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**Biometeorological Research
in
Canadian Forest
Entomology - A Review**

by

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FORESTRY BRANCH

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A RETROSPECTIVE SURVEY OF ORIGINAL AIMS AND METHODS

A long-term program to investigate the effects of weather on forest insects in Canada was first organized in 1945. It began with a series of biometeorological studies of the spruce budworm in Canadian forests (Wellington, 1948, 1949,a,b, 1954b; Wellington and Henson, 1947). During the next 4 years, principles derived from these investigations were used to develop the broader program required for work on other kinds of forest insects. And this expanded program, with added refinements, is still operating today.

When we were planning the first outline for this program, we rejected the most common pre-war methods of determining weather's influence on insects. Most, though by no means all, of the earlier workers had approached their problems by using the methods of classical climatology, and by concentrating on insect development or mortality, or on some isolated biological event, such as emergence. We felt that this approach was too limited, because it ignored one of the most obvious features of weather and of living insects; the continual behavioral changes in both systems.

We adopted this point of view because we believed that there was a useful analogy between weather and living organisms that had never been exploited before. Viewed as systems, both weather and organisms have properties in common. Both are dynamic, not static. They also may form populations of sorts, that undergo changes in distribution and abundance. They each include pervasive historical elements that make their present (and their future) dependent on their past. And their fate -- i.e., extinction -- is both certain and uncertain, in that the sequence of events leading to it may be unpredictable if very narrow limits of accuracy are imposed on the predictive statements.

We can expect only limited success if we attempt to study the impact of one dynamic system on another by using static methods. Nor can we neglect their histories when we try to understand their present relationship or predict its outcome. But the techniques of classical climatology have always minimized the dynamic aspects of weather, often to the point of obscuring the historical element. Similarly, on the biological side, concentrating on development and mortality often has obscured the fact that proper development and ultimate survival both may depend entirely on correct behavior at critical moments. To avoid these pitfalls, we preferred to define our problems in dynamic terms. Thus we approached each problem with techniques drawn from synoptic meteorology, instead of classical climatology, and with methods designed to reveal changes in insect behavior and activity in different environments.

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We certainly did not, and do not, deride studies of development per se. But we preferred first to re-examine the whole field with our new approach, so that we could return finally to studies of development or survival with a sounder knowledge of the impact of weather on all the biological processes that may lead to success or failure in a changing environment. Our first task, however, was to divide the field into more tractable sub-fields. We did this by alternating between problems involving individuals and those concerning populations, on the biological side, and by relating events in the microenvironment to larger-scale weather processes, on the meteorological side. Each aspect was approached by concurrent laboratory and field investigations, in which techniques and attitudes developed in the laboratory were fully exploited in the field. In other words, we tended to view the field as an outdoor laboratory whenever and wherever possible. The results of these early investigations have all been published, and we need not go into their details here (Green, 1954a,b,c; Henson, 1951; Sullivan and Wellington, 1953; Wellington, 1950a,b; Wellington, Sullivan and Green, 1951). Only a few generalities require notice now.

At the level of the individual, for example, we studied the microenvironment, not by earlier methods of recording the march of air temperature or other variables at different levels, but by taking our records where each stage of the insect spent its time. These records were related to the different types of weather systems that were present then. In addition, wherever possible we made simultaneous observations of the microenvironment and of how the insects spent their time in two adjacent, but extreme habitats.

This field method allowed us to assess the impact of weather on the success of individuals with different ecological histories and requirements. But it also helped us to record annual changes in the frequencies of favorable or unfavorable types of weather systems within the region during critical periods of the insect's life cycle. Accompanied or preceded by behavioral and other biological studies in the laboratory, this approach proved to be a very powerful analytical tool. It was first used in the spruce-budworm studies (Henson, 1951; Shepherd, 1958-59; Wellington, 1948, 1954b; Wellington and Henson, 1947), and variations of it have appeared many times since (Green, 1962a,b, 1965; Green and de Freitas, 1955; Henson, 1958, 1962; Stark, 1959a,b; Sullivan, 1959, 1960, 1961a,b, 1965; Sullivan and Wallace, 1965; Turnock, 1955; Turnock and Ives, 1962; Wallace and Sullivan, 1963, 1966; Wellington, 1955, 1957b, 1964; Wellington, Sullivan and Henson, 1954).

