LES DONNÉES RÉCENTES DE LA MICROCLIMATOLOGIE ET LEUR IMPORTANCE EN ÉCOLOGIE ENTOMOLOGIQUE

PAR

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RECENT CONTRIBUTIONS TO MICROCLIMATOLOGY AND THEIR IMPORTANCE IN ECOLOGICAL ENTOMOLOGY

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(Translated from French by R.W. Stark.)

Many faunisticians and biogeographers believe it is sufficient to note the origin and name of the plant on which captures are made. But there has developed, in the last few years, and especially in Germany, a school of meteorologists specializing in microclimatology and the study of the layer of air just above the soil (bodannen Luftschicht). Their measurements, too often ignored by zoologists and agricultural entomologists, completely overthrow the theories the latter had made on the relation of insects to climate: for example, temperature differences as high as 10 degrees can exist between a point a few centimeters above the ground and 1.5 metres above; these differences can be increased under different conditions, such as in the interior of wheat fields, or in forest undergrowth. The insect lives in a climatic universe entirely different from ours, and we do not pay enough attention to it.

THE INSTRUMENTS IN MICROMETEOROLOGY

The instruments of the microclimatologist are much different than those of the meteorologist, sensu lato. In measuring temperature, for example, they cannot use a shelter, they are too large and by their presence modify the microclimate. In a general way, it is scarcely possible, except in cloudy weather, to measure air temperature with a thermometer, even by covering the reservoir with a nickel screen. A better technique, by Selltzer, is the use of thermo-electric points enclosed in a nickel cylinder several centimetres in diameter, in which there is a small air inlet. The use of sling thermometers is prohibited, because of the turbulence which they cause in the restricted air layer. As for humidity, ordinary hair hygrometers are too large and they prefer models where the hairs are enclosed in a perforated tube which can be inserted in small places. One of the best types is the aspiration psychrometer of Asmann, in which a small ventilator permits a weak current of air to pass over the wet and dry thermometers. Analagous models made in France are unsuitable. The measurement of illumination cannot be made with a light meter, except in open country; in the midst of vegetation it is no longer white light which reaches the photo-electric cell but, as we shall see, an aggregate of radiations, predominantly green and infra-red. The light meter calibrated for white light will not give the desired results and rather than use special filters, as recommended by the Americans, it is preferable to use a pyrrheliometer, where all the radiations, transformed to heat by the blackened thermo-electric cell, are measured by the deviations of a galvanometer. There are transportable models with a small thermo-electric element. This, alternatively turned towards the sky, then towards the soil, can be used to measure the differences between incidental and reflected radiation or the albedo. Rainfall can be evaluated by a series of small, elongated zinc jars, of a determined size, equally spaced on the soil and which can be compared with an analogous series placed under the vegetation. As for wind, it is usually too light near the places measured by the microclimatologist to activate an anemometer and there is a perfected apparatus where the air movement is measured by the cooling of an electrically heated plate. This apparatus has other uses as well. Air movement can exercise a noteable influence on evaporation, which can be measured with the aid of a standard recording evaporimeter.

I In the review which follows we use the term 'microclimate' instead of 'ecoclimate' which some favour. It is the term used exclusively by Geiger and by all authors which have followed his work.

THE MICROCLIMATE OF THE BARE SOIL

One can define and distinguish it from the macroclimate by two principal characters: an accentuated thermal gradient near the soil, and more marked thermal extremes than in the zone of the macroclimate. During the day the temperature increases in proportion to its nearness to the soil. The Hindu school of agricultural meteorologists has studied, with the aid of very precise physical methods, the distribution of temperature every 1/10 millimeters above the hot surface. Their results are shown in the following table:

mm.	0	0.05	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
T°	87.5	79.0	77.4	74.0	71.2	68.8	66.6	64.4	62.0	60.0	58.0	56.8

From the table it can be seen that there is a temperature drop of more than 10° in the first tenth of a millimetre. In the deserts, the large pimelids, with their long legs and the small ants therefore, obviously do not live in the same temperature regime, even if moved on the same day at the same time, to the same place. Furthermore, there are frequently some temperature drops greater than 6° between 1mm. and 10 mm. above the soil. The microclimate depends also on the conductivity and colour of the soil, as we shall see later. The layers of warm air close to the soil probably explain the behaviour of certain thermophilic flies like the Sarcophagids, which one frequently sees in summer, flattened against the earth, the legs spread out as if to get as close as possible to the heated surface.

A little before sundown, and sooner in calm air, there occurs a <u>thermal inversion</u>. The air becomes colder near the soil, the air may be 4 ° higher 5 to 10 cms. above the ground. This phenomenon is affected by the nature of the soil: a good conducting soil accumulates much heat during the day but loses it readily at night. The nocturnal inversion curve shows some anomalies however, when there are deposits of dew, because of the heat of condensation liberated by the air moisture especially near the soil. The inversion cannot be produced, for example, in the Indian desert where the daily heat is so high that the soil remains warm all night, on the other hand it can occur during the day. This is more frequently the case in the Siberian Steppes according to Pavlosk. The soil covering exerts a great influence on the microclimate. We will deal later with the microclimate of the field and forest, but will observe now that a thin layer of close-cropped grass is sufficient to narrow the range between thermal extremes, owing to the obstacle it presents to radiation. Not only the air, but the soil itself, shows the smallest variations; temperatures have been recorded on a fine summer day: 25° at 1 cm. deep in fine sand; 23° at the same depth in the same soil but with a light moss cover and only 12° where the same soil had a dense grass cover. Correlatively, when a soil is denuded and plowed, its climate becomes more "continental". For example, it has been noted that in a cleared field half the potato plants were frozen, while in the neighbouring field, not cleared, the plants were unharmed. This may also be connected with the behaviour of the adults of <u>Ulemia melanoplus</u> which take refuge at the first chill in old trees or at the foot of clumps of grass (<u>Gramine</u> spp.). They undoubtedly seek there the lesser extremes of temperature, particularily the lower. These modifications of the microclimate of the soil probably explain the drop in populations of terrestrial Elaterid larvae, noticed by English authors, after putting under cultivation fields previously occupied by prairie. In a field containing initially 500,000 larvae per acre, there was noted a drop of 25 per cent at the end of the first year and 50 per cent at the end of the second. It appears that the larvae are very sensitive to heat and drought, and a climate which is too "continental" for them is fatal. For the same reason the larvae of the June bug penetrate only 2 or 3 cms. in the prairies and up to 50 cms. in bare, looses soil (Jancke, 1927). The poorest conducter of all coverings is dead leaf litter, even poorer than snow. Interior temperatures of 43° have been recorded in May in Germany, and it is the leaf piles which are the last to thaw in spring. Undoubtedly, it is the low conductivity of the piles which activates so many insects to hibernate in them, or even to pass the whole year there. We can compare these with kelp beds deposited on the seashore, where an abundant and peculiar fauna is developed. One of the best ecological studies we know was carried out by Backlund (1945) in the kelp beds of Sweden and Finland. The microclimatic conditions are very different at the surface of the kelp, which, due to their black colour, absorb much of the radiation and stay very warm during the day, and in the deeper layers, which are more humid, cooler, and bathed in a special atmosphere due to innumerable decompositions and fermentations which go on there. The upper layer shelters a population which prefer high temperatures, are photopositive and drought resistant; those in the lower layers possess entirely different characters. In winter, the temperature of the kelp is higher and more stable than the ambient air, so much so that a number of animals remain active and develop all year. An exhaustive discussion of the consitution of the different biocenoses and of their relation with the microclimate may be found in this magnificent work, a work impossible to summarize and which all ecologists should read.

Rainwater penetrating the soil gradually raises or lowers the soil temperature to conform with its own, if the rain is heavy enough. However, it is slow process; it has been observed that it takes 19 minutes to observe a modification in the temperature one centimetre below the soil surface. The degree of moisture in the soil affects its calorific conductibility. The smaller the puddles left by the rain on the surface of the soil, the greater the temperature; as the puddles become larger, the temperature lowers. There is a minimal size beyond which the temperature increase at the surface of the puddles is the same.

The temperature diminishes rapidly with soil depth. At several metres depth, there is a curious thermal inversion. At 7 metres it can be warmer in the winter than in the summer and in this zone the differences of temperature in the course of the two seasons are but 1.5 degrees.

The greatest intensity of radiation emitted by the sun is found to be about 0.5u, that is to say in the visible light, while radiation emitted by the earth at night, mostly infra-red has a maximum of about 10 u. However, the water vapour and carbon dioxide which are more abundant at night near the soil, reabsorb a great part of this radiation. During the day, the composition of the radiation reflected varies with the nature of the substratum. For example, snow reflects 80 percent of the ultra-violet, whereas all the other substrates reflect very little (granite 25%; garden soil 6%). Grey, dry, sand reflected 18% of total radiation and only 9% when wet; grass reflected 32% dry and 20% wet. Generally the longer wave lengths are absorbed, white sand reflects only 11%, grey stone 8-9%, snow 0.5%. Evidently a surface becomes warmer when it absorbs more rays and reflects less. The albedo is equally variable with substratum as the following table shows:

	Dry	Wet
Black earth	0.14	0.08
Grey sand	0.18	0.09
High grass	0.32	0.22

However the substratum rarely has a smooth and homogenous surface, it has projections, hollows, tufts of grass, etc. All these introduce wide variations in the radiation and cause great turbulence of the thermal layers as evidenced by the poor visibility of distant objects when viewed along ground level. At night, this agitation is a little less pronounced, but the least current of air induces turbulence which is slow to settle.

The thermal extremes are more marked in the microclimate of mountains than in the prairies.

Moisture variations are also more marked near the ground. The difference in the vapour pressure of the moisture close to the soil between sundown and noon can be 5 times that at three metres above the ground. The air is more humid in the layer next to the soil during the day, but drier during the night on account of the condensation as dew. The measurements made by Büdel near Munich show, that during the summer, the dewpoint is reached as early as sundown at 5 cm. above the soil, when at the same time at 1.75 metres above the soil, the humidity is only 55%.

