PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Significance of Low-Density Populations of the African Armyworm Spodoptera exempta (Walk.)

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The significance of low-density populations of the African armyworm *Spodoptera exempta* (Walk.)

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Mass emergences of moths from conspicuous gregarious-phase caterpillars in high densities are important sources of migrant moths, which are borne downwind to cause a progression of armyworm outbreaks northwards from Tanzania to Ethiopia, and southwards from Rhodesia to South Africa. This progression might possibly be checked by destroying outbreak caterpillars.

The sources of moths which cause the first outbreaks before the progression starts are not known, and the possibility is examined that these come from scattered populations of solitary-phase caterpillars hidden at the bases of green grasses, where they are sometimes found at considerable density.

Recent analyses of weather patterns on the estimated dates of arrival of the moths responsible for fourteen groups of outbreaks in Rhodesia suggest that outbreaks could often be caused by convergent windflow concentrating low-density moth populations from sources between Rhodesia and the Mozambique coast, and that these sources may persist for several months.

A model is presented which attempts to relate the phase forms found in the field with the life system of the armyworm.

1. Introduction

The African armyworm, *Spodoptera exempta* (Walk.) may occur in one of two very different forms in the larval stage. Caterpillars crowded together during development become dark and ultimately black with pale yellow stripes; and those reared singly remain green, or pink and green, until they pupate (Faure 1943). By analogy with locusts, Faure distinguished these as gregarious- and solitary-phase forms respectively, although no phase difference has so far been found in the moths, and the nearest approach to gregarious behaviour is the unidirectional marching sometimes shown by larvae at high densities.

The differences in the field behaviour of the two forms are even more striking. The gregarious-phase caterpillars seem to appear suddenly in very large numbers; they become conspicuous, changing colour from green to black, usually at their third moult, with an associated increase in their activity and feeding rate. The sudden appearance of infestations, often on many farms in one region at the same time, is known as an armyworm outbreak. Large outbreaks of high densities of caterpillars on cereals and pastures may cause serious damage before control is achieved. Larval development within an outbreak is well synchronized, and most caterpillars disappear into the ground to pupate during a period of only a few days. The sudden appearance and equally sudden disappearance of the gregarious-phase larvae is characteristic, and hence the name mystery worm used by some farmers. The subsequent mass emergence of moths from outbreak areas is an important source from which infestations develop elsewhere, and part of

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the strategy for control of armyworm on a regional basis would depend on the eradication of such sources.

By contrast, the solitary-phase caterpillars are rarely noticed in the field. They are sluggish, often curled; they feed at the bases of grasses, often beneath a sward of perennials such as *Cynodon dactylon* (L.) Pers., feeding and developing more slowly than the gregarious-phase, perhaps because they are less exposed to radiant heat from the sun. Even when seen by farmers they are not recognized as they are not easily distinguished from other caterpillars, such as the lawn caterpillar, *Spodoptera cilium* Guen.

The terms *active* and *passive* were coined by Whellan (1954) to describe field populations of predominantly gregarious- or solitary-phase larvae, to stress the differences in behaviour of the populations and to avoid the implication that solitary-phase caterpillars occur only in low densities. Passive populations may exist at fairly high densities, provided that the larvae are feeding within a thick mat of grasses and are not crowded during development.

Areas in which armyworm breed continuously throughout the year, year after year, have not been found. Survival over unfavourable seasons of the year seems to be mostly by migration, although a small proportion of armyworm populations may survive the dry season as long-term pupae (S. Khasimuddin, unpublished observations).