At the population level, we preferred at first to consider local populations separately from regional or subcontinental groups of populations encompassing much of the range of a species. For example, in the spruce-budworm studies it proved to be most convenient to move directly from studies of individuals to an historical treatment of the constellation of populations occupying northeastern North America (Wellington, 1952, 1954a,b; Wellington et al., 1950). These were synoptic climatological studies that used available U.S. Weather Bureau records of fluctuations in the routes and numbers of major weather systems. The results called for confirmation by a different approach, however, and in the Maritime Provinces Greenbank (1956-57) made the first tests by observing a few populations in an area small enough to be influenced by weather systems of only regional size; i.e., ordinary cyclonic storms or portions of high-pressure cells. In Alberta, Shepherd (1958-59) also confirmed the results by studying the behavior, development, and survival of individuals in extreme habitats before comparing the course of local outbreaks with changes in the sub-regional climatic pattern.

Approaches to the study of one or a few local populations have been extremely varied, but they soon began to demand inclusion of the final element required for successful biometeorological analysis of mesoscale, as opposed to macro- or micro-scale systems: the influence of the surrounding, as well as strictly local, terrain on passing weather systems. This concept was first exploited during a study of the overwintering mortality of the lodgepole needle miner in the Bow Valley of Banff National Park (Henson, Stark and Wellington, 1954; Stark, 1959a, b). By taking into account the influence of high mountain barriers and complex pass system on the speeds of entry, passage, and exit of warm and cold air masses during mid-winter, we were

able to show that annual and local changes in the amounts of mortality at valley bottom and on the slopes were linked with changes in the frequency with which Pacific and Arctic air masses invaded the region, because these air masses responded differently to the Bow Valley terrain, and so produced different vertical distributions of minimum temperatures.

In population ecology, however, terrain influences on meso-scale weather can be exploited in methodological as well as interpretive ways. By exploiting the visual evidence of these influences -- that is, the stable or recurrent cloud patterns that result from terrain effects -- one can improve the design and implementation of any ecological study, especially one requiring deep involvement in population dynamics. This application of terrain influences was first developed during studies of the western tent caterpillar on southern Vancouver Island (Wellington, 1957a,b, 1958, 1960b, 1962, 1964, 1965b). In this population study, the boundaries of the stable cloud patterns that appeared over hills and ridges when westerly airflow prevailed were mapped and used to distinguish areas with different local climates. The mosaic of warm-dry and cool-moist local climates that could be mapped by this method proved to be so realistic that networks of meteorological instruments were not required to record climatic data during the study. Even without instruments, it was still possible to determine the effects of weather on the annual changes in the distribution and abundance of the insect (Wellington, 1965b).

SOME METHODS APPLIED TO RECENT REGIONAL PROBLEMS

We turn now to more detailed examples of the ways in which we apply the methods outlined in the previous section. Our first example is drawn from work on the white pine weevil in Ontario (Belyea and Sullivan, 1956; Sullivan, 1953, 1959-61b).

THE WHITE PINE WEEVIL: For many years the white pine weevil has seriously interfered with the growing of white pine in eastern North America. Casual observations long ago indicated that white pine was damaged much less in shade than in the open. Consequently, there were many attempts to manipulate the stand climates of plantations by growing pine with various mixtures of other trees. Many of these attempts failed, however, because no one really understood how shade deters weevils. Ultimately, therefore, planting of white pine as a plantation species was largely abandoned because the trees were damaged so frequently.

Our work began with studies of weevil behavior and development in the microenvironments of open-growing stands of white pine. In contrast to some of the colonial insects we had studied previously (Green, 1954a,c; Green and De Freitas, 1955; Sullivan and Wellington, 1953; Wellington, 1952; Wellington, Sullivan and Henson, 1954), the adult weevils were solitary feeders. Thus the feeding, oviposition, or flight of individuals could be correlated with microclimatic and ambient conditions in the field. Fitting 2nd-, 3rd- and 4th-degree polynomials to the accumulated data showed that temperature, solar radiation, and atmospheric moisture had important effects on weevil activity and development. We found, however, that these variables sometimes had combined effects that had to be taken into account when we wanted to predict changes in activity. Accordingly, we constructed activity isopleths that showed the zones in which interactions occurred, and these charts gave us a basis for defining the probability of attack in mixed (i.e., shaded) stands (Sullivan, 1959, 1960). We moved then to one of these shaded stands to record pertinent weather factors under different aspen-canopy densities throughout the critical season of weevil activity, and to calculate the maximum level of activity that could be expected from the information gained in the open-growing stands.

