and 2½ months' larval development. These generations closely fit the population changes except in the period May–July 1967; events here would be explained if part of the generation that began from eggs laid in December underwent arrested development in the adult or egg stage during harmattan. The abruptly curtailed peak of numbers that followed increase in late December suggests there was much larval mortality; this may have been an effect of harmattan in the exposed sampling area. In 1966 optimum conditions were apparently encountered at the end of May by the first generation of larvae that hatched after the dry season, but in 1967 it was not until July, when second generation larvae were developing, that population increase, much smaller than in 1966, was possible. It is impossible to say which of the many weather differences between the corresponding parts of the 2 years might have indirectly influenced *Anaxipha* populations.

Sometimes the population curve of a species varied between areas as well as between years. In 1966 the gryllacridid *Afrogyllacris africana* (Fig. 3b) had one period of population increase in block H and two in block P. In block R, numbers of meconemines (Fig. 2) showed no periods of major increase, but remained similar to the minima in the other blocks where seasonal improvement in conditions was presumably more marked. Nevertheless, even in block R separate counts of adults and larvae (not included in Fig. 2) showed that the succession of generations was uninterrupted.

These relationships postulate a direct response by the population of an insect to changes in food supply. The possibility that the response is not direct, but is mediated by some token stimulus that precedes the food change cannot be excluded. The large variations in times of optimum conditions makes this unlikely in species that are able to maintain an uninterrupted succession of generations. In some other species, however, arrested development at some stage of the life cycle may occur. In particular, vulnerability of eggs and larvae to desiccation may result in arrested development of adults, or eggs, in the dry sunny season. Numbers of the litter-inhibiting cricket *Ornebius* (Fig. 11a), for example, were very small in this season when, under the thin cocoa leaf litter, the soil was hard and dry. It is unlikely that normal development continued under these conditions. We suspect that mortality due directly to desiccation in spells of harmattan may be important in some species. There is strong circumstantial evidence for it in cocoa capsids on exposed trees (Gibbs *et al.* 1968).

ACKNOWLEDGMENTS

This study arose from the programme of the International Capsid Research Team (International Office of Cocoa and Chocolate) at the Cocoa Research Institute of Ghana. We are indebted to many assistants at C.R.I.G. for their help. Much of our material was identified by Dr L. Chopard (Muséum national d'histoire naturelle, Paris), Mr D. J. Clark (British Museum, Natural History), Commonwealth Institute of Entomology, Dr L. Hoberlandt (Národní Museum v Praze, Prague), Mr John Huxley (British Museum, Natural History), Dr R. Roy (Institut fondamental d'Afrique noire, Dakar), Dr G. Schmitz (Musée Royal de l'Afrique centrale, Tervuren), Dr H. G. E. Scudder (University of British Columbia), Dr J. A. Slater (University of Connecticut) and Dr R. W. Taylor (C.S.I.R.O., Canberra). Dr C. G. Johnson kindly gave valuable criticisms of the manuscript.

SUMMARY

Sampling by light trap, insecticide knockdown and other methods has given data on seasonal population changes in many insects and a few spiders in an area of semi-deciduous high forest largely devoted to cocoa growing at Tafo, Ghana.

Populations of most species showed seasonal change and in every month some species were in a period of major increase. There are several characteristic seasonal population curves which, when associated with botanic and climatic events, lead to the conclusion that six seasons should be recognized. These can be defined by a combination of mean rainfall (more or less than 4 in./month) and mean monthly sunshine (more or less than 5.5 h/day). The seasons, listed together with some of the events we have discussed, are:

(1) Dry sunny. Maximum fruit production, abundance of fruit-feeding and seed-feeding

insects, continuing into the following season. Species thought to be favoured by effects of drought and related stress factors on host-plant nutrition also increase.

(2) First wet sunny. Maximum leaf production; abundance of leaf-feeding insects and their predators. Maximum breakdown of leaf litter; abundance of litter-feeding and fungus-feeding insects.

(3) First wet dull. Decline in leaf feeders and their predators. Abundance of timber-borers.

(4) Dry dull. Biologically similar to wet dull seasons; forms with numbers closely correlated with rainfall, for example timber-borers, may decline.