Wind velocity diminishes considerably near the soil, for by contact with the soil, it produces a series of eddies which check it. The number of hours when the air is calm increases with proximity to the soil.

Height above the soil - cms.	Hours								Hours of calm Ave.
	0 - 3	3 - 6	6 - 9	9-12	12-15	15-18	18-21	21-24	
200	13	12	5	0	0	1	12	15	7
100	18	13	2	1	0	2	16	19	9
50	22	18	4	1	0	3	22	25	12
25	31	26	10	1	0	7	33	34	18
5	41	36	25	6	5	16	46	43	27

Observations made during 10 days in May

According to some authors, the limits of the layer of air next to the ground (Bodannen Luftschicht) extends 1 or 2 metres above the soil, above this height wind velocity increases noticeably. But although this assertion is maintained with wind velocity it is inaccurate for the other microclimatic factors, where the effect caused by the proximity of the soil ceases at a height much less than that.

Recent studies on the distribution of radium and thorium emanations near the soil showed:

Height above the ground in cms.	1	10	100	1,000	10,000
Emanation of radium	100	98	95	87	69
Emanation of Thorium	100	82	50	9	0
Emanation of Thorium B	100	97	91	76	49

From the table it is obvious that the emanations are stronger close to the soil, it is lowered with high humidity and low temperature, it is zero when there are even a few cms. of snow covering the ground.

Fig. I

A Temperature at different depths in the sand near Pawlowsk in May (Leyst).

B The nocturnal inversion in the layer 300 metres above the ground (July 20, 1925) near Rostock (Steiner).

C Temperatures in the sand (not snow-covered) at Pawlowsk in January (Leyst).

D Daily temperature, at noon, near Koenigsburg, at different heights above the ground (Leyst).

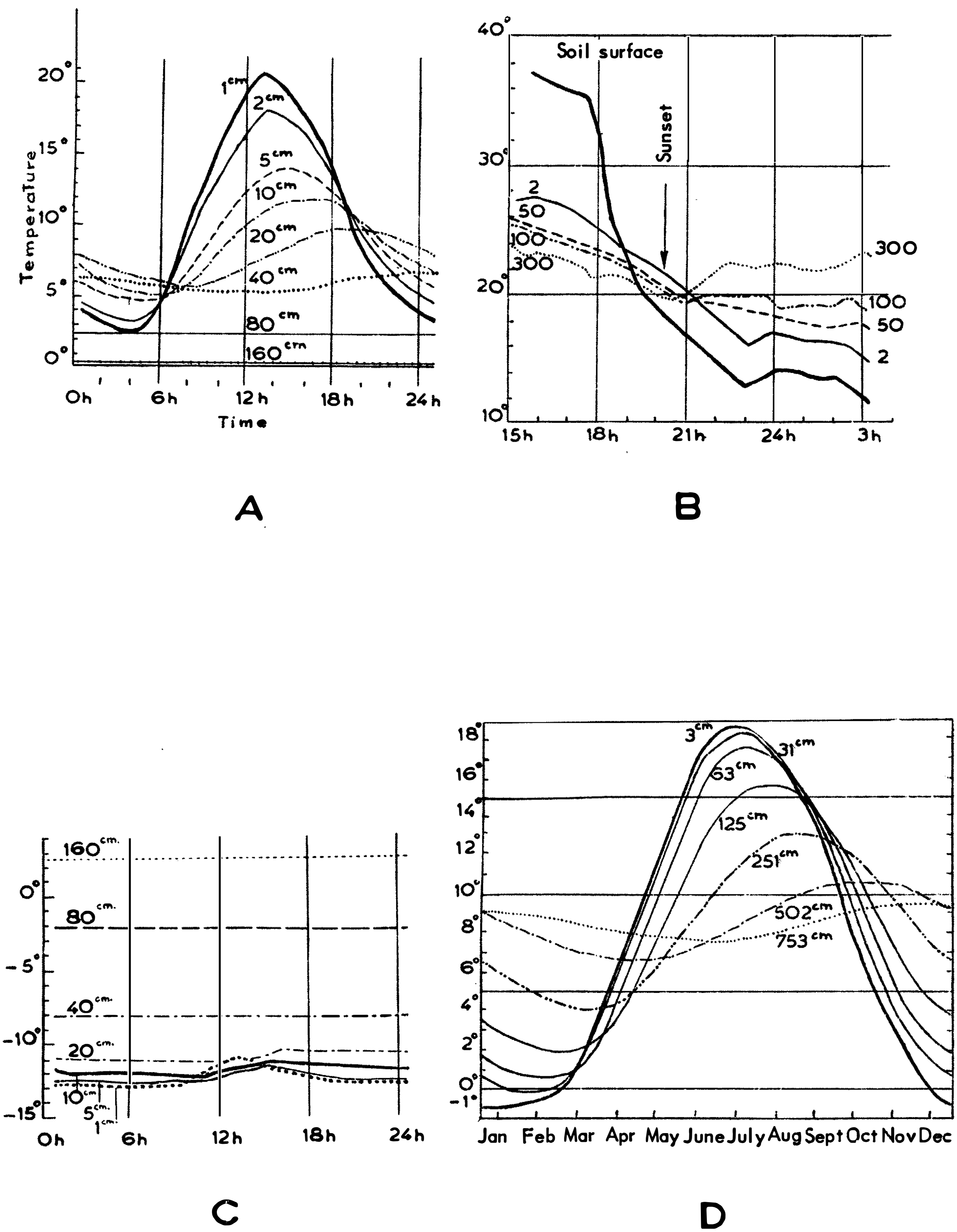

A
Temperature
Time
1 cm
2 cm
5 cm
10 cm
20 cm
40 cm
80 cm
160 cm
B
Soil surface
Sunset
2
50
100
300
C
160 cm.
80 cm.
40 cm.
20 cm.
10 cm.
5 cm.
1 cm.
D
3 cm
31 cm
63 cm
125 cm
251 cm
502 cm
753 cm
Jan Feb Mar Apr May June July Aug Sept Oct Nov Dec

Fig. I

Fig. 2

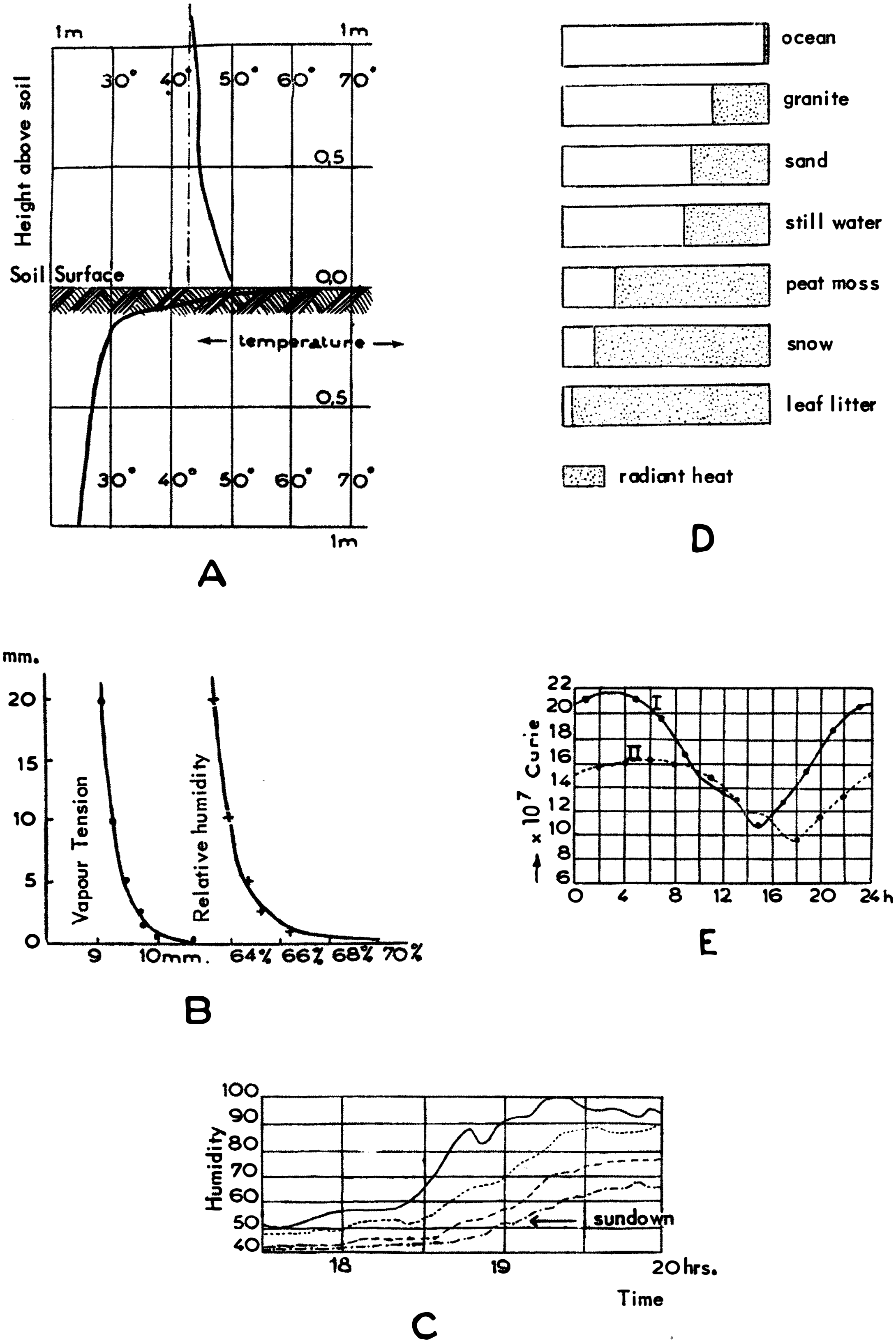
A Distribution of temperatures above and below the soil surface at Tucson Arizona, June 21, 1915, at 1 o'clock (Sinclair).

B Distribution of relative humidity and vapour tension above the soil (Rossi).