Marked changes in the microclimates of shaded habitats occur as the foliage of an aspen overstory develops, because insolation is reduced in proportion to the amount of foliage growth in the canopy. Such changes affect the seasonal trend of temperature differences between the bark of overtopped and exposed white-pine leaders, as recorded on relatively clear, calm days from mid-April to late June. Before the aspen leaves open, increasing solar elevation and radiant heating bring the temperatures

of overtopped leaders closer and closer to those of the fully exposed leaders of pines growing in the open. When the leaves of the aspen overstory begin to appear in early May, however, bark temperatures of the overtopped stems begin to lag behind those in the open. In June, when the overstory canopy is fully developed, the overtopped white-pine stems may be as much as 11°C below comparable stems in exposed stands.

Only a very low level of weevil activity can be expected in such shaded places, and effective activity is likely to be eliminated entirely when the microenvironmental effects combine with the effects of the growth characteristics of white-pine stems on weevil behavior. Weevils show a preference for stems that have upper diameters greater than 6 mm and bark thicker than 1.5 mm, but stems with such characteristics rarely develop in the most shaded stands. Consequently, in many parts of a properly shaded stand, low levels of activity combined with weak responses to the type of pine stem available greatly reduce the number of eggs a female will lay. If too few eggs are deposited in a stem, there are not enough larvae to form the ring-like feeding aggregation that is so essential for the survival and development of young larvae in the resinous leader of a pine tree (Sullivan, 1961b).

These studies were done before we had portable sources of electricity, so that we could not obtain continuous records of bark temperatures in all the stands in which we worked. Consequently, we determined the relationship between bark temperatures and the temperatures of unshielded and blackened bimetals of ordinary thermographs (Sullivan, 1961b; Wellington, 1949c, 1950a). Temperatures recorded by such thermographs closely approximated actual bark temperatures of white-pine leaders, and this greatly facilitated our work.

Measurements of light in young white-pine understories showed that weevil damage is negligible if clear-day insolation is reduced 60 to 80 % by a fully developed overstory canopy (e.g., one that consists of red oak, closely spaced aspen, or mixed hardwoods and softwoods). When the canopy consists of widely spaced aspen, insolation is reduced only 25 to 50 %, and weevil damage then may be appreciable. (In such stands, however, it may still be only some 10 % of the damage encountered on trees in the open).

In order to test these results, we had to introduce weevils into some of the more extreme habitats so that we could observe behavior and survival. Weevils liberated in heavily shaded areas left before they had done more than nominal damage. Leader vigor and microclimate varied in relation to the patchy distribution of shade, however, so that some of the more exposed pines in a mixed stand provided the weevils with conditions closer to those in open-growing, fully exposed pine stands. If the weevils found such trees, they attacked.

The shade factor, therefore, certainly can be used as a criterion for determining the degree of protection afforded understory pine, even though earlier, uncritical attempts to exploit it failed. Establishing and maintaining the necessary amount of shade when young pines are most susceptible to attack is mainly a silvicultural problem. But it is now possible to approach it with more exact information concerning what conditions must be created and when they are required. Two extensive silvicultural programs currently are testing our conclusions to determine what further refinements may be necessary. Meanwhile, the shade factor determined by this study is being used as a guide in the establishment of most of our new white-pine plantations. In addition, the defined physical characteristics of white-pine leaders that influence weevil attack are currently being used by tree breeders in their attempts to create weevil-resistant hybrids.