2. Evidence for the existence of low-density populations

The highest recorded densities of solitary-phase caterpillars have been on pasture grasses and lawns in Rhodesia (Whellan 1954, Rose 1975). During the 1953–4 wet season a sequence of three generations of armyworm was sampled daily at the Salisbury Research Station. A widespread outbreak of armyworm occurred throughout Rhodesia at the time of the first generation, no outbreaks were reported at the time of the second generation, and only a few during the third generation. Detailed observations of the second and third generations of passive populations were made in a paddock of mixed grasses of *Cynodon dactylon* (L.) Pers., *Eleusine indica* (L.), *Trochlea panicoides* Beauv., *Sporobulos pyramidalis* Beauv., *Setaria pallidifusca* (Schumach.) Stapf & Hubbard and *Digitaria abyssinica* (Hochst. *ex* A. Rich.) Stapf. The first and second generation larvae were at densities exceeding 100 m^{-2}. Those of the second generation were greatly reduced by parasites, notably *Euplectrus laphygmae* Ferr.; moths from this generation, trapped in cages on emergence from the ground, were at an average density of 4.6 m^{-2}. Samples of the third generation pupae and prepupae in the ground were taken from a passive population hidden in pasture grasses and also from a nearby active population in an oatfield. The numbers of pupae and prepupae under pasture grasses averaged 54 m^{-2}, about twice the density of those in the oatfield (Rose 1975). On this occasion more moths emerged from the hidden population in the pasture (5.8 m^{-2}) than from the conspicuous population in the oats (4.2 m^{-2}).

A similar density of solitary-phase caterpillars was found under a sward of the annual grass *Eleusine indica* during the same season; and during January 1976 large numbers were found in a *Cynodon dactylon* lawn at Shamva, Rhodesia.

Such densities have been found only during seasons of armyworm outbreaks; generally solitary-phase caterpillars are at very low densities. The best documented accounts of field searches for low-density populations are those given by Faure (1943) and Matthée (1952). During the years 1942–7, hundreds of man-hours were spent on searches for armyworm larvae in the bases of *Cynodon dactylon* and other grasses in the vicinity of Pretoria and other parts of South Africa where survival of resident populations was considered possible. None were found during the dry seasons and the conclusion reached was that outbreaks were caused by migration of moths from areas where there were more suitable conditions for continuous breeding.

Even so, both Faure and Matthée found some solitary-phase caterpillars in each of the 5 years, during several months of each wet season when grasses were suitable. Searches in other parts of Africa have been less systematic, but have revealed patchy, very low-density populations of solitary-phase larvae during wet months of the year; one or two larvae have been found by the author, after extensive search, in Rhodesia in most years between 1955 and 1977. Dr S. Khasimuddin (unpublished observations) has found solitary-phase larvae in Kenya each year from 1974 to 1977, and has suspected that there may be several generations of low-density populations during the wet season in the Lambwe valley. Solitary-phase caterpillars have also been found by numbers of other entomologists working in East Africa (E. S. Brown, unpublished observations), but generally little importance has been attached to them because of their seeming rarity.

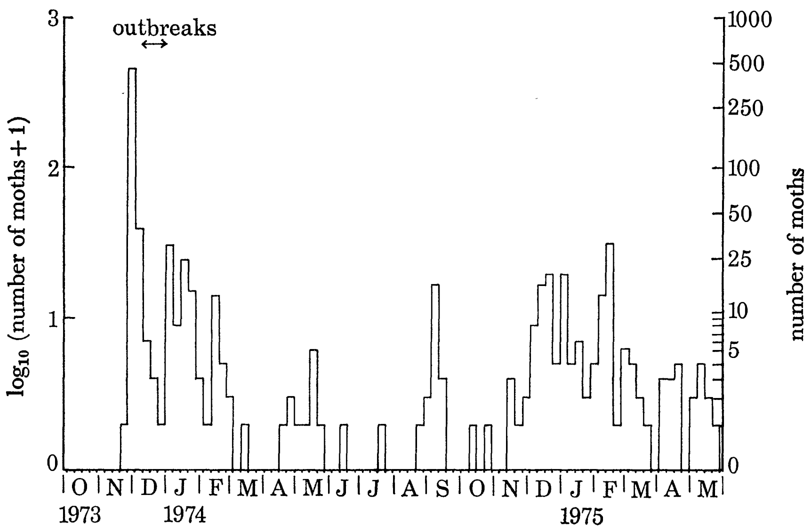

Figure 1. Number of armyworm moths in the light-trap at Salisbury, Rhodesia: weekly totals from October 1973 to May 1975.