C Distribution of relative humidity in the air layer near the ground on a summer evening (July 22, 1929), measured from 10 cm. (solid line) to one metre (Lowest dotted line) (Geiger).

D Radient heat from different substrata (Schmidt).

E These curves represent the radium content of the layer of air above the soil at different times of day. The solid line is one metre above the ground, the dotted line 13 metres above (Becker).



1m
1m
Height above soil
30° 40° 50° 60° 70°
0.5
Soil Surface
0.0
temperature
0.5
30° 40° 50° 60° 70°
1m
A
ocean
granite
sand
still water
peat moss
snow
leaf litter
radiant heat
D
mm.
20
15
10
5
0
Vapour Tension
Relative humidity
9
10mm.
64% 66% 68% 70%
B
22
20
18
16
14
12
10
8
6
× 10^7 Curie
I
II
0 4 8 12 16 20 24h
E
100
90
80
70
60
50
40
Humidity
sundown
18
19
20hrs.
Time
C

Fig. II

We do not have any measurements of the variations in ionization and drop of potential near the soil.

All microclimatic factors govern the distribution of insects near the soil. The movements of grasshoppers which climb up the plant stalks at sundown and descend a little when the first star appears are indubitably correlated with the phenomenon of the nocturnal inversion. The authors which recognize this are wrong only in that they consider only temperature, whereas moisture cannot be without influence (Gunn, Perry, Seymour, Telford, Wright, Yeo, 1945).

Also connected with the microclimate must be the curious phenomena observed by Williams during four years of investigation at the Rothamsted Experimental Station. It is believed that generally, light traps attract only Lepidopterous males, with a small proportion of females. But Williams, in disposing his traps at different heights above the ground, found that above 10 metres, a very high proportion of females (especially among the Noctuids) was obtained. The males and the females thus fly in different strata of the atmosphere, which indicates without doubt, different climatic preferences. These studies are of tremendous importance in applied entomology.

<u>To summarize, the 'geophilic' insects live in a climate much more 'continental' than man, a climate where there is continuous thermal variations, where there is hardly ever wind, and where the abundant emanations of radium introduces on certain sites a very peculiar element, which has an effect on the development (particularily on mutations) which can be appreciated only with difficulty. The insect undergoes climateric variations whenever it is displaced on the soil, variations all the more marked when one considers its small size.</u>

MICROCLIMATE AND MESOCLIMATE

All the microclimatic peculiarities which characterize a region of determined physical geography (hill, valley, banks of a river) can be grouped under the title <u>mesoclimate</u>. It is necessary to remember that the heavier, cold, air stays close to the soil surface and flows like water with the slope; it fills the small hollows and there forms "cold lakes" detected in winter by the high proportion of frozen plants found there. A difference in level of several centimetres is often enough to introduce a difference of temperature: <u>Argytes</u> <u>bicolour</u>, (Coleoptera: Silphidae), commonly found in larval masses of <u>Bibio</u>, are also found in the adult state in accumulations of dead leaves in small, deep cavities. Is it not attracted there by the lower temperature and the peculiarly stable climatic conditions, more or less analagous to those that it found in the <u>Bibio</u> larval masses?

All the contributions discussed so far have applied to almost level soil surfaces. Everything changes when the surface is strongly inclined, and the first factor to consider is therefore <u>the</u> <u>orientation</u>

of the slope, for the heating of the soil is dependent upon that. However, a slope oriented towards the east can receive the same quantity of heat as one inclined at the same angle but to the west. The one receives the rays of the rising sun, the other, the rays of the setting sun. When it is a question of vertical walls (such as trellis walls) that are facing south, they will receive their maximum radiation in winter and the beginning of spring. But, in the lower layers of soil and interior of masses, the maximum temperatures are reached sooner in south-west exposures, owing to the supplemental influences of precipitation and evaporation. This obtains only in our climate, the orientation of slopes having a lesser importance in the tropics, the sun being nearer the zenith. Maximum humidity is reached in our climate on west-facing slopes.

In the interior of a valley, the phenomena are more complicated. The variations of temperature and humidity are greater in the bottoms of valleys than at the summits of the slopes; conditions are intermediate at mid-height of the slopes. The influence of mesoclimate is so strong that it can surpass differences at sea-level. Geiger has measured, in the valleys of the Bavarian Alps, some temperatures which exceeded by 3 degrees, throughout the whole day, those of the neighbouring summits, higher by 1,400 metres. Also, the valley was colder by 3 degrees during the night. A peculiar element of the biotype of the valleys is the existence of special winds, valley winds and slope winds. They are caused by variations in temperature on the slopes and their direction reverses during the night. The bottom of the valley is always much colder during the night than the slopes owing to the fact that cold air accumulates there. That is why frost is often much more serious in the bottoms of the valleys. The construction of a simple railroad embankment across a valley, can modify the microclimate completely, if the valley bottom is slightly inclined. The cold air flowing along the valley bottom collects behind the embankment and the plants situated further below escape the frost, whereas those situated 'upstream' will be destroyed.

It is certain that these conditions affect the distribution of plants. Gradually only the more cold-resistant ones stay in the valley bottoms, the more cold sensitive are confined to the slopes. The insect distribution will evidently be modelled to that of the plants, but there is also, from the entomological point of view, a climatological effect. Franz, working in a valley near Zurndorf, not far from Vienna, where the vegetation on the slopes and in the valley bottom are almost identical, has noticed a definate difference in distribution of Orthoptera, which is only explainable by microclimatic differences. Thus, Edalus nigrofasciatus is found only on the edges of plateaus, as is Dociostaurus brevicollis which descends sometimes into the higher limits of the slopes. The latter are populated by Calliptamus italicus, Gamphocerus maculatus, Stenobothris nigiomaculatus; a little lower occurs Edipoda coerulescens. At the bottom of the valley abound Chorthippus dorsatus and elegans, as well as C. parallelus, species which are wanting entirely on the plateau and on the slopes. One finds there also, a hygrophilic Phasgonurid, Xiphidium dorsale, not found on the slopes. The author considers the Orthoptera as excellent indicators of microclimate, and it would be int-

Fig. 3. Intensity of solar radiation on some slopes of different slope and exposure (Gessler).

Fig. 4.

A. Curve of temperatures in a valley on a frosty night in calm weather (Schmidt).

B. The nocturnal "valley wind" (large dots in bottom of valley) and the "slope winds" (fine dots) (Wagner).

C. How cold air flows on two sides of a railway embankment (Geiger).

D. Distribution of relative humidity on a mountain on a warm day in spring; the dotted line is at the bottom of the valley at 645 metres; D. -...; the broken line on a slope at 946 metres and the solid line, on a plateau at 1,447 metres (Woeikof).

E. Representing how cold air collects behind the walls separating vineyards (Geiger).

F. Daily temperatures on a mountain on a warm spring day; solid line the bottom of the valley at 645 metres; dotted line on a slope at 108 (Poss. misprint 1080) (Ed.) metres; broken line (dashes) on the plateau at 1,447 metres (Woeikof).