THE EUROPEAN PINE SHOOT MOTH AND THE EUROPEAN PINE SAWFLY: Our next examples are drawn from work on the European pine shoot moth and the European pine sawfly in Ontario (Campbell and Sullivan, 1963; Green, 1962a,b, 1965; Green, Baldwin and Sullivan, 1957; Green and Pointing, 1962; Lyons, 1964; Pointing and Green, 1962; Sullivan, 1965; Sullivan and Wallace, 1965; Wallace and Sullivan, 1963, 1966). These insects cause extensive damage to pine plantations in their native lands. Both species have appeared recently in Canada, and as so often happens with introduced insects,

they seem to have unique population characteristics, possibly associated with initial freedom from their original parasites and predators. There are other elements besides predation and parasitism, however, that may affect the success of introduced insects. For example, availability of host material, adaptation to new hosts, and ability to withstand climatic extremes also may be involved. In Ontario, therefore, both species are the joint concern of entomologists and foresters, because of the pine plantations on reclaimed agricultural lands in the south, and the natural stands of pines that extend into the cooler northern parts of the province. Teams of investigators have been formed to examine the bionimics of the insects in their new environment and to elucidate their population dynamics as a prerequisite to effective control. Biometeorologists on each team have been concerned with detailed studies of behavior, activity, and development in relation to environmental factors.

We thought that the effect of temperature on the rate of development of shoot-moth pupae might have an important effect on fecundity. To obtain a reliable measure of developmental rate during variable weather, we re-assessed the well-known degree-day technique (Glenn, 1922, 1931; Shelford, 1927; Simpson, 1903). Although thermal sums, developmental units, and degree-days are useful approximations of the probable dates of appearance of the various stages of an insect, they can be misleading. What we required was a method for adjusting Stevenson Screen temperatures to equivalent bud temperatures to provide parameters closer to the true temperature threshold for development and the true thermal constant, respectively. When this adjustment was obtained, parameters derived from laboratory experiments were used in equations to calculate development of pupae at varying temperatures. When the final results were applied to field situations, the rate of development we could predict very closely approximated that which actually occurred.

Information on the movements of insects is important in any study of population dynamics, and it must be acquired first through an understanding of the effects of physical factors on flight behavior, so that the mechanics of transport may be adequately assessed and interpreted in terms of distribution and abundance. For gravid females to take part in a dispersive flight, for example, environmental factors must permit or even initiate flight, and such factors must be identified.

Shoot-moth flight commences as overhead light intensities drop below 1000 ft-c, reaches a peak near 125 ft-c, and ceases in full darkness. There is no flight below 12°C; the optimum temperature for flight activity is 22°C, and the activity declines again above that temperature. In Ontario, warm overcast evenings associated with air masses from the Gulf of Mexico, the Great Basin, or parts of the Pacific Ocean are most favorable for mating and for flight. The summer weather of arctic or polar continental air masses tends to restrict flight and reduce mating.

No completely satisfactory method of tagging, releasing, and recapturing large numbers of adults in the field was available to obtain quantitative data on the dispersal range of the moths. Consequently, several techniques that would provide information on dispersal tendencies had to be employed instead. For example, radioactive tagging techniques permitted observation of female dispersal throughout restricted areas and allowed the observer to make inferences concerning the possibility of more widespread dispersal (Green, Baldwin and Sullivan, 1957; Green and Poin-ting, 1962).

We had to return to the laboratory, however, to supplement field data on dispersal. A flight mill similar to one described by Hocking (1953) was used to determine the intrinsic range and speed of flight. With this technique we found that large, egg-laden females could make non-stop flights equivalent to some 4 miles of travel through still air. In the field, we had already observed that such females frequently rose well above the tree tops before they began to fly down-wind. Therefore, in winds of 8 to 12 mph, mated and gravid females could easily travel 10 to 15 miles in a single flight. By combining these results with others concerning the dispersal of larvae in the field, we concluded that flight by mated females is the major factor in the natural dispersal of shoot moths in Ontario. Similar studies of the pine sawfly also have shown that female flight is the main factor in its regional spread.

Our preliminary surveys also suggested that both the shoot moth and the sawfly often would be exposed to the low winter temperatures that occur in many parts of Ontario. In contrast to insects that hibernate in well-insulated places, these species overwinter where insulation by snow is, at best, sporadic, so that they must be able to tolerate periods of extreme cold and rapid temperature changes if they are to survive. It was necessary, therefore, to determine the extent to which low temperature might limit their distribution and abundance.