Light-trap records of moth catches also suggest that armyworm populations persist while suitable grasses exist. High numbers at the beginning of a wet season probably indicate large scale invasion of moths into the area and warn of subsequent outbreaks. Nightly capture of moths during the remainder of the wet season may indicate continued invasion of moths, and/or the presence of armyworm living in low-density populations in the vicinity. At present there is no way of distinguishing between moths from these sources. In figure 1 the peak catch of moths in December 1973 occurred at the beginning of the wet season after a period of several months drought. Armyworm outbreaks were predicted, and occurred shortly afterwards. During the early part of 1974 rains were exceptionally heavy and prolonged, and grasses remained green for longer than usual during the 1974 dry season. Moths were captured at the trap fairly continuously for a period of 75 weeks, the longest gap being of four weeks during the dry season. Many female moths were dissected and found to contain spermatophores; it is inconceivable that none of these moths laid eggs in the Salisbury area where host grasses were abundant, yet no further outbreaks occurred in Rhodesia.† Most probably low-density populations were present, undetected in the solitary phase.

The importance of the low-density populations in seasonally green grasses is not known; there is no practicable way of measuring their numbers, nor of comparing these with numbers of gregarious-phase larvae in outbreaks. Nevertheless the grasslands of Africa are vast, and the populations of solitary-phase caterpillars and moths emerging from them may be large on a geographic scale.

3. Possible sources of moths which cause armyworm outbreaks

(a) *The importance of moths emerging from known outbreaks*

Outbreaks of very dense populations of gregarious-phase larvae provide sources from which large numbers of moths emerge together over a relatively short period of time (Brown & Swaine 1966). Those that migrate are likely to be carried down-wind together, and the larvae developing from the eggs they lay are likely to become crowded and cause further outbreaks. Any strategy for control of armyworm on a regional basis must recognize the importance of moths emerging from large outbreaks.

During years of serious armyworm infestation, the first outbreaks often start in Tanzania, Rhodesia and Malawi at about the beginning of the wet season in December, and are followed by a progression of outbreaks at about one generation time-intervals from Tanzania through Kenya, Uganda, Ethiopia, Somalia to the Yemen (Brown, Betts & Rainey 1969; Betts 1976) and from Rhodesia to South Africa (T. J. Naudé, unpublished observations; Blair & Catling 1974). Once outbreaks have started, the progression might possibly be checked by destroying outbreak caterpillars.

(b) *The significance of moths developing from low-density populations*

As the first outbreak of the season cannot be related to moths from previously known outbreak centres, it is possible that they come from inconspicuous caterpillars, either in low densities scattered in seasonally green grasses, or in denser populations where grasses are green and temperatures are favourable most of the year. *Cynodon* grasses and *Cyperus* sedges on flood plains are possible places (Tinley 1971), or grasslands with rainfall in most months of the year.

The first outbreaks of the African season are often recorded in Rhodesia, for which recent records have been analysed to find out whether outbreaks coincided in time and place with weather patterns which could have concentrated wind-borne moths from low-density populations by mechanisms similar to those described by Rainey (1976) and Joyce (1976). The date of laying, taken as that of arrival of the parent moths, has been estimated from the age of samples of larvae from each infestation, from mean head-capsule widths, with the aid of population development curves previously constructed for solitary- and gregarious-phase field populations (Rose 1975). The outbreaks which have the same moth-arrival date had been plotted (D. J. W. Rose, B. W. Blair and A. B. Law, in preparation) on the relevant daily wind streamline charts for 04.00 h G.M.T. (06.00 local time) and 850 mbar‡ pressure heights, of the Meteorological Department. The synoptic charts for the days before and after

† Indeed, from January 1974 to May 1975 the nearest reported infestations were some 1200 km away, in Natal (January 1975) and in southwest Tanzania (January 1974 and January 1975).

‡ 1 mbar = 10^2 Pa.

the moth arrival date were also examined, and as moth arrival generally seems to coincide with rainfall in the vicinity (Brown, Betts & Rainey 1969), light-trap and rainfall records were also studied to check the reliability of the estimated date.