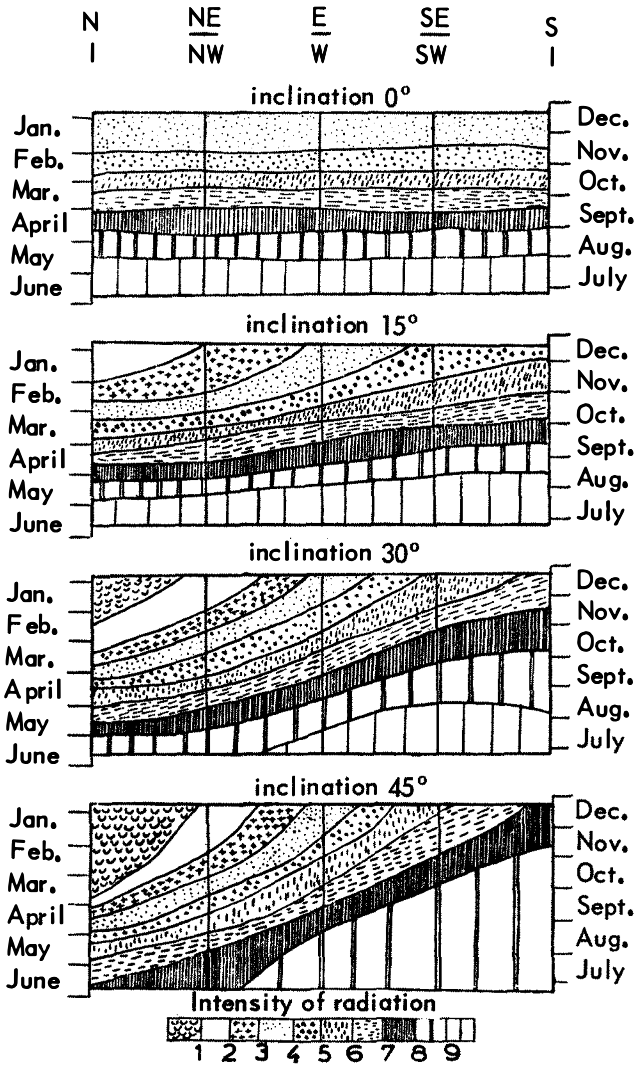


Fig. III

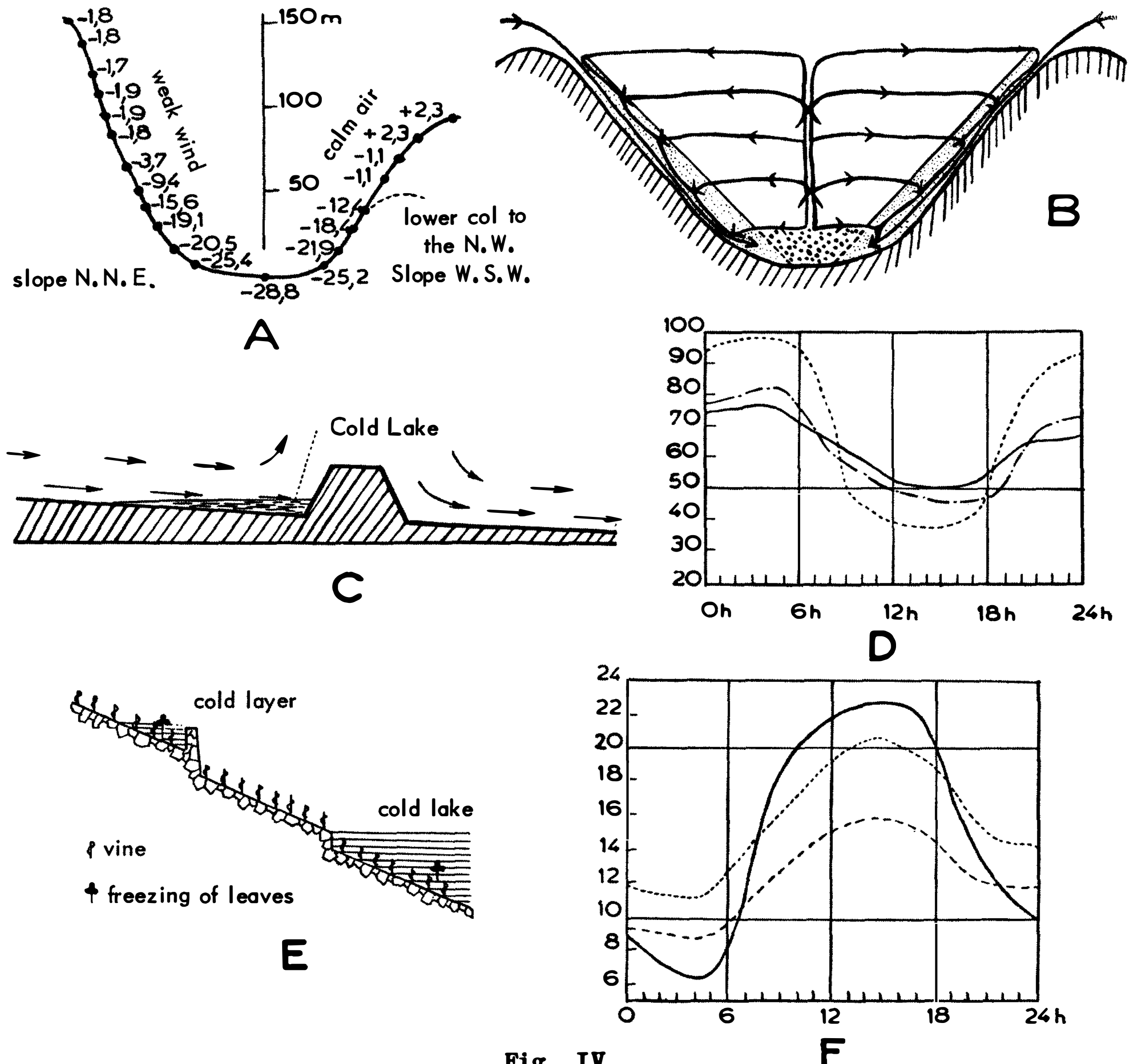


Fig. IV

eresting to discover the analogous distribution in other valleys. The Orthoptera are not however, the only insects whose distribution depends on microclimate. In the same region, the larva Evetria turionana is not rare at the summit of slopes, but one can rarely find it 10 metres below, 30 metres below, it is exceptional, the majority being killed by cold. A Coleoptera, Pityogenes conjunctus lays on the higher slopes of the valleys, but at the summit all the generations are annual while lower down they are biennual, with a very heavy mortality due to cold.

Microclimatic conditions certainly contribute to the formation of natural refuges and it is without doubt the explanation of the distribution of Hylemyia coarctata, which, in the Paris region at least, is normally contained within certain favourable environs; when the external medium becomes favourable, it spreads rapidily and does considerable damage.

Hollows and caves:- These evidently form a very special microclimatic environment. We know very little of the microclimate of small hollows, such as the nests of moles, for example, except that it is very different from the outside environment. As for caves, we are much better informed on this subject thanks to the works of R. Jeannel, but these are too well known to summarize here.

I The variations of humidity, not only of temperature, can also have a great influence on Orthoptera distribution as Grassé has shown with the native species of Perigord.

MICROCLIMATE OF CULTIVATED FIELDS

The Germans have been working the past few years on intensive studies concerning the microclimatology of the cultivated field. The installation technique of Prof. Tamm of Berlin is, from this point of view, a model of its kind. Electric cables transmit the impulses of many reading apparatuses to a central building, where at all times is given the variations in temperature, humidity, radiations etc., at different heights above the soil and at different depths in the soil. It is evident that such an installation, unhappily non-existent in France, would be a veritable mine of precise measurements. The microclimatic peculiarities of fields of potatoes, wheat, rye, barley, maize, clover, alfalfa, oats, soya bean, tobacco, hemp, and flax have been described by Tamm and his school. Having mentioned this work, it is important to study the general modifications that the presence of vegetation produces on the microclimate.

When solar radiation falls on the leaves, a portion is reflected, another absorbed, and another part, very small, goes through the leaf. The leaves reflect scarcely any of the ultra-violet, no more than sand or bare earth, but they reflect 8 to 20 percent of the visible (the white portion of parti-colored leaves can reflect up to 60 percent). The fields and the forest therefore, return only one-fifth or one-quarter of the visible incidental light. As for the portion of the spectrum near the infra-red, it is entirely reflected and it is because of this that vegetation appears white when photographed through a filter passing only infra-red light. On the other hand, the reflecting ability of leaves is very low for long infra-red waves, the foliage is nearly transparent for these rays. The light transmitted by a leaf therefore, is not only greenish, it is mainly infra-red.

As for the absorbed radiation, the values are 90 percent for ultra-violet, climbing very slowly with the longer waves; a minimum in the yellow-green (5%) and from 5-10 percent towards 1u they increase again to 65 percent towards 2.4u.

Because of their special behaviour in respect to radiation and also because of transpiration which lowers their temperatures, plants do not have the same temperature as ambient air. Generally they are warmer than the air during the day and cooler during the night. Observations about one leaf of the castor-oil plant have shown a layer of cold air about 1 mm. thick. The surface area of the leaf has a great importance; a small leaf cools more quickly than a larger. A meadow is covered with white frost before a cultivated field, in which the crop leaves are, on the average larger. Moreover, the leaves closest to the ground are always colder than the ambient air at the same level (up to 50 difference). The aphids and the scale insects therefore, live in a microclimate much more 'continental' than the surrounding atmosphere. The mining insects exist in even more peculiar conditions. The leaves are heated when struck by the rays of the sun, particularily if they are thick, (a temperature of 55° was measured in a leaf of house leek when the air temperature was 35°). The miners must be especially resistant to heat or confined to the shade. It must be the latter which explains why the dipterous Drosophilid Scaplomyza apicolis mines only the lower leaves of rape.

In a cultivated field, the temperature varies with the nature of the crop, the density of stalks, the orientation of the lines of sowing and whether the plants have storied leaves (like the potato) or vertical leaves (like rye). In barley fields in winter, for example, the stalks form a dense palisade which prohibits free air movement, the daily maximum temperature is found then near the soil and the minimum at the midpoint of the height of the stalks. Related to this fact is the observation that the eggs of Pyrausta nubilalis are laid in the axils of the leaves (partly median on the maize plants) and they all die if they fall to the ground. As they are very sensitive to heat it is not impossible to think that it is the microclimatic maximum temperature which kills them. In a field of snapdragons (Antirrhinum) on the other hand, where the air can circulate more easily, the maximum temperature is found at the top of the stalks and the minimum near the soil.

In the tropics, analagous measurements have been made by the school of Ramdas in fields of sugar cane and millet grass. The table below shows the temperature differences between the cane field and the ambient air, also cooling influence of irrigation. I

Height above ground (cms.)	Ambient Air	Millet grass (non-irrigated)	Sugar cane (irrigated)
183	29.8	30.0	27.5
122	30.0	29.9	27.0
91	30.1	29.8	26.4
61	31.0	29.7	25.5
31	31.6	29.9	24.6
15	32.5	29.7	23.8
8	33.6	29.4	23.3
3	34.8	29.3	23.0
1	36.7	29.3	22.7

I A very clear example of the modifying influence of irrigation on the microclimate can be found in the distribution of Epilachna cornuta (Coleoptera) present at all times in the warm and humid climate of Mexico and in the arid prairies of Western United States. These entirely different environmental conditions have led authors to maintain that the insect was indifferent to its environment, until Sweetman showed that the localised distribution in the United States was in irrigated fields in which microclimate is altogether different from the rest of the area. Analagous observations could be made concerning the distribution of Prodenia eitura and of the thrips of cotton, two others influenced by irrigation.

In a field of coffee in German East Africa, the measurements of Wien show that the temperature (at an altitude of 1,750 metres) reached 11° outside and 20° in the field, even though the plants are quite widely spaced.

Up to this point it has been impossible to cite the work of any French microclimatologist, but there has been some remarkable work done by the phytosociologists of the school of Braun-Blanquet concerning the microclimate of certain Southern Brachypodium grass associations. Here, the temperature depends particularily on the density of the vegetation and as the species of Brachypodium are always more dense than those of Bromus, for example, the differences of temperature between the soil and in the upper strata of the vegetation are much more marked in the latter (56° at 2 cms. above the soil against 44° at 25 cms. in July in an association of Bromus. In the clearer summer days, the lower layers of the Brachypodietum receive only half the solar radiation of the higher strata. But these measurements have been made with a light metre calibrated only for white light, whereas the light transmitted by the leaves is green and infra-red as we have seen. It would have been preferable to use a pyrrheliometer.

The humidity is very high between plant stalks. On June 18, 1920, at a temperature of 29°, humidity measurements were made near Frieburg: in free air, 50% R.H., 100 cms. above the soil; 78% at 13 cms. between some stalks of clover, and 96% at 2 cms. in the grass. The turf emits, on the average, twice as much water vapour as the bare soil, but for some plant associations up to 5 or even 8 times more. It essentially depends on the density of the vegetation. In spite of all this, the air between the leaves does not attain the point of saturation; on a rainy day between the stalks, the humidity was found to be only 98%, the highest value recorded there.