(5) Second wet dull.

(6) Second wet sunny. Shorter than the first wet sunny season, but period of sub-maximum leaf production; abundance of leaf feeders and their predators.

Species that depend for food on primary production of plant tissues in the form of leaves or fruits have maximum numbers in the three sunny seasons. Their populations appear to respond directly to seasonal changes in the amount of food.

REFERENCES

- Alibert, N. (1951). Les insectes vivant sur les cacaoyers en Afrique occidentale. *Mém. Inst. fr. Afr. noire* **15**, 1-174.
- Allee, W. C., Emerson, A. E., Park, O., Park, T. & Schmidt, K. P. (1949). *Principles of Animal Ecology*. Philadelphia and London.
- Alvim, P. de T. (1967). Eco-physiology of the cacao tree. *Proc. Conf. int. Rech. agron. Cacao, Abidjan*, 1965, 23-35.
- Baker, J. R. & Baker, I. (1936). The seasons in a tropical rain-forest (New Hebrides). Part 2. Botany. *J. Linn. Soc. (Zool.)*, **39**, 507-19.
- Baker, J. R. & Harrison, T. H. (1936). The seasons in a tropical rain-forest (New Hebrides). Part 1. Meteorology. *J. Linn. Soc. (Zool.)*, **39**, 443-63.
- Beard, J. S. (1944). Climax vegetation in tropical America. *Ecology*, **25**, 127-58.
- Bernard, E. (1945). *Le climat écologiques de la Cuvette centrale congolaise*. Bruxelles.
- Boateng, B. A. (1959). *A Geography of Ghana*. Cambridge.
- Chamney, N. P. (1928). The climatology of the Gold Coast. *Bull. Dep. Agric. Gold Cst*, **15**, 1-62.
- Chamney, N. P. (1930). The hourly distribution of rainfall in the Gold Coast. *Bull. Dep. Agric. Gold Cst*, **22**, 360-63.
- Charter, C. F. (1941). *A Reconnaissance Survey of the Soils of British Honduras*. Trinidad.
- Church, R. J. H. (1957). *West Africa*. London.
- Corner, E. J. H. (1952). *Wayside Trees of Malaya*, Vols 1 and 2. Singapore.
- Cotterell, G. S. (1927). Pests of cocoa in the Gold Coast. *Proc. W. Afr. agric. Conf.*, 1927, 98-112.
- Danilevskii, A. S. (1965). *Photoperiodism and Seasonal Development of Insects*. Edinburgh and London.
- Davis, D. E. (1945). The annual cycle of plants, mosquitoes, birds, and mammals in two Brazilian forests. *Ecol. Monogr.* **15**, 243-95.
- Eastop, V. F. (1958). Flight periodicity of some aphids and psyllids in Nigeria. *Entomologist's mon. Mag.* **44**, 32-3.
- Entwistle, P. F. (1962-63). Entomology. *Rep. W. Afr. Cocoa Res. Inst.* 1960-61, 81-92; 1961-62, 100-113.
- Entwistle, P. F. (1964). Entomology. *Rep. W. Afr. Cocoa Res. Inst.* 1962-63, 48-58.
- Entwistle, P. F. (1965). *Earias biplaga*; minor pests. *Rep. W. Afr. Cocoa Res. Inst.* 1963-64, 66-72.
- Foggie, A. (1947). Some ecological observations on a tropical forest type in the Gold Coast. *J. Ecol.* **34**, 88-106.
- Forsyth, J. (1966). *Agricultural Insects of Ghana*. Accra.
- Gibbs, D. G., Pickett, A. D. & Leston, D. (1968). Seasonal population changes in cocoa capsids (Hemiptera, Miridae) in Ghana. *Bull. ent. Res.* **58**, 279-93.
- Greenwood, M. & Posnette, A. F. (1950). The growth flushes of cacao. *J. hort. Sci.* **25**, 164-74.
- Hocking, B. & Depner, K. R. (1961). Larval nutrition in *Agrotis orthogonia* (Lepidoptera: Phalaenidae): digestive enzymes. *Ann. ent. Soc. Am.* **54**, 86-9.
- Hopkins, B. (1966). Vegetation of the Olokomeji Forest Reserve, Nigeria. IV. The litter and soil with special reference to their seasonal changes. *J. Ecol.* **54**, 687-703.