Salt (1950, 1953, 1955, 1957, 1958a,b, 1961a,b, 1964) has contributed a wealth of excellent and fundamental information on the freezing process in insects. Questions that concerned us were: at what temperatures will the overwintering stages succumb? Are Ontario populations becoming more cold-hardy and thus capable of extending their ranges northward? What duration of exposure to cold affects survival? How much protection is afforded by snow cover? Can we use screen temperatures to predict mortality? To answer these questions, we had to determine temperatures at which individuals of both species froze. And to do this, we used a modification of earlier techniques that allowed us to observe directly the freezing process in groups of eggs or larvae (Sullivan and Green, 1964); thus we did not have to record the freezing of a series of isolated individuals by the usual and very laborious contact methods (Green, 1962b; Robinson, 1928; Salt, 1953).

In the shoot moth, we found no evidence of inherent differences in capacity to supercool among the different populations inhabiting different temperature zones. More cold-hardy races of this species thus do not seem to be developing. But shoot-moth larvae and sawfly eggs both are capable of acclimating to low temperatures above lethal levels in such a way that their supercooling points shift to a significantly lower temperature (Green, 1962b; Sullivan, 1965). This ability sometimes will promote survival in natural populations.

When we subjected sawfly eggs from various European, Asian and Canadian populations to cold-hardiness tests, we found a range in cold-hardiness among specimens from 4 different countries. The Canadian population apparently has not yet achieved the degree of hardiness already possessed by Latvian populations, but it is harder than the other populations we tested. For example, exposure to a temperature of -32°C will kill some 22 % of the Latvian insects, 52 % of the Canadian ones, 71 % of a German population and 92 % of the Japanese insects. There is some evidence that some of the present Ontario populations of pine sawflies, in contrast to the pine shoot moths, are increasing their cold-hardiness in response to selective pressures from low winter temperatures. If this proves true, the Canadian stock may become as cold-hardy as the Latvian.

Studies of cold-hardiness have considerable value in attempts to assess the probable range of distribution of an insect. To make such assessments, we used standard climatological data published by the Canadian Meteorological Service. Monthly mean extreme-isotherm maps were prepared from the records of selected weather stations for the period, 1926-63. The lowest temperatures in northern Ontario occur in January, but the deepest southerly penetration of cold air occurs during February. Because of this difference between January and February, we used maps for both months in conjunction with freezing-point determinations to assess the probable northward spread of the shoot moth and the sawfly (Green, 1962b; Sullivan, 1965).

Whatever their acclimation level, larvae of the shoot moth cannot tolerate temperatures below -30°C . Therefore, the northern limit of the species in Ontario is not likely to extend for long beyond the line of the January -30° isotherm. The shoot moth thus should continue to be restricted to the pine plantations of southern Ontario. In contrast, we expect the sawfly to extend its range farther northward because of its tendency to increase in cold-hardiness. At present it is as far north as the -29° isotherm, and ordinary dispersal should carry it farther towards the -34° isotherm, which would match its present level of cold-hardiness. If selection for more cold-hardiness ultimately occurs, there is no reason why the insect should not penetrate as far as the -40° isotherm, which lies north of many of the present natural stands of red and jack-pine in Ontario. Even now, the insect in one place needs only a short flight northward to reach some of these stands.

Although such studies help to locate range boundaries and to assess mortality due to freezing within these boundaries, they demonstrate only one part of the process whereby an insect may adapt to a new environment. Within the established range, many other factors affect the abundance of a species, and these also must be considered in detail if we are ever to understand the dynamics of insect populations. In our studies (Green and Sullivan, unpublished; Wellington, 1957b, 1960a,b, 1962, 1964, 1965a,c) and more recently in those by W.R. Henson (unpublished), it has become increasingly evident that qualitative differences among individuals affect the success of whole populations.

Some of the qualitative differences observed in populations seem to contribute to regulation (although the situation may be complicated by changes in the habitat and by the effects of regional climatic changes on local climatic mosaics). In the shoot moth, for example, population models have shown that winter survival often is inversely proportional to summer survival (P.J. Pointing, unpublished). When there are optimum conditions for egg production, oviposition, hatching, and survival of the younger larvae, overwintering mortality tends to be greater than expected. Conversely, when overwintering mortality is severe, survival through the subsequent spring and summer and into the following generation often is better than expected. When we examine this situation more closely, we find that the adult female population consists of groups of individuals that differ markedly in weight and fecundity, and in the size of the eggs they produce. Some females produce a small number of eggs per unit weight, and others produce a larger number of smaller eggs. The small eggs produce larvae that are initially smaller than those that emerge from larger eggs; and this size differential persists throughout subsequent larval development, even in the presence of abundant food. The effect that such differences may have on shoot-moth population dynamics is now being investigated, and the results we obtain may very well interlock with those already available for the spruce budworm (Campbell, 1962) and the western tent caterpillar (Wellington, 1965a).