Field of cereals - density	Dense	Medium	Sparse	Free air
Relative humidity	73	64	51	40
Surface foliage in cms^2/ cu. cm. of air	1.81	0.82	0.38	0

In the very dry biomes, like the deserts, there is no increase of the moisture content between the leaves, because of influence of dessication, winds between the sparse plants and above all, because of the temperature. The latter can be so high, that the air between the lower plants may be drier than in the open. The Mediterranean grasses studied by Sorsceanu seem to approach this condition.

As for the wind, we have seen that its velocity falls considerably near the soil. This drop is accentuated by the presence of vegetation. In the country of East Prussia which is battered by winds, the wind can drop 9.3 metres /sec. at 1.8 metres height to 1 metre /sec. between tufts of Calluna. Generally, rarely are speeds above 1 metre /sec. recorded between tufts of vegetation. This is important when considering evaporation, which is greatly increased by air movement. It will be weak between plant stalks except in grasses of dry sunny regions, where the role of temperature predominates.

Wind velocity in metres per sec.	Loss in percent of the velocity at 25 cms.		
	Wheat	Beans	Potatoes
Below 1	24	20	30
1 - 2	15	23	24
2 - 3	11	15	23
Above 3	9	11	--

Fig. 5.

A. The distribution of daily temperatures at different levels in a field of rye; the figures in the illustrations are proportional to the temperature (Geiger).

B. Light reaching the soil in different cultivated fields. From top to bottom: in free air, in barley fields, in a rye field, in a field of clover. Height of the barley 12-15 cms.; of the rye 80 cms.; of the clover 30 cms. Measurements taken in May (Sauberer).

Fig. 6.

A. Distributions of temperatures in cultivated fields at different heights. Temperature increase to the right of the figure: 1 degree corresponds to 0.5 cms.

B. Field of Antirrhinum (Snapdragons).

C. Rye field, from left to right: in April, from the first to the tenth of May; 11th to the 20th of May; the 21st to the 31st; first of June to the 10th of July; 26th of July to the 12th of August. All temperatures are measured about noon.

D. Nocturnal temperatures in a field of Antirrhinum.

E. Nocturnal temperatures in a field of rye. From left to right (as in C - Ed.). All temperatures measured about midnight. (Geiger).

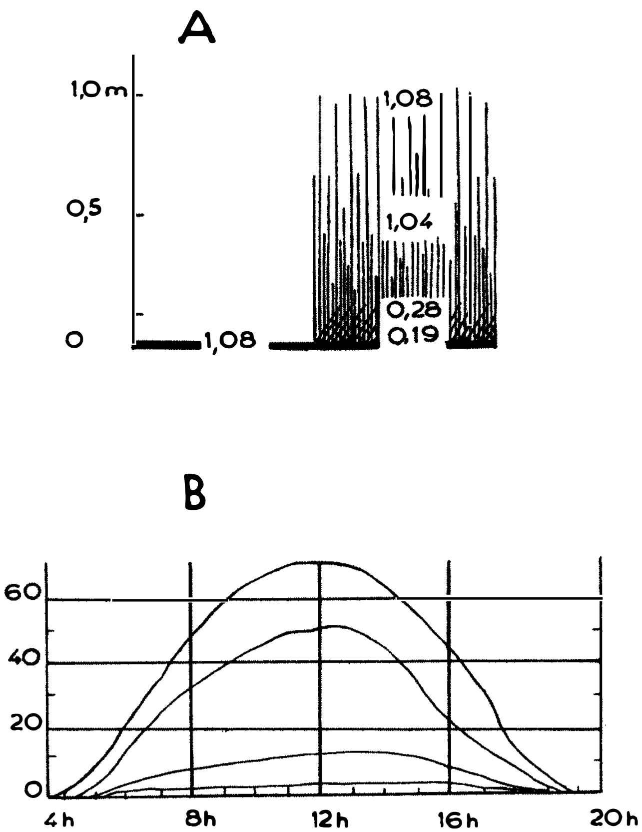

A
1,0 m
0,5
0
1,08
1,08
1,04
0,28
0,19
B
60
40
20
0
4h
8h
12h
16h
20h

Fig. V

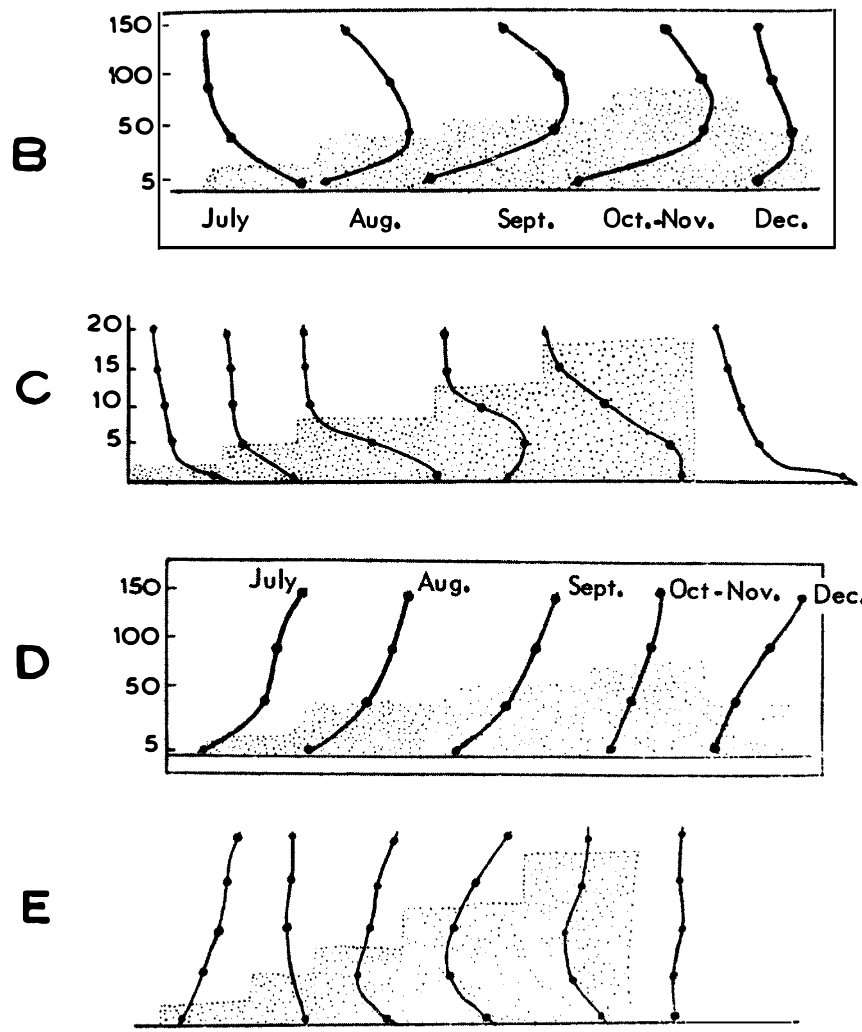

B
150
100
50
5
July
Aug.
Sept.
Oct.-Nov.
Dec.
C
20
15
10
5
D
150
100
50
5
July
Aug.
Sept.
Oct-Nov.
Dec.
E

Fig. VI

Fig. 7.

A. Vapor tension in a field of sugar cane a. in free air; b. in a field of millet; c. at Poona in India. Along the ordinate, height above the soil; on the abscissa vapor tension in mms. Measurements taken at sunrise (left) and at noon (right) (Ramdas).

B. Distribution of temperatures at noon (left) and midnight (right) in a vineyard (Geiger).

Fig. 8. Zones of equal wind velocity above different vegetation in horizontal section to illustrate the different turbulence of the air according to the type of vegetation. The turbulence caused by the presence of beets is more violent, but does not extend as high as that above the stubble. (Schmidt).

Fig. 9.

B. Permeability to radiation, in respect to wave length, using leaves from 3 different plant species. On the abscissa, wave length in mu; on the ordinate, permeability in percent. 2 - a red beet leaf; b - Cowslip; c - hellebore (Angstrom).

C. Light in the interior of the grove of red beech at first leaf (dotted line) and in full leaf (solid line). Ordinate: height in metres above the ground; abscissa percent of light in the free air. The three horizontal divisions correspond to lower shrubby layer, Zone of the tree trunks and to the crown (Trapp).