Fourteen distinct groups of armyworms outbreaks in Rhodesia have now been examined in this way, and thirteen corresponded remarkably closely in time and location with regions of wind-convergence as drawn on the routine synoptic charts. For example, before the beginning of the wet season in Rhodesia there are many weeks with unbroken wind-flow and no rain; then the association of date of moth arrival with a convergence line is convincing. Even so, within the general regions of convergence the sites of armyworm outbreaks are localized. Frequently these sites are where rain has fallen, often corresponding closely with the locations of hail storms about the date of moth arrival. The mechanisms which concentrate oviposition to restricted areas within the regions of wind-convergence are not fully understood, but may be associated with moth behaviour after arrival, or with localized weather disturbances.

During October 1955 two distinct outbreaks of armyworm in Rhodesia developed where heavy hail storms had occurred. The late E. O. Pearson, former Director, Commonwealth Institute of Entomology, commenting on these coincidences, was the first to suggest that armyworm moths may be concentrated by wind-convergence (personal communication, 1955) in a similar manner to locusts (Rainey 1951). Recent analysis has confirmed that moth arrival did indeed coincide with wind-convergence for more than 24 h in the locality of the outbreaks, and back-tracking the winds from the outbreak areas on those dates suggests that the moths may have come from Mozambique (Rose & Law 1976).

Figures 2 and 3 show two groups of armyworm outbreaks plotted on the relevant wind streamline charts for estimated dates of moth arrival: the detailed analysis is given elsewhere (D. J. W. Rose, B. W. Blair & A. B. Law, in preparation). A peak catch of moths was recorded in the light-trap at Limbe, Malawi on 10 January 1976, coincident with the passage of the asymptote of convergence which on the 11th lay in close proximity to the positions of the infestations believed to have been caused by arrival of moths on that day (figure 2). Again, the positions of the outbreaks associated with moth arrival on 15 January 1976 (figure 3) were in a zone of wind speed-convergence. In both cases back-track of winds indicates that Mozambique was a possible source of the moths, although at an asymptote of convergence moths may also have been carried from another direction.

Table 1 summarizes the analyses of recognized, separate waves of armyworm outbreaks in Rhodesia between October 1976 and April 1977. The positions of each outbreak for each separate group have been plotted on the wind streamline charts for estimated dates of moth arrival, and show a close association of moth arrival with convergent wind patterns. On the only occasion when there was no association, moth pheromone traps and direct observations in Malawi indicated that there was mass emergence of moths from heavy infestations there on about 5 January (J. Marks, personal communication); the prevailing wind was from Malawi, and the outbreaks which subsequently developed were widespread in Rhodesia.

As the armyworm outbreaks of 1976–7 occurred at irregular intervals when weather patterns were available for concentration of parent moths in the vicinity, it is likely that moth sources were persistent for several months, and that on many days flying moths were scattered downwind, not concentrated, and failed to cause outbreaks. Thus these analyses show that in Rhodesia the positions and timing of the first outbreaks are determined by vagaries of weather patterns, in contrast with the apparent situation once major outbreaks have occurred and the northerly

