STATE OF ILLINOIS
DEPARTMENT OF REGISTRATION AND EDUCATION

DIVISION OF THE
NATURAL HISTORY SURVEY
STEPHEN A. FORBES, *Chief*

Vol. XVI. BULLETIN Article VII.

The General Entomological Ecology of the Indian Corn Plant

BY

STEPHEN A. FORBES

PRINTED BY AUTHORITY OF THE STATE OF ILLINOIS

URBANA, ILLINOIS
April, 1927

STATE OF ILLINOIS

DEPARTMENT OF REGISTRATION AND EDUCATION

A. M. Shelton, *Director*

BOARD OF

NATURAL RESOURCES AND CONSERVATION

A. M. Shelton, *Chairman*

THE NATURAL HISTORY SURVEY DIVISION

Stephen A. Forbes, *Chief*

Schnepp & Barnes, Printers
Springfield, Ill.
1927

65530—500

Article VII.—*The General Entomological Ecology of the Indian Corn Plant.** By Stephen A. Forbes.

Ecology being the science of the interactions between an organism or a group of organisms and its environment, and between organisms in general and their environment in general, this complex of relations may, of course, be divided in various ways. The division here used implies a centripetal grouping of the facts of relationship around single kinds of organisms, and the group of facts to be discussed is that of which the corn plant is the center and the insects of its environment are the active factors.

A prolonged study, extending over many years, of the entomology of the corn plant, the economic results of which have been published in my seventh and twelfth reports as State Entomologist of Illinois (the Eighteenth and Twenty-third of the office series), has left in my possession a considerable body of information capable of treatment from the standpoint of pure ecology, and the beginnings of such a treatment are here assembled because of the rising interest in ecological investigation and the promise which it gives of interesting and important results, and because of a wish to illustrate in some measure the general scientific value of such materials of which, it scarcely need be said, the economic entomologists of this country have accumulated a large amount.

Insect Infestation of the Corn Plant

We know of some two hundred and twenty-five species of insects in the United States which are evidently attracted to the corn plant because of some benefit or advantage which they are able to derive from it. The principal groups of this series are ninety species of Coleoptera, fifty-six species of larvæ of Lepidoptera, forty-five species of Hemiptera and twenty-five species of Orthoptera. The other insect orders are represented by seven or eight species of Diptera and one or two of Hymenoptera. Every part of the plant is liable to infestation by these insects, but the leaves and the roots yield the principal supplies of insect food, either in the form of sap and protoplasm sucked from their substance by Hemiptera or in that of tissues and cells devoured by the subterranean larvæ of Coleoptera and by caterpillars, grasshoppers and beetles feeding above ground.

Lack of Special Adaptations

Notwithstanding the great number of these insects and the variety and importance of the injuries which they frequently inflict upon the corn plant, there is little in its structure or its life history to suggest any spe-

* Reprinted from The American Naturalist, Vol. XLIII, No. 509, May, 1909.

cial adaptation of the plant to its insect visitants—no lure to insects capable of service to it or special apparatus of defense against those able to injure it. The fertilization of its seed is fully provided for without reference to the agency of insects. It has no armature of spines or bristly hairs to embarrass their movements over its surface or to defend against their attack its softer and more succulent foliage. It secretes no viscid fluids to entangle them and forms no chemical poisons or distasteful compounds in its tissues to destroy or to repel them. The cuticle of its leaf is neither hardened nor thickened by special deposits; its anthers are neither protected nor concealed; and its delicate styles are as fully exposed as if they were the least essential of its organs. Minute sucking insects are able at all times to pierce its roots and its leaves with their flexible beaks, and, with the single exception of its fruit, there is no part of it which is not freely accessible at any time to any hungry enemy. Only the kernel, which is supposed to have been lightly covered in the wild corn plant by a single chaffy scale or glume, has become in the long course of development securely inclosed beneath a thick coat of husks, impenetrable by nearly all insects; and we may perhaps reasonably infer that, among the possible injuries against which this conspicuous protective structure defends the soft young kernel, those of insects are to be taken into account.