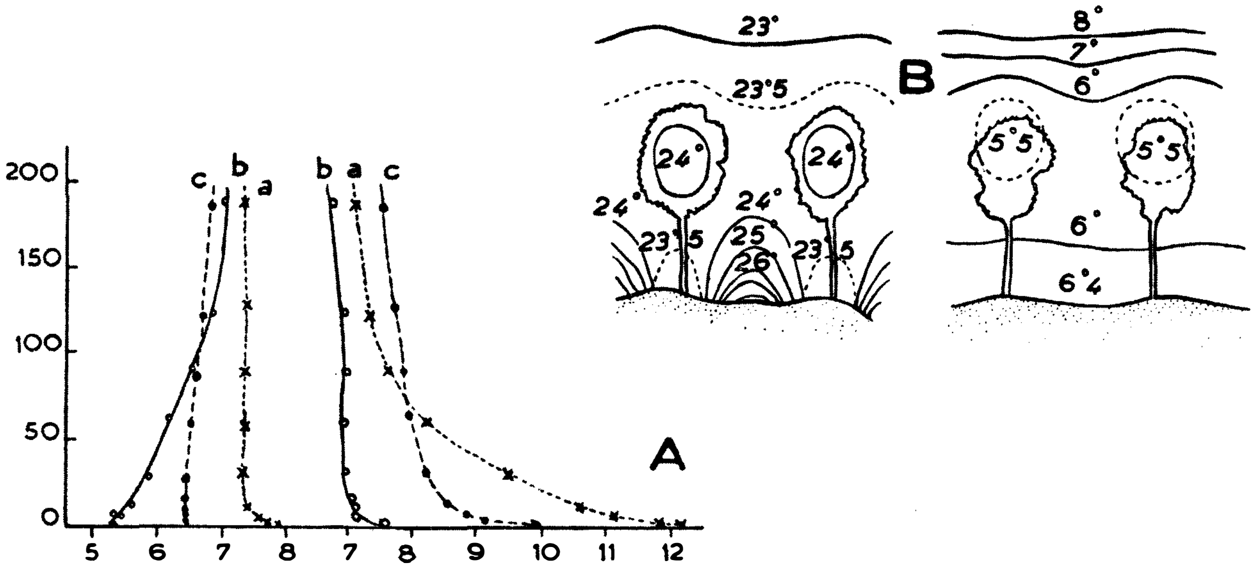


Fig. VII

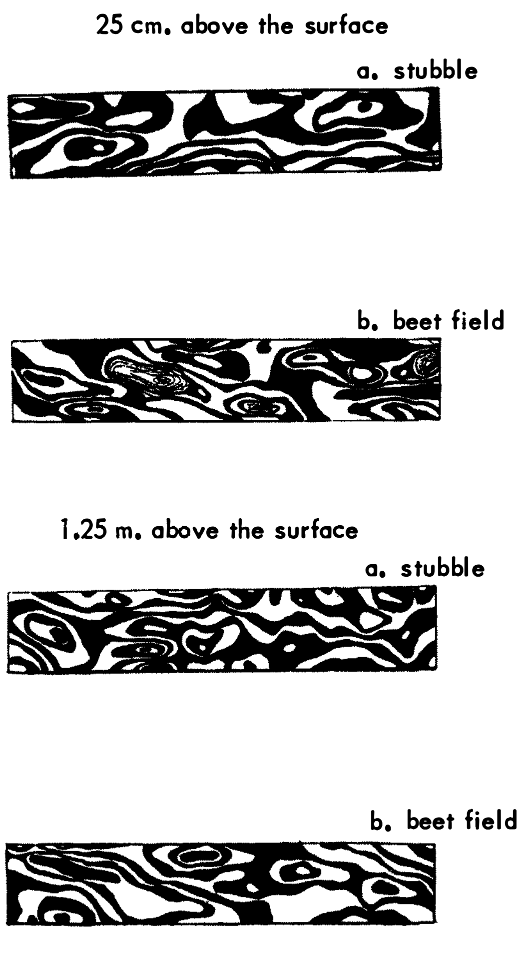


Fig. VIII

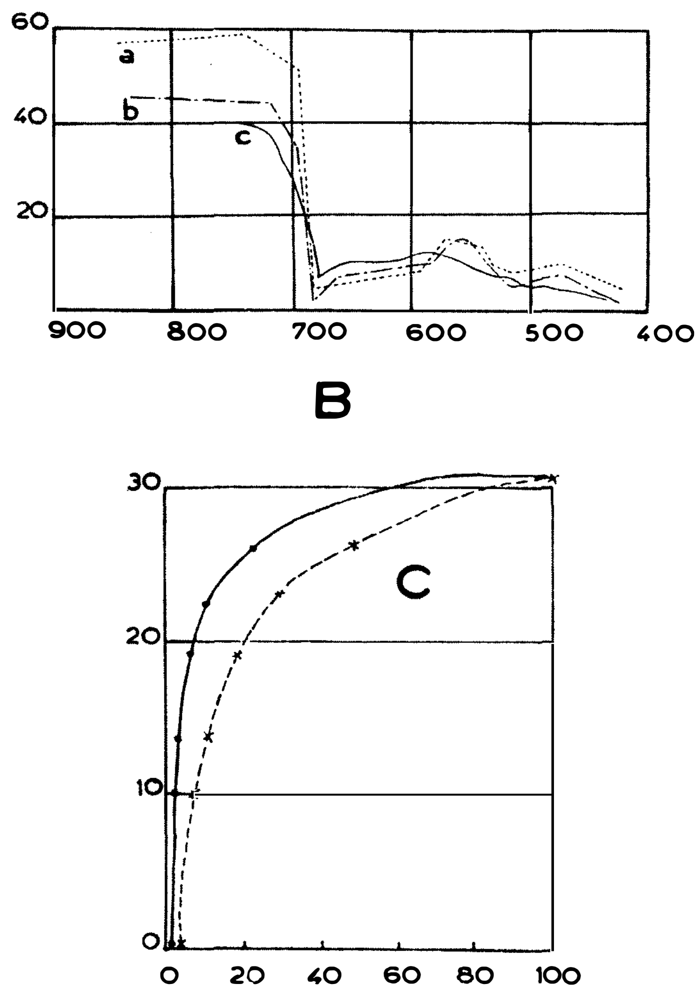


Fig. IX

Other factors, less studied, may be of great importance. The masses of ionized air, in particular, do not penetrate into the plant masses, which constitute a sort of Faraday's cage. On the other hand it is difficult to conceive that between the densely woven leaves of a field of alfalfa, for example, that there would not be any difference in the content of oxygen during the day and at night, and between that of the interior of the field and in the open, the more so as diffusion is slow and there is no wind, but no one has yet looked at it from this angle.

The microclimate of the field is not homogenous; the shaded portions differ considerably from the sunny parts, and the border of the field (or rather the borders, as the orientation must be considered) have not the same temperature or humidity. These peculiarities appear to be connected with the behaviour of Cephus pygmaeus which attacks primarily in the shaded corners of the fields, under trees and along hedges, as well as the shaded borders of rows.

Soil temperature depends, as we have already seen, on the nature of the plants covering, therefore the temperature of the soils of plots of Bromus erectus are higher than that of the soil below Brachypodium. However, the most important point to note is the general dryness of soils covered with vegetation. The intercepting rain guages of Clark (1940) have shown that in a field of oats, 43 to 75 percent of the water from showers did not reach the soil; in a field of wheat 60 to 100 percent of the water from heavy rain and 90-100 percent of light rain are stopped. The surface area of leaves is 3 to 20 times larger than that of the soil and the interception is almost analagous to that of trees.

In summary, insects of cultivated fields live in a very humid climate, practically devoid of wind, where masses of ionized air do not penetrate and where they are bathed in infra-red rays. The gas content undoubtedly differs from that of free air and the temperature varies considerably from the normal. As for the insects which enter the soil, for example for pupation, they enter an environment which is very dry, practically a desert.

MICROCLIMATE OF THE FORESTS

The climate of the forests, in contrast to that which we have just studied, has lesser extremes than the free air. The daily maximum and the nocturnal minimum is higher than in the open. The tree crowns constitute the warmest zone in the forest. However, the temperature of the leaves varies tremendously depending on their position. The difference between leaves at the top of the crown and those at the bottom, rarely exposed to the sun, can surpass six ^{o}. Moreover, the maximum temperature changes location during the day. In the morning, it is found in the higher portions of the crown, about one o'clock in the mid-crown region and later it is found again towards the top. If the crowns are closed, they form an "effective soil" with a thermal gradient and a special nocturnal inversion different from that of the ground below. Even in winter, when the trees no longer have leaves, the characteristics of this "effective soil" do not disappear entirely. During the night the leaves at the centre of the crown cool less quickly than those of the periphery.

The illumination is obviously much less in the forest than in the open and depends on the nature of the vegetation.

Tree	Illumination in percent of the open light	
	Defoliated	Foliated
Red beech	26 - 66	2 - 40
Oak	43 - 69	3 - 35
Ash	39 - 80	8 - 60
Birch		20 - 30
Spruce		2 - 20
Pine		4 - 40

Braun-Blanquet, studying the forests of Mediterranean evergreen oak has noted that the superior shrubby stratum (150 cms. below oak crowns) received only one-thirty-fifth of the exterior light, the lower shrubby stratum (70 cms.) only one-seventieth. As we have seen above, the light is not only screened but filtered, as shown by the following table, the data for which was taken under deciduous trees.

Wave length	0.71	0.65	0.57	0.52	0.45	0.36
	Red	Orange	Yellow	Green	Blue	Violet
March 12	61	54	51	48	46	44
April 15	59	39	36	33	32	30
May 10	19	6	7	6	6	5
June 4	14	4	5	4	3	3
	Percent of radiation reaching the soil					

On the other hand, all that has been said on the permeability of leaves to infra-red can be repeated as appropiate to forests, thus, the undergrowth is bathed in green and especially infra-red light. Related to the lesser light, is the fact that the days are shorter in the forest than in the open, the difference can reach an hour in cloudy or rainy weather.

Humidity is generally higher in the forest, especially during the night and at the time of dew deposit of which the greater part falls on the tree crowns. As in free air, the humidity increases as we approach the soil. In a pine wood measurements of humidity showed 84% at 6 cms. in tufts of Oxalis, 67% at 30 cms. between some Myosotis and 59% in the trees at trunk height. However, there is a second maximum at the level of the crowns. As above, the moisture and thermal minima are less accentuated in the plants of the forest. Precipitation plays a small part in maintaining a reasonably high average moisture content, which is maintained mainly due to low evaporation. In fact, in coniferous forests two-thirds of a light rain are kept back by the crowns and at least a fifth of rain storms. This interception is much greater under deciduous trees in leaf. Evaporation is greater in the crown zone than in the plant-moss strata, which is caused by the unequal air-movement in the different strata. This is illustrated by the following table:

Height in Metres	Location	Ave. wind velocity in metres /sec.	
16.85	Above the crowns	1.61)	Measurements in a pine forest.
13.70	At crown top level	0.90)	
10.55	In the crowns	0.69)	
7.40	Just at bottom of crown	0.67)	
4.25	At middle of trunk	0.69)	
1.10	Near the soil	0.60)	

The distribution of certain insects must be connected with the peculiar distribution of the microclimatic strata, such as Hoemagogus capricornus carrier of the "jungle fever". This mosquito is much more abundant in the vicinity of the crown tops than at soil level. When it is found at soil level it is more abundant in the exposed areas than in the undergrowth. In the rainy season, the insect is more abundant at soil level, towards mid-day. It is not known what the microclimatic peculiarities are that regulate this distribution, but it seems premature to place it exclusively to moisture.