When we examine the European pine sawfly from this point of view, we find a more intimate linkage between the properties of the insect and the physical environment. Preliminary studies have shown that the interaction of temperature and photoperiod during growth and development may produce differences in the period spent in the cocoon, and these differences also are reflected in reproductive potential (Campbell and Sullivan, 1963; Sullivan and Wallace, 1965; Wallace and Sullivan, 1963). Females from cocoons spun in shaded, moderately cool places in the field frequently emerge much earlier in the season and have more mature eggs than females from cocoons spun in more exposed, warmer places. The females with smaller egg complements never use some of the fat-body content that would normally be devoted to egg production.

Laboratory studies also have revealed some of the ways in which the duration of diapause and morphogenesis depend upon temperature. The agreement between the estimated and observed durations of diapause is especially striking; the sequence of adult emergence in the field is what we would expect from laboratory results. But the same field data also have shown that the true course of morphogenesis is somewhat different from that indicated by laboratory observations; the process is completed in the field more rapidly than laboratory observations suggest. In the preliminary laboratory studies it seemed convenient to assume that eonymphal and pronymphal stages each involved single processes with single temperature responses, even though we recognized that the real situation must be more complicated than that. Now that we know we cannot use the first laboratory results to predict morphogenesis in the field, however, we will have to allow for the complexity that really exists when we plan further laboratory studies of morphogenesis, if we are to match the predictive value of the observations on diapause.

Even though we can make some predictions concerning the diapause of this sawfly, we still need more information on the role of photoperiod in the induction of diapause, and on the interaction of temperature and photoperiod in the regulation of seasonal development and diapause. When cocoons from larvae reared at 21°C with 0, 16, 20, and 24-hr photoperiods were taken to 10°C, the prepupae underwent a diapause of two to three weeks before morphogenesis, and finally emerged as adults 83-89 days after

spinning. In contrast, individuals reared in photoperiods of 4 to 15 hr at 21°C spent from 2 weeks to 2 years in prepupal diapause when their cocoons were held at 10°C. Studies now in progress should provide further information on the factors that prolong diapause so greatly, and on the effects such prolongation may have on the quality of natural populations.

CONCLUDING REMARKS: AN APPRAISAL AND A PROSPECT

We began this review with a retrospective consideration of the aims of our program as we saw them some 20 years ago. At that time we rejected most earlier approaches to biometeorological studies of insects because they seemed too narrow. We thought our approach would lead to more realistic results -- and we believe that it has. But the reader will have noticed the trend of the last few pages. There we were not speaking solely as biometeorologists concerned with insects. Instead, we had to mention other aspects of insect ecology and physiology not usually associated with the influence of weather; and in our present work, in fact, we have been trying to include aspects of insect nutrition and kindred subjects that really require a biochemical approach. It is clear that our original approach also was too narrow to handle the very complex real world of weather and living insects.

In all our studies, we have observed that insects, despite their armored exteriors, usually maintain enough flexibility to cope with their changing environment. After this glance at the past and at the present, what concerns us most is whether the armored exteriors of biometeorologists will be sufficiently flexible to cope with the approaching changes in their environment. There are many papers in the current literature that still employ the pre-war approaches we rejected. If armor is so rigid, can its wearer bend with the changes that are coming?

To make worth-while contributions in the future, we believe that a biometeorologist working with insects will have to concern himself with many more disciplines than we have to date. And to exploit these disciplines fully, we believe that he will have to turn to systems analysis and simulation studies with computers in order to attain the higher degrees of precision, realism, and completeness that the solution of future problems will demand. In prospect, therefore, the approach we have presented here will soon be as outmoded as its predecessors. We need not be dismayed by signs that the future will require a much broader approach. But dismayed or not, we will be challenged.