- Humphries, E. C. (1944). A consideration of the factors controlling the opening of buds in the cacao tree (*Theobroma cacao*). *Ann. Bot.*, n.s. **8**, 260-7.
- Hurd, R. G. & Cunningham, R. K. (1961). A cocoa shade and manurial experiment at the West African Cocoa Research Institute. 3. Physiological results. *J. hort. Sci.* **36**, 126-37.
- Hutchinson, J. & Dalziel, J. M. (1954 et seq). *Flora of West Tropical Africa*, 2nd edn (Ed. by R. W. J. Keay & F. N. Hepper). London.
- Keay, R. W. J. (Ed.) (1959). *Vegetation Map of Africa South of the Tropic of Cancer*. London.
- Kendrew, W. G. (1961). *The Climate of the Continents*, 5th edn. Oxford.
- Leston, D. (1968). Heteroptera of Ghana: Largidae. *Entomologist's mon. Mag.* **104**, 225-7.
- Leston, D. & Gibbs, D. G. (1968). A new deraeocorine (Hemiptera: Miridae) predacious on *Mesohomotoma tessmanni* (Aulmann) (Hemiptera: Psyllidae) on cocoa. *Proc. R. ent. Soc. B.* **37**, 73-9.
- Leston, D. & Hughs, B. (1968). The snakes of Tafo, a forest cocoa-farm locality in Ghana. *Bull. Inst. fondam. Afrique noire* (Ser. A), **30**, 737-70.
- Lodos, N. (1967). Studies on *Bathycoelia thalassina* (H.-S.) (Hemiptera, Pentatomidae), the cause of premature ripening of cocoa pods in Ghana. *Bull. ent. Res.* **57**, 289-99.
- McKelvie, A. D. (1962). Cocoa: B. Physiology. *Agriculture and Land Use in Ghana* (Ed. by J. B. Wills), pp. 256-60. London.
- Martinson, J. S. (1929). The edible-snail industry. *Bull. Dep. Agric. Gold Cst*, **16**, 231-5.
- Miller, A. A. (1961). *Climatology*, 9th edn. London.
- Njoku, E. (1963). Seasonal periodicity in the growth and development of some forest trees in Nigeria. I. Observations on mature trees. *J. Ecol.* **51**, 617-24.
- Owen, D. F. (1966). *Animal Ecology in Tropical Africa*. Edinburgh.
- Papadakis, J. (1966). *Climates of the World and their Agricultural Potentialities*. Buenos Aires.
- Paulian, R. (1947). *Observations écologiques en forêt de Basse Côte-d'Ivoire*. Paris.
- Richards, P. W. (1952). *The Tropical Rain Forest. An Ecological Study*. Cambridge.
- Roberts, H. (1961). Seasonal variation in the attack of ambrosia beetles in the Bobiri Forest Reserve, Kumasi, Ghana, and the effect of tree poisoning on the level of the ambrosia beetle population. *Rep. W. Afr. Timb. Borer Res. Unit*, **4**, 53-60.
- Schimper, A. F. W. (1903). *Plant-geography upon a Physiological Basis*. Oxford.
- Taylor, C. J. (1952). The vegetation zones of the Gold Coast. *Bull. For. Dep. Gold Cst*, **4**, 1-12.
- Taylor, C. J. (1962). *Synecology and Silviculture in Ghana*. London.
- Usinger, R. L. & Matsuda, R. (1959). *Classification of the Aradidae (Hemiptera-Heteroptera)*. London.
- Walker, H. O. (1962). Weather and Climate. *Agriculture and Land Use in Ghana* (Ed. by J. B. Wills), pp. 7-50. London.
- Wills, J. B. (1962). The General Pattern of Land Use. *Agriculture and Land Use in Ghana* (Ed. by J. B. Wills), pp. 201-25. London.

(Received 18 June 1968; revision received 19 January 1970)