All the other mosquitoes of the tropical forests also have a well-defined strata of distribution, some at ground level, some like Hoemagogus in the crown zone (Marston Bates, 1944). This is comparable with the case of Potosia speciosissima which, in the forests of Fontainbleau, stays distinctly in the crown region.

The Orthoptera of the forest, studied by Grassé (1929) show a very characteristic distribution. It is particularly interesting to note the relations of Pholidoptera griseo-aptera and of Nemobius sylvestris with the plant-moss zone. It is probable that the conditions of weak light, high moisture content and of the temperature peculiar to this strata governs, as Grassé thinks, the distribution of these species. It is regrettable that the photo- and hygrotropisms of these insects (and especially of Nemobious, which is so dependent on the undergrowth) have never been studied. As in cultivated fields, the carbon dioxide content of the air must be higher near the soil of forests, because of the specific gravity of this gas and of the poor mixing of the air (Braun-Blanquet).

Because of the special conditions in which they are found, all the chemical phenomena of the forest trees are modified with regard to those same species growing in the free air, in the isolated states. Thus the osmotic pressure of beech shows lesser variations in the forest than in the isolated state, in an open field. This applies to a stronger degree to the plants of the lower strata. We know what influence these modifications can have on parasites, an influence well illustrated by the classical experiments of Wladinirsky. Another example is in the damage done by Pissodes pini which is much less in pines shaded by deciduous trees, than on solitary pines in the sun.

The results of all these contributions is that the animals of the forest live in a well-tempered climate, less "continental" than those in the open, with thermal and moisture extremes less accentuated. The average temperature is lower, the average moisture content higher than in the open, the air movements slighter, the illumination much less than in the open and very rich in long-wave infra-red. There are fairly strong differences in the microclimates of the different strata.

We must, however, distinguish in the forest a series of particular biotypes, especially the clear-cut areas and clearings. Their microclimate depends above all on their size or extent. However, in a general way, it is more continental than that of the surrounding forest. A consideration of the size of the clearing related to the height of the surrounding trees is very important, because of the possible penetration of wind, increased exposure to the sun, etc. The temperature extremes can exceed those of open country and shrubs in the clearings freeze very easily in winter. They are drier than bare fields for an important part of the rainfall (which rarely falls vertically) is stopped by the branches of the surrounding trees. Small clearings are the driest.

The edge of the forests, like the edges of fields is not similar to the rest; its orientation is of great importance from the point of view of microclimate, but it is in general, in our latitudes, more humid than the rest.

The orientation of the tree trunks influence their own microclimate and that of the xylophagous insects on them. Those living on trees in the shade develope less quickly than those in the sun. It is somewhat similar to the condition found in fallen trees. In our climate, a fallen tree oriented N.W.-S.E., would have a warm south-west surface and a cold north-east surface. Some xylophagous insects like Ips typographus develop in a very different way on the two surfaces. In zone 1 Fig. 14 where the temperature reaches 50 deg. in the air and 35 deg. in the bark, oviposition does not occur. In zone 2 the eggs are laid but all die. In zone 3 they are able to hatch but the young larvae, less resistant, die from dessication. In zone 4 the development is normal, but in zone 5, because of the high moisture content, the mortality ranges from 75 to 92 percent.

The innumerable cavities of the trunks consitute a series of

Fig. 10. Distribution of temperatures in a grove of oak in August from 5.15 to 8.30 A.M. Sunrise at 5.15 A.M. a - 27 metres high, above crown top; b - in the midst of the crown top at 23 metres; c - 19 metres; d - 11 metres; e - 1 metre.

Fig. 11. Distribution of temperature in the same wood from 2.15 P.M. to 6.30 P.M. (Geiger and Asmann).

Fig. 12. Distribution of Arthropod populations of the nettle (Larium sp.) in the shade (A) and in the sun (B) (Vladimirsky).

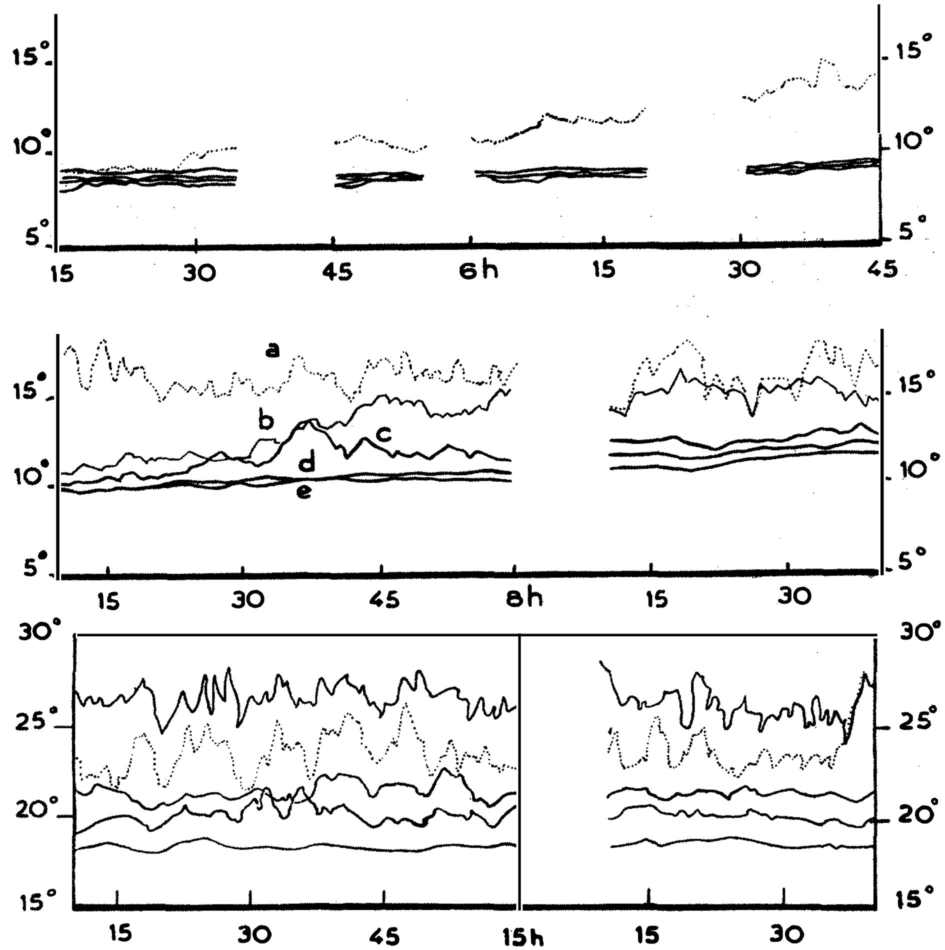


Fig. X

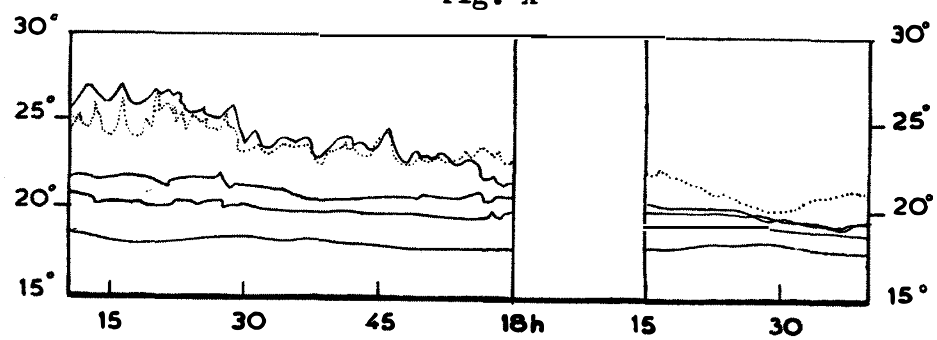


Fig. XI

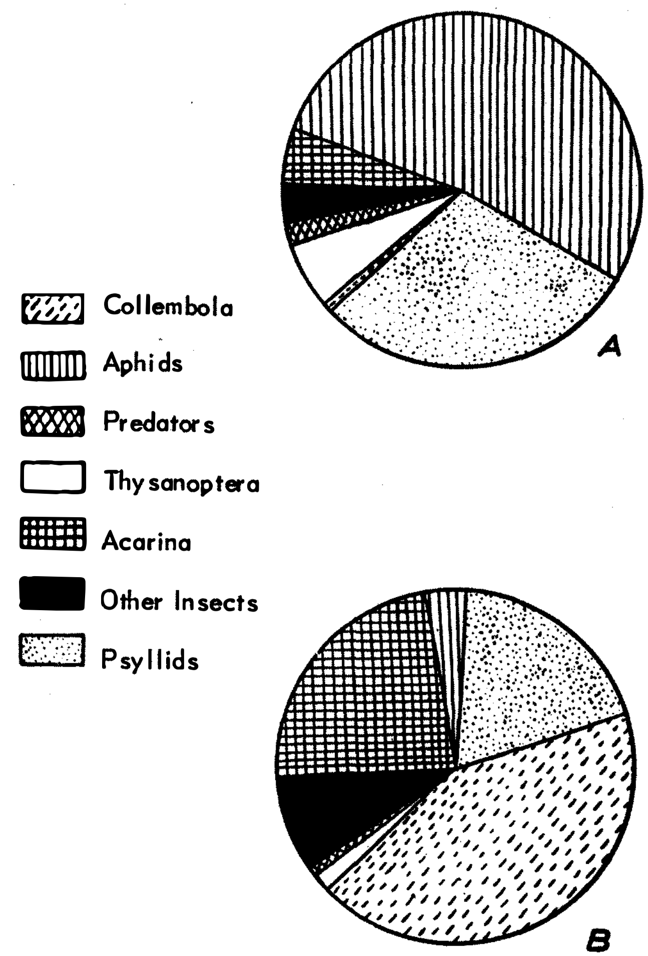


Fig. XII

Fig. 13. The danger of frost in relation to the dimension of clearings. On the ordinate, observed nocturnal minima; on the abscissa, reading from top to bottom; diameter of the clearings in metres; surface of the clearing in hectares (2.471 acres); ratio of diameter to height of surrounding trees. The top curve shows the average of the 17 coldest nights in spring of 1940; the bottom the coldest nights observed about June 6, 1940. Observations made in Germany (Geiger).