There are, of course, many insect species, even among those which habitually frequent the plant, which are unable to appropriate certain parts of its substance to their use, but this is because of the absence of adaptation on their part and not because of any special defensive adaptation on the side of the plant. Thus we may say that, with the exception of the ear, the whole plant lies open and free to insect depredation, and that it is able to maintain itself in the midst of its entomological dependents only by virtue of its unusual power of vigorous, rapid and superabundant growth. Like every other plant which is normally subject to a regular drain upon its substance from insect injury, it must grow a surplus necessary for no other purpose than to appease its enemies; and this, in a favorable season, the corn plant does with an energetic profusion unexampled among our cultivated plants. Insects, indeed, grow rapidly as a rule, and most of them soon reach their full size. Many species multiply with great rapidity, but even these the corn plant will outgrow if given a fair chance, provided they are limited to corn itself for food.

Turning to the other side of the relationship, we may say that the corn insects exhibit no structural adaptations to their life on the corn plant—no structures, that is to say, which fit them any better to live and feed on corn than on any one of many other kinds of vegetation. This was, of course, to be expected of the great list of insects which find in corn only one element of a various food, and that not necessarily the most important; but it seems equally true of those which, like the corn root-worm or the corn root-aphis, live on it by strong preference, if not by absolute necessity.

Aphis maidiradicis, the so-called corn root-aphis, is not especially different in adaptive characters from the other root-lice generally, and it lives, indeed, in early spring on plants extremely unlike corn. Finding its first food on smartweed (Polygonum) and on the field grasses (Setaria, Panicum, etc.), it is scarcely more than a piece of good fortune for it and for its attendant ants if the ground in which it hatches is sometimes planted to corn, in which it finds a more sustained and generous food-supply than in the comparatively small, dry and slow-growing plants to which it would otherwise be restricted.

The larva of *Diabrotica longicornis*, usually known as the corn root-worm, is, of course, well constructed to burrow young corn roots, but it differs from related Diabrotica larvæ in no way that I know of to suggest a special adaptation to this operation except in the mere matter of size. If it were larger it would probably eat the roots entire, as does the closely related and very similar larva of *D. 12-punctata*. Indeed, there is some reason to believe that *D. longicornis* may breed in large swamp grasses, since the beetle has been found abundant in New Brunswick in situations where it is difficult to suppose that it originated in fields of corn and where such grasses are extremely common. Even the special corn insects seem, in short, structurally adapted to much more general conditions than those supplied by the corn plant alone, and if they are restricted largely or wholly to this plant for food, this seems due to other conditions than those supplied by special structural adaptations.

In short, in the entomological ecology of the corn plant we see nothing whatever of that nice fitting of one thing to another, specialization answering to specialization, either on the insect side or on that of the plant, which we sometimes find illustrated in the relations of plants and insects. The system of relations existing in the corn field seems simple, general and primitive, on the whole, like that which doubtless originally obtained between plants in general and insects in general in the early stages of their association.

Such adaptations to corn as we get glimpses of are almost without exception adaptations to considerable groups of food plants, in which corn is included—some of these groups select and definite, like the families of the grasses and the sedges to which the chinch-bug is strictly limited, and others large and vague, like the almost unlimited food resources of the larvæ of Lachnosterna and Cyclocephala under ground. These are evidently adaptations established without any reference to corn as a food plant, most of them very likely long before it became an inhabitant of our region, and applying to corn simply because of its resemblance, as food for insects, to certain groups of plants already native here.

Entomological Ecology of Corn and the Strawberry

Corn being, in fact, an exotic or intrusive plant which seems to have brought none, or at most but one,[1] of its native insects with it into its new

[1] *Diabrotica longicornis* Say.

environment, it will be profitable to compare the entomological ecology of this introduced but long-established and widely cultivated plant with that of some native species which is also generally and, in some districts, extensively grown.