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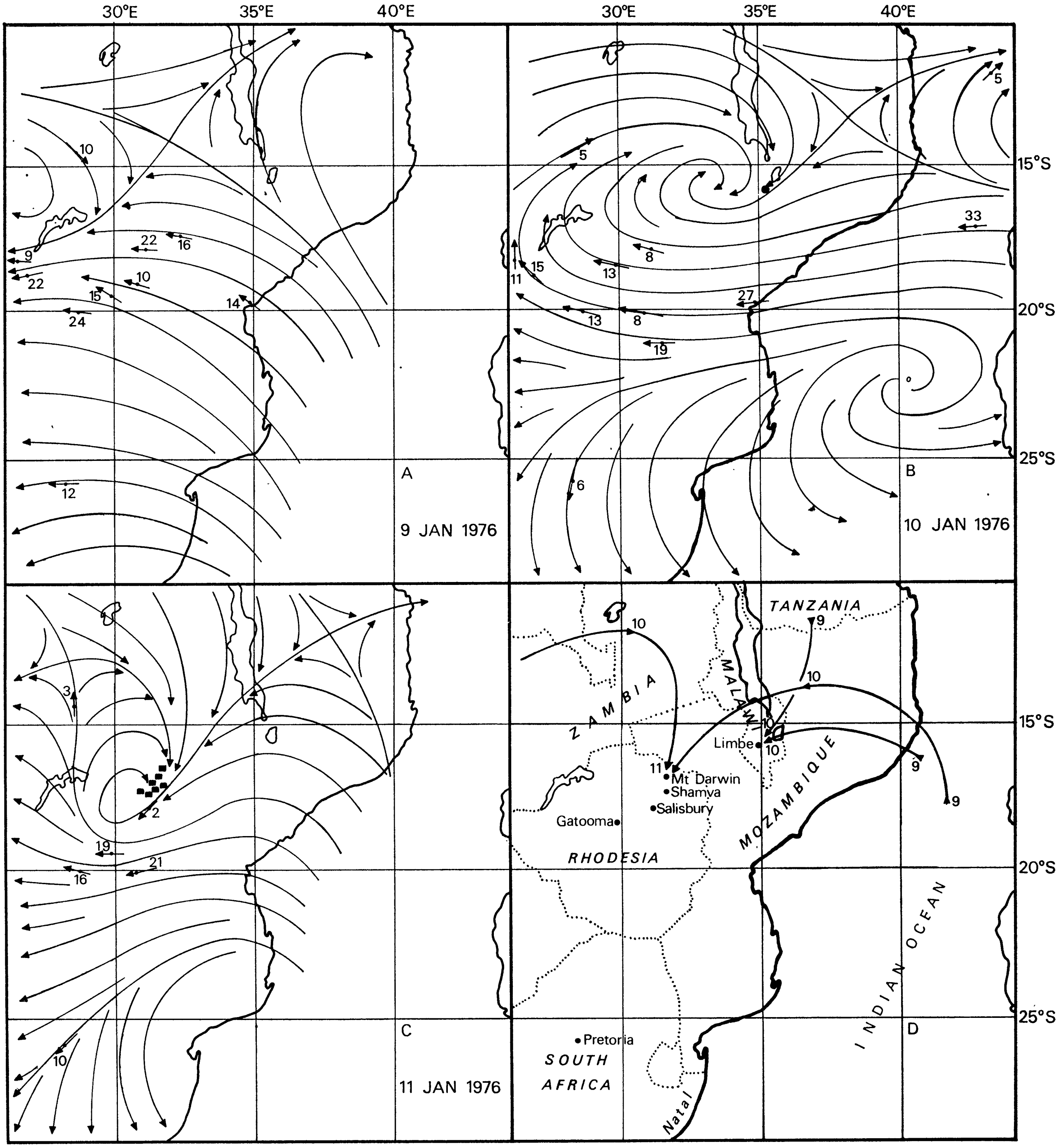

FIGURE 2. (*a*)–(*c*) Windstreams at pressure height of 850 mbar (1 mbar = 10^2 Pa) at 04.00 h G.M.T. on 9, 10 and 11 January 1976 respectively. Arrows show wind direction with speed in knots. (1 knot ≈ 0.515 m/s.) ■, Positions of outbreaks of larvae on 10 January in Malawi and on 11 January 1976 in Rhodesia, shown on (*b*) and (*c*) respectively. (*d*) Trajectory of air arriving in the vicinity of Mount Darwin at 04.00 h G.M.T. on 11 January, and of Limbe on 10 January 1976, with dates.