Fig. 14.

A. How the buds of an isolated pine 15 years old open according to aspect of the crown. (May, 1937, Eberswalde). Black discs:- buds not open the 17th of May; black and white:- opening the afternoon of the 16th; white discs:- opening the morning of the 16th; starred discs:- eclosian on the 15th (Scamoni).

B. Zones attacked by <u>Ips typographus</u> in a fallen trunk.

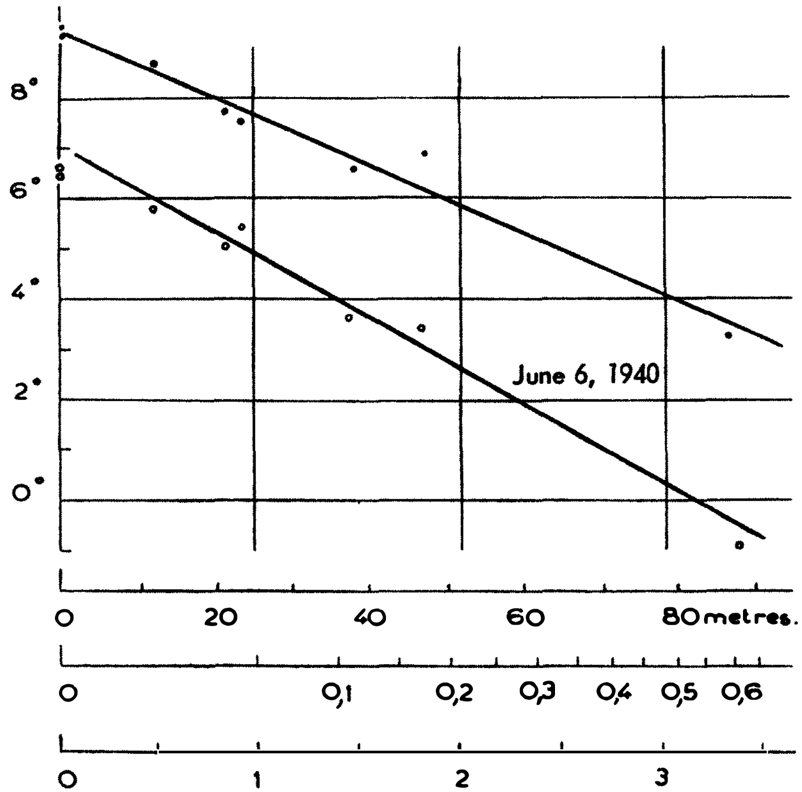


Fig. XIII

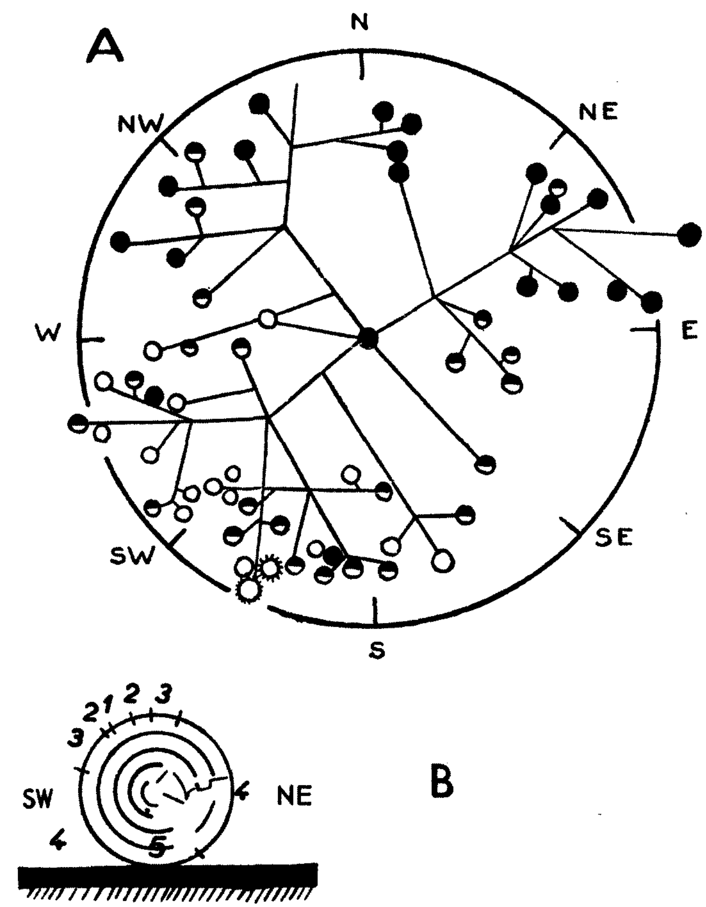


Fig. XIV

microcaves, the characteristics of which have been recently studied by A. Kh. Iablokov in his remarkable work on Elaterids in the Fontainebleau forests. Many southern diurnal Elaterids on flowers are also found at Fontainebleau, but exclusively in the bark cavities of old trees which they leave only at night. Without a doubt they find there microclimatic conditions which, although different from those of southern France, permit survival. However, on particularly sunny and warm days, the Elaterids leave en masse and are captured in full light on whitebean flowers. By the precise analysis of the climatic conditions at the time of capture of reputedly rare Elaterids, Iablokov has been able to collect large quantities, and to build thus collections probably unique in France. It is one of the best proofs of the importance of climatic contributions for the faunistic entomologist.

SOME SPECIAL MICROCLIMATES.

There remains only to discuss the microclimatic characters of cavities such as those covered by little stones, nests of mammals and of the insects in them. There has been much work done on those of the social insects, (extensively covered by Uvarov). We will discuss only the fragmentary and incomplete data scantily covered by investigations. According to Agrell (1945) the Collemba of birds' nests and mole burrows have very different environments and the conditions vary according to the height of the nest above the ground. The underground nests are evidently characterized by constant thermal and moisture characters, whereas in the nests of birds, the temperature is that of the body of the female when she is nesting. The Collembola which frequent the nest during this period show an obvious preference for higher temperatures.

All the nests are dry biotypes, the humidity rarely exceeding 30 percent. Therefore the Collembola of these nests must be resistant to dessication (something rather astonishing for Collembola).

Buxton (1932) has studied the microclimate of rat holes, in relation to the life history of the bubonic plague-carrying flea, Xenopsylla cheopsis. He found that generally the temperature was regularly higher in the holes and also in empty spaces between crates of stored merchandise in warehouses, than in the open. The humidity is also higher. Thanks to special microclimates existing in this manner, conditions permitting the development of the larvae of the bubonic plague-carrying flea are realized more often than one would think. Buxton thinks that by designing a special warehouse, roofed with glass to permit the penetration of infra-red rays and well-ventilated, the microclimate in the small spaces would be modified sufficiently to inhibit the development of Xenopsylla.

Temperature and Moisture Content of Rat-holes

A. In a stable (in Jerusalem.) B. Rat-hole No. 1 C. Hole No. 2

Time	Temp.	Vapour pressure	Sat'n deficit	Temp.	Vapour pressure	Sat'n deficit	Temp.	Vapour pressure	Sat'n deficit
9.00 a.m.	29.2	13.6	16.8	27	26.0	0.6	27	17.0	9.6
8.30 a.m.	28.6	11.4	18.0	27	25.2	1.4	27	23.1	3.5
8.30 a.m.	27.0	14.7	11.8	27	21.6	5.0	27	14.5	12.1
8.30 a.m.	25.6	15.4	9.2	27	23.7	2.9	27	16.5	10.1
5.00 P.M.	27.8	15.6	12.2	27	16.5	10.1	27	15.5	11.1
AVE.	27.4	14.4	12.9	27	21.9	4.7	27	16.7	9.9

CONCLUSIONS

The several biological examples cited in this paper (and to which all faunisticians will be able to add from their own experience) all show the importance of the work of Geiger and his school to applied entomology. Who knows whether it is impossible, by adjusting the density of the stalks in a cultivated field, to so modify the microclimate that the multiplication of certain parasites is impeded? From another point of view, if the young entomologist, instead of following at random the ramifications, restricted himself to a limited number of avenues of research, such as measurements at the same height, on the same plant association, at several times of the day and on different days, and also by taking the statistics of the species recovered and noting the precise microclimatic conditions at the time of capture, he would rapidly amass contributions of great scientific interest. It is no longer sufficient to indicate in the collections the locality and plant on which the capture was made; it is indispensable, after the work of modern micrometeorologists, to note in addition, the temperature, moisture content of the air, approximate wind velocity, time of day and sky cover at the time of capture. In addition to their systematic interest, contributions collected in this manner add to building up the knowledge of this tremendously interesting science and also serve to fill in the blanks in our knowledge of insect and animal ecology.

Laboratory of the Evolution of Organized
Life and the Central Station of Agricultural
Zoology.

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The references indicated by an asterisk are not from Geiger. Instrumentation:- for temperature measurements, we used the apparatus of Schmidt (Z. Instrumentenk., 46, 1936, 432) (instantaneous measurements). For recording instruments see Johnson (Geophys. Mem., 46, 1929) and Albrecht (Met. Z. 1937, 420). For radiation measurements consult Falckenberg (Met. Z., 1928, 422). For the adaptation of the hair hygrometer to microclimatic work, see Geiger (Met. Z., 1929, 539), Howell and Craig (Science, 89, 1939, 544), Neilson and Thamdrup (Biokl. B., 6, 1939, 180). For the measure of the wind velocities of low values see the work of Schmidt (WienerSitz. Ber., 85, 1929 and Met. Z., 1929, 495). For the measure of dewpoint, see Hiltner (Wissen. Arch. Lanwirtsch., A,3,1930,1) and Adrianoff (Met. Z., 1927, 425).

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