We may take for this purpose the strawberry plant, whose insect visitants and injuries I studied carefully several years ago. About fifty insects species are now listed as injurious to the strawberry and about twenty of these also infest corn. Two fifths of the known strawberry insects are thus so little specialized to that food that they feed on other plants as widely removed from the strawberry as is Indian corn. On the other hand, six species, all native, are found, so far as known, only, or almost wholly, on the strawberry, at least in that stage in which they are most injurious to that plant. These are the strawberry slug (*Emphytus maculatus*); the strawberry leaf-roller (*Phoxopteris comptana*), occasionally abundant on blackberry and raspberry, to which it spreads from infested strawberry plants adjacent; two of the strawberry root-worms—the larvæ of *Typophorus aterrimus* and of *Scelodonta nebulosus;* the strawberry crown-borer (*Tyloderma fragariæ*); and the strawberry aphis (*Aphis forbesi*).

Not even one of this considerable list exhibits, so far as I can see, any special structural adaptation to life on the *strawberry* plant. The two root-worms mentioned, for example, are no better fitted to feed on strawberry roots than is a third strawberry root-worm—the larva of *Colaspis brunnea* which lives on the roots of corn and timothy also. *Emphytus maculatus* might feed, for all the structural peculiarities which one can see, on the leaves of roses as well as does the common slug or false-worm of those shrubs, and so of the others of the list. Even the strawberry crown-borer, which lives in all stages solely on that plant, might, so far as structure and life history are concerned, feed and develop in any other thick-rooted perennial. The difference seems to be one of habit or preference solely, and not of structural adaptation.

Our impressions of the extent, nicety and frequency with which insects and plants are mutually adapted are indeed commonly much exaggerated, owing to the fact that our attention is especially drawn to notable cases of curious, precise or particularly advantageous adjustments between organisms, while no general study is made of the entire system of relations obtaining between all the members of an associate group, varying widely, as these do, in respect to the intimacy, importance and exclusiveness of the association. For this same reason in part, we ordinarily have no accurate idea of the relative frequency and primacy of structural, or static, adaptations—particularly obvious, especially interesting, and seemingly ingenious as they often are—and of those more obcure adaptations of preference, behavior, habit and the like, which, taken together, we may call dynamic.

Classification of Adaptations to Food

A plant-insect group—a group, that is, composed of a plant and its insect visitants—is not in fact usually marked, either as a whole or in any of its several parts, by the presence of adaptive structures special to that group. The structural adaptations of insects are as a rule much too broadly shaped to fit them closely to any one plant, and where such a fitting is found, it is clearly due to some other than the structural factor. Such facts bring us to a consideration of the whole subject of the variations and classification of the adaptations of insects to their food resources.

These adaptations may be classed as structural, physiological, psychological, synethic,[2] local, biographical and numerical. All structural adaptations are, of course, physiological in a sense, but I use the word physiological, as a matter of convenience, for functional adaptations not based on obvious structural peculiarities, as where an insect equally capable of feeding on the sap of two plants and readily availing itself of either, nevertheless thrives and multiplies better on one than on the other, the adaptation being evidently digestive or assimilative rather than obviously structural. The San José scale, for example, feeds readily on a great variety of trees and shrubs, on some of which it thrives poorly and spreads but little, while on others it multiplies enormously and spreads with great rapidity. The word psychological may be applied to cases of apparent choice or evident inclination, as between the various available food plants of the environment. Those fixed peculiarities of habit or behavior which adapt an insect to one food plant or class of food plants rather than to another we may call synethic adaptations, in the absence of any existing word applicable in this sense; local adaptations are those in which the usual haunts and places of resort of an insect species, however determined, bring it into common contact with an available food plant, the frequency of this contact being quite independent of the degree of the fitness of such plant for its food; biographical adaptations are those based on a correspondence between the life history of the insect and its organic food supply, such that the latter shall always be accessible in sufficient quantity to meet the varying needs of the dependent insect at the various stages of its growth; and numerical adaptations are the consequence of such an adjustment of the rate of insect multiplication to the plants or animals of its food that only the unessential surplus of this food shall be appropriated, its maximum essential product being left undiminished.

These several classes of adaptations limit each other variously, the most desirable food of an insect being that which is found within the area common to all of them. That is, the most important food plants of a vegetarian species will be those which are well within its structural capacities of discovery, access and appropriation; within its physiologi-

[2] Adaptations of habit.

cal powers of easy digestion and profitable assimilation; and within its habitual range and location; and which are consistent with its usual preferences and habits of action, and are well adapted to furnish continuously amounts of food answering to its varying necessities during the different stages of its life.