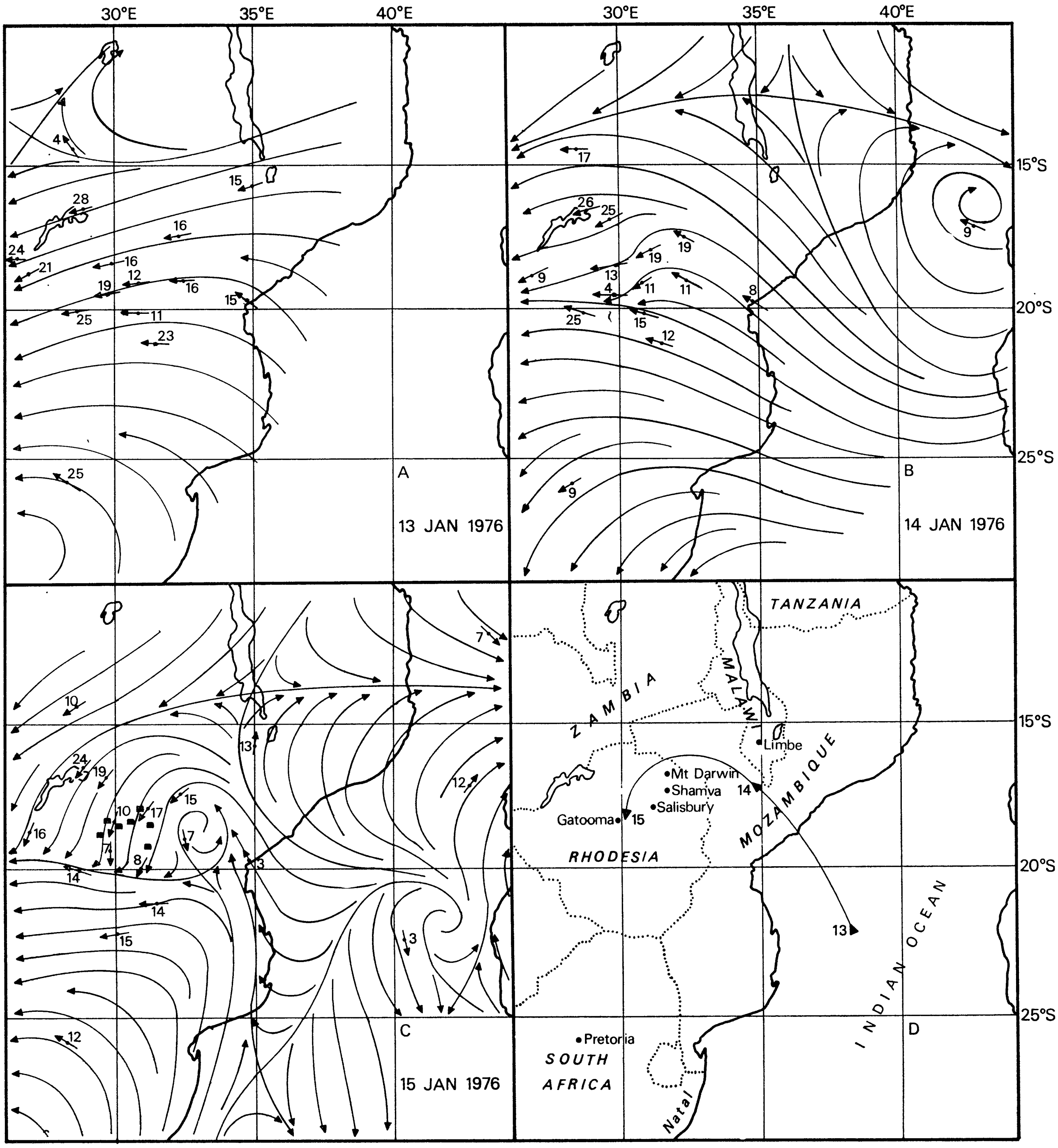

FIGURE 3. (*a*)–(*c*) Windstreams at pressure height of 850 mbar at 04.00 h G.M.T. on 13, 14 and 15 January 1976 respectively. Arrows show wind direction with speed in knots. ■, Positions of outbreaks in Rhodesia on 15 January 1976, shown on (*c*). (*d*) Trajectory of air arriving in the vicinity of Gatooma at 04.00 h G.M.T. on 15 January 1976, with dates.

(Brown *et al.* 1969) or southerly (Blair & Catling 1974) progression of outbreaks has started. Then the progression of infestations is at a time interval of about one generation, as would be expected if these areas were important sources of outbreak moths. Many of the outbreaks occur before the Inter-Tropical Convergence Zone has moved south to anywhere near Rhodesia, and there is no evidence that initial outbreaks are regularly started by wind-borne moths from the north. The analyses made so far have consistently pointed to moth sources between Rhodesia and the Mozambique coast.