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Over the years spanned by this review there have been many colleagues intimately associated with the development and implementation of the program we have sketched so briefly here. In presenting this, we have been speaking for them as much as for ourselves. In such limited space, we have not been able to give details of all the contributions made to the program by D.K. Edwards, D.O. Greenbank, W.R. Henson, J.M. Powell, R.F. Shepherd, R.W. Stark and W.J. Turnock; but we want to acknowledge them here. We also want to thank P.J. Pointing for allowing us to refer to some unpublished data. And in particular, we want to thank M.L. Prebble for the strong support he gave to the program during the many years he was directly concerned with forest entomology in Canada.

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ABSTRACT. - This is a review of the methods and results of a large number of biometeorological studies during the last 20 years in Canada. The intensive biometeorological program developed for Canadian forest entomology just after World War II rejected generally accepted pre-war approaches to problems involving weather and insects, because they used classical climatological methods, and were concentrated on insect development and survival. Our initial approach emphasized instead the effects of weather on behavior and activity. Meteorological methods were derived mainly from synoptic meteorology and climatology. They included descriptions of events in the microenvironment in terms of air-mass weather, and techniques for determining annual or seasonal changes in the numbers and types of weather systems that passed over large and sparsely settled forested areas. Biological methods included simultaneous laboratory and field studies of insects in extreme situations. By exploiting these methods we have been able to return to the larger problems of the impact of weather on development and survival with sounder knowledge of biological and meteorological events in the microenvironment where insects live, and where they must act effectively if they are to survive and reproduce.

ZUSAMMENFASSUNG. - Die ist ein Bericht über die Methoden und Ergebnisse einer grossen Zahl biometeorologischer Untersuchungen in den letzten 20 Jahren in Canada. Das intensive biometeorologische Programm, dass in der Forstentomologie nach dem 2. Weltkrieg aufgestellt wurde, verwarf alle Vorkriegsmethoden, die der klassischen Klimatologie entstammten und sich auf die Entwicklung und das Überleben von Insekten konzentrierten. In dem neuen Programm konzentrierten sich die Untersuchungen auf das Verhalten und die Aktivität der Insekten. Die meteorologischen Methoden wurden von der synoptischen Meteorologie und Klimatologie übernommen. Dabei wurden Beschreibungen

gen der Ereignisse in der Mikro-Umwelt über Luftmassen und Verfahren zur Bestimmung der jährlichen und jahreszeitlichen Veränderungen nach Zahl und Art von Wetterabläufen über grossen und dünn besetzten Forstgebieten mit berücksichtigt. Die biologischen Untersuchungen erfolgten an Insekten unter extremen Bedingungen im Feld und Laboratorium gleichzeitig. Unter Ausnutzung dieser Methoden war es möglich die Hauptprobleme bei der Wirkung von Wetter auf die Entwicklung und das Überleben von Insekten in ihrer Mikro-Umwelt mit gut fundiertem meteorologischem und biologischem Wissen neu aufzugreifen.

RESUME. - On passe ici en revue les méthodes et les résultats d'un grand nombre de recherches effectuées au Canada durant ces 20 dernières années. Le programme biométéorologique développé par l'entomologie forestière canadienne après la deuxième guerre mondiale rejetait généralement les idées auparavant acceptées concernant les problèmes du temps et des insectes. En effet seules les méthodes classiques de la climatologie étaient utilisés et les recherches se concentraient sur le développement et l'existence des insectes. Notre méthode avec l'accent sur les effets du temps sur leur comportement et leur activité. Les méthodes météorologiques dérivait de la météorologie et de la climatologie synoptique. Elles comprenaient les descriptions des événements dans les micro-environs en termes de masses d'air des techniques permettant de déterminer les variations annuelles et saisonnières des nombres et types de systèmes climatiques qui avaient passé au dessus des grandes régions forestières peu peuplées. Notre méthode biologique étudie les insectes dans des conditions extrêmes tant en laboratoires que dans les conditions naturelles. Par cette méthode, on a pu revenir aux problèmes les plus importants, concernant l'influence du temps sur le développement et l'existence, par une meilleure connaissance des événements biologiques et météorologiques rignants dans les environs habités par les insectes.