Advantages of Biographical Adaptation

It is obviously to the advantage of any insect species that it shall have its largest possible food supply coincident with its own largest demand for food—that is, at the climax of its period of growth. In a species restricted to one annual food plant the most favorable relation will usually be that in which the life history of the plant and that of the insect coincide, the egg-laying period of the one corresponding to the seeding period of the other, the hatching of the insect being virtually simultaneous with the germinating period of the plant, and the period of most rapid growth being coincident in both. This kind of adaptation is well illustrated by the life histories of *Diabrotica longicornis* and the corn plant. This beetle lays its eggs in fall when the ear is maturing, and the larvæ hatch in spring when the corn plant is young and growing slowly, and they feed on the roots during the entire growing season of the plant. It is evident that such a well-adjusted insect will have an advantage, other things being equal, over a poorly adjusted competitor for food from the same plant, since it will be able, as a rule, to leave a more vigorous and abundant progeny; and similarly, any part of a species which, by aberration of life history, may come to be poorly adjusted to its food plant, will suffer as a consequence in comparison with the normal members of the species, with the result that these biographical characters of the insect will tend to become permanent and characteristic in the same sense in which its structural characters are.

It should be noticed also that such an adjustment is an advantage to the host plant as well as to the dependent insect, since it distributes the depredations of the latter in a way to make them relatively slight when but little injury can be borne, and concentrates them, on the other hand, where the largest injury can be supported with the least serious consequences. Such a well-adjusted insect will get the maximum amount of food with the minimum injury to the plant, and such a plant-insect pair will have a competitive advantage over a poorly adjusted pair in which a greater injury is done to the plant than is necessary to the maintenance of the insect.

The same reasoning applies and the same rule holds good for species with a more heterogeneous food, except that in respect to them we must substitute for the single plant the entire group of plants to which the insect resorts for food. At this point, however, the facts become too complicated for successful analysis, especially in view of the difference of abundance from year to year of the plants of a considerable list and the effects on the food supply of variable competitions among the various species resorting to it. It may be said in general terms, however, that when the life history of a food plant or the common history of a group of such plants exhibits sufficiently constant characters to serve as an adaptive matrix, an adaptation to it of the life history of those insects strictly or mainly dependent on it for food is more or less likely to follow.

Mutual Biographical Adjustments of Competitors

An example of the competitive relations into which corn insects of widely different character, origin, habit and life history may be brought by their dependence on the same food plant may be found in *Diabrotica longicornis* and *Aphis maidiradicis*. Both pass the winter as eggs in the earth of the corn field, the aphis hatching sooner than the root-worm and developing two or more of its short-lived generations before the Diabrotica larva is out of the egg, gaining thus the advantage of an earlier attack in greater numbers. It is also able to take much more rapid possession of a field of corn because of its command of the services of ants in finding its way to the roots of the plants which the tiny and feeble Diabrotica larva must search out for itself.

Later the root-aphis gives origin to young, many of which acquire wings and may thus disperse as their local attack upon the plant becomes unduly heavy, while the root-worm must take its chances for the year in the field where the eggs were left the previous fall. The aphis feeds at first on the sap of young weeds common in spring in all cultivated fields, and may thus save itself even though the ground is planted to wheat, or oats, an event which causes the death by starvation of every root-worm hatching from the egg.

In respect to rate of multiplication, the root-aphis has of course a truly enormous advantage as compared with the corn root-worm, and yet, notwithstanding all these facts favorable to the aphis, its injuries to corn in Illinois are seemingly no greater than those done by the corn root-worm. This is due partly to the fact that, through the winged members of the early generations, the percentage of which increases as conditions become locally less favorable, the aphis largely leaves the field in which it originally started and early breaks the force of its attack by a general distribution of it. The depredations of the root-worm, on the other hand, increase with the growth of the insect until about September first, and increase also at a rapid rate from year to year in a field kept continuously in corn. It follows as a consequence that the principal damage by *Aphis maidiradicis* is done to the corn while it is young, and that by Diabrotica to the well-grown plant.