Table 1. Armyworm outbreak localities and convergent weather patterns in Rhodesia

(Charts with positions of outbreaks in relation to wind streamlines at 850 mbar pressure height at 04.00 h on estimated date of moth arrival are available from the author.)

estimated date of moth arrival	location of outbreak	wind-convergence in locality on date of moth arrival	remarks
11 October 1976	Salisbury south to Enkeldoorn	weak speed convergence	
27 October	Umvukwes to Karoi	well marked asymptote	
4 November	Mtoko to Bulawayo	speed convergence	
10–14 November	Salisbury	asymptote on 10 November and 14 November	possible local emergence
27 December	Mtoko to Chipinga	well marked asymptote	
5–7 January 1977	Karoi-Mtoko-Chipinga-Gatooma	nil	northeasterlies: moths from Malawi
2 February	Fort Victoria-Chiredzi-Beit Bridge	well marked asymptote	
11 February	Karoi and Gwelo	cyclonic	
2–3 March	Karoi to Chipinga	well marked asymptote	
18 March	Gwebi	asymptote	possible local emergence

4. Conclusions

At present it is only possible to suggest that wind-convergence, plus more localized weather and moth behaviour, may provide a mechanism for transporting and concentrating moths emerging from low-density armyworm populations. In an insect with pronounced phase change in the larval stage, environmental factors largely determine whether caterpillars become crowded and therefore conspicuous, or remain unseen. Local increase in numbers may sometimes cause outbreaks, and Hattingh (1941) believed that this could happen. However if low-density populations are important sources of outbreaks, it now seems more likely that these are caused by concentration of moths so that oviposition takes place in restricted areas (Joyce 1976).

The density of solitary-phase caterpillars may vary considerably according to habitat and host plants before crowding is induced. One can postulate places where grass mats are green and thick, where conditions for armyworm are suitable most of the year, and where fairly high densities may occur before populations become crowded on their food plants and thus conspicuous.

Years of major armyworm outbreaks are most likely to start when low-density populations of armyworm are large, producing many moths available for concentration by weather patterns. The sizes of the low-density populations are likely to vary from year to year in response to many environmental factors which are little known, and new techniques are badly needed for their study.

Figure 4 is a simple model summarizing some of the environmental factors which may determine whether moths cause an outbreak. It assumes that the moth influx is constant at densities too low to cause an outbreak unless the moths are firstly concentrated to oviposit in a restricted area, that many convergent weather patterns will not cause outbreaks because there are not enough moths flying or because concentration mechanisms are not strong enough, and that at other times large numbers of eggs may be laid but the larvae will not become crowded, either because of high mortality, or because the nature of the host grass prevents crowding.

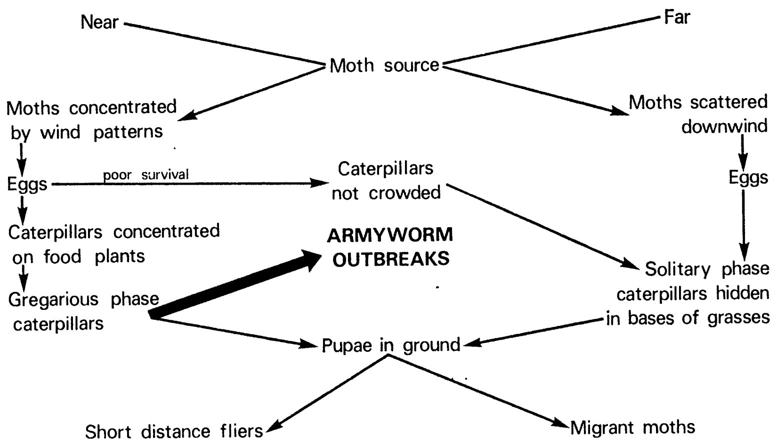

Figure 4. A simple model of some aspects of the life system of the African armyworm.

Figure 4 is a reminder of the holistic approach which has to be made in order to understand the relationships between outbreak and low-density populations of the African armyworm.

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