This serial order of injuries to the corn plant, due to the relation of the life histories and rates of multiplication of these two competing insects, is an advantage to both of them and, indeed, to all three, corn included, since the plant would be more seriously injured or more certainly destroyed if both its insect enemies attacked it together than it is where their attacks are made successively. Competitors for food from a living plant find it to their advantage, and to that of the plant they feed upon, to avoid a simultaneous competition ; and such a plant-insect group would, of course, prevail, other things being equal, over a competing group not so adjusted. Natural selection tends, no doubt, to establish these mutually advantageous relations between a plant and its constant insect visitants. With respect to these two corn insects, however, it must be admitted that no proof is apparent that such adaptation of life histories and habits as we here see is due to anything more than an accidental collocation of species whose significant peculiarities were already established when they came together.

A similar but more striking example of a serial succession of injuries to the same plant is to be found among the strawberry insects, as I showed several years ago.[3] Three coleopterous larvæ belonging to the same family (Chrysomelidæ) but to different genera (Colaspis, Graphops and Typophorus), and to species native in the United States, are all so closely adapted to underground life and to the root-feeding habit that they are distinguishable from one another only by rather slight and inconspicuous characters. They are often associated in large numbers in the same fields, living wholly on the roots of strawberry plants, which they affect in an identical manner, so that from the appearance of the injury itself one could not possibly tell which of the three species was present in the field. One of these root-worms, the Colaspis larva, feeds also on the roots of other plants, especially on those of timothy and corn, but the other two larvæ have been found only among strawberry roots. They seem thus to be strict competitors for food from the same part of the same plant, and as their locomotive capacity is poor, they are unable to avoid one another's company by migration under ground.

The strawberry plant, however, grows continuously throughout the season, and each of these three insects, having a short larval period, feeds on strawberry roots for only a part of this growing season. It is an interesting and striking fact that the life histories of the three competing insects are so related that the larvæ do not infest the plant at the same time, but follow one another in close succession, beginning early in May and ending late in fall. The first of the species, the Colaspis larva, feeds from about May to the end of June, the Typophorus larva follows in July and August, and the Graphops larva begins in August and continues until fall.

Consistently with this difference, the species concerned hibernate in different stages of development—Colaspis apparently as an egg, Typophorus undoubtedly as an adult, and Graphops as a larva in its subterranean cell, from which adults emerge the following June to lay their eggs in July. With such a distribution of their attack, each of these three species is able to maintain itself on the strawberry in numbers as

[3] "On the Life Histories and Immature Stages of Three Eumolpini," *Psyche*, Vol. 4, Nos. 117-118, January-February, 1884 ; and No. 121, May, 1884.

large as would be possible for all three taken together if they made their assault on the plant simultaneously. The advantage to both plant and insects of this adjustment of life histories—if one may call it such—is obvious at once.

That some actual adjustment of larval periods has here been made is rendered somewhat more probable by the fact that a closely related species of Graphops which infests the wild primrose (*Œnothera biennis*) in southern Illinois, has a life history different from that of the species which breeds in the strawberry—hibernating as an adult, like Typophorus, and not as larva, like the strawberry species of its own genus.

Maladjustment of Competitions

The corn plant is in greater danger from insect ravage during the first month of its life than at any later time. This is because it offers then a comparatively scanty supply of food, so that a small number of insects may work great destruction; because the single small plant is much more easily killed than a larger one; and because a larger number of active rival insects infest corn when it is young than at any other time, some of them beginning with the recently planted or just sprouting seed. The young roots, the underground part of the stalk, the stalk above ground, and the leaves, both before and after they unfold, are all liable to infestation by several species at the same time. The seed is injured by the wireworms, the seed-maggot, the Sciara larva and the larva of *Systena blanda;* the roots, by the wireworms, the root-aphis, the corn root-worms, and the white-grubs; the stalk under ground, by the wireworms, the root-aphis, the southern corn root-worm, and the bill-bugs; the stalk above ground, by the bill-bugs, the cutworms, the web-worms, the stalk-borers, and the army-worm—sometimes by the chinch-bug also; and the leaves, by the bill-bugs, the web-worms, the cutworms, the army-worm and the first generation of the ear-worm.

This concentration of injury upon the corn when it is young is a case of maladaptation, since the plant has least to offer when it is most heavily drawn upon. It will be noticed, however, that this early spring attack is mainly delivered by insects which come into corn from some other vegetation, chiefly from grass, and whose occurrence in the corn field is scarcely more than accidental. The motive to an adjustment of habits and life histories to the capacities of the plant is therefore virtually wanting, and seems at any rate impossible, owing to the variability and inconstancy of the several factors involved.

Conclusion

From the foregoing it will be seen that the corn plant is not only an exotic in its origin, but that, aside from its relation to man, it still remains an unnaturalized foreigner, not sufficiently adapted to our conditions to survive without the constant supervision of a guardian and the services of a nurse. The corn field contains an artificial "association" persistently maintained by human agency in the midst of a hostile environment to which it would promptly succumb if left to itself, and as such it would seem to offer to the ecologist all the advantages of a vast and long-continued experiment, by a study of whose results he may learn something of the manner in which ecological relations may be affected when a plant takes advantage of a single favoring condition to push its way into a territory foreign to its former habits.

This corn plant, at least, which has certainly lived in our territory under the care of man for several centuries, and perhaps for some millenniums, has even yet no specialized friends active in its service, and no structurally adapted enemies enlisted against it, such specializations of injurious relationship as one detects being clearly due to other than structural differentiations. During all this long period, it has been widely and steadily forced into a strange ecological system which has nevertheless scarcely yielded to it at any point. It has produced, it is true, by its enormous multiplication and extension, a profound effect on the numbers and distribution of some insect species, reducing the area of multiplication for several, which, like the cutworms and the army-worm, formerly bred in the turf of our native prairies but can not breed in fields of corn; and immensely extending the range and increasing the number of others which have found in this plant a better and far more abundant food supply than that originally available to them. Insect species which, like *Diabrotica longicornis* and *Aphis maidiradicis*, were almost unknown fifty years ago within our territory, have now, through their increase in corn fields, arisen to the rank of dominant species.

But the few discernible insect adaptations to the offerings of the corn plant are physiological, psychological, synethic and biographical, and apparently not structural at all. Slight and seemingly incipient as they are, we have no sufficient reason to conclude that they are recent results of the association of the corn plant with the insect; both parties of the association may have been substantially what they now are when they first found each other, and such mutual fitness as they exhibit may be merely like that of angular stones shaken together in a box until like surfaces seem to cohere, simply because in this position the fragments can not readily be shaken apart.

We may also derive from this discussion support for the idea that adaptations of insects to their environment are largely, and often primarily, psychological—that they are often, in the first instance, specializations of preference or choice, or, as we may perhaps more safely say, of tropic reaction. Species which would otherwise compete with each other, with disadvantageous consequences to each, escape these disadvantages by acquiring, one or both, different habits of reaction, under the influence of which they separate, one going for its principal food to the corn plant, for example, and the other continuing on the strawberry, although structurally each remains equally fit to feed on either. Physiological, or even structural, adaptation may follow the psychological, but as secondary to it. This is only saying in other words that the central nervous system, on whose special functioning peculiarities of habit depend, is subject, like any other, to adaptive variations, and that these variations may either follow and reinforce those of some other organ or organs tending to the same end, or that they may arise independently of any other; and this is merely extending to insects a generalization very obvious with respect to man, finding warrant for the extension, as we do, in the facts disclosed by an examination of the general economy of insect life.

NOTE.—Changes of nomenclature since this paper was written call for the following data of synonymy:

Pp. 449, 453, 456.

Aphis maidiradicis = *Anuraphis maidi-radicis* (Forbes).
Lachnosterna = *Phyllophaga*.

Pp. 450, 454, 455.

Emphytus maculatus = *Empria maculata* (Norton).
Phoxopteris comptana = *Ancylis comptana* (Fröhl.).
Typophorus aterrimus = *Paria canella* (Fab.).
Scelodonta nebulosus = *Graphops nebulosus* (Lec.).