



The field biology of *Camnula pellucida* Scud
by Paul W Riegert

A THESIS Submitted to the Graduate Committee In partial fulfillment of the requirements for the degree of Master of Science in Entomology
Montana State University
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Abstract:

The general behavior of insects is discussed in relation to the physical environmental factors, as well as the biological; and the probable influencing factors in the behavior of *Camnula pellucida* Scud, reviewed.

The work site, methods of observation and equipment used In the study of the behavior of this species are discussed and described In detail.

Population densities, within localized areas, may be correlated to the stage of morphological and sexual development, and to the activity of the insect.

Data are presented showing specific environmental factors such as temperature, humidity, light, and wind velocity, which were measured when such activities as 'start of movement', 'general movement', 'maximum movement', 'start of climbing', 'frenzied movement', 'heat torpor', 'movement stopped', and 'no activity' were noted for *C. pellucida*. Such activities can best be correlated to temperature.

Data presented indicate that the feeding response, in relation to the stage of development of the insect, seems to be largely dependent upon temperature; in that, as development increases, feeding occurs at increased temperature also.

Winds having average velocities over 2-3 and 5-6 m.p.h. appear to have interrupting effects on the feeding of nymphs and the flight of adults, respectively.

Observations on migrations of *C. pellucida* seem to indicate that although gregarious inertia and optical responses may keep a band migrating simultaneously, air and soil surface temperatures (within a range of 24.8-36.0 °C (76.6- 96.8 °F) and 25.5-44.2 °O (77.9-111.6 °F), respectively), a positive phototaxis and relative humidity may guide the grasshopper during migration bearing in mind its left-handed light-compass reaction to the sun and maintaining an angle of 30-110 degrees between the direction of migration and the position of the sun.

Field experiments, using crushed *Agropyron smithii* to evoke an olfactory stimulus-response reaction, showed that the reaction-time (and probably sensory receptivity of stimuli) is closely associated with development in that the higher instars had faster reaction-times.

Observations of their climbing habits disclosed that *pellucida* appeared to respond more actively to heat (thermotaxis and thermo-kinesis), while *Melanoplus bivittatus* Say. appeared to respond more pronouncedly to illumination (phototaxis and photokinesis).

The color changes, from darker to lighter pigmentation of the exoskeleton of *C. pellucida*. as development progresses, may be due to Increased temperature as the season advances.

Partial or complete damage of the flight appendages of the females is caused by the males when

hyperexcited during sexual stimulation.

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PAUL W. RIEGERT

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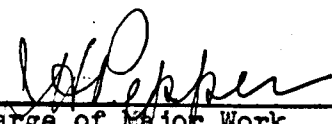
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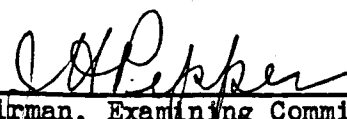
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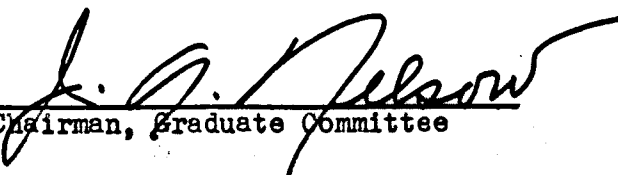
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ABSTRACT

The general behavior of insects is discussed in relation to the physical environmental factors, as well as the biological; and the probable influencing factors in the behavior of Camnula pellucida Scud. reviewed.

The work site, methods of observation and equipment used in the study of the behavior of this species are discussed and described in detail.

Population densities, within localized areas, may be correlated to the stage of morphological and sexual development, and to the activity of the insect.

Data are presented showing specific environmental factors such as temperature, humidity, light, and wind velocity, which were measured when such activities as 'start of movement', 'general movement', 'maximum movement', 'start of climbing', 'frenzied movement', 'heat torpor', 'movement stopped', and 'no activity' were noted for C. pellucida. Such activities can best be correlated to temperature.

Data presented indicate that the feeding response, in relation to the stage of development of the insect, seems to be largely dependent upon temperature; in that, as development increases, feeding occurs at increased temperature also.

Winds having average velocities over 2-3 and 5-6 m.p.h. appear to have interrupting effects on the feeding of nymphs and the flight of adults, respectively.

Observations on migrations of C. pellucida seem to indicate that although gregarious inertia and optical responses may keep a band migrating simultaneously, air and soil surface temperatures (within a range of 24.8-36.0 °C (76.6- 96.8 °F) and 25.5-44.2 °C (77.9-111.6 °F), respectively), a positive phototaxis and relative humidity may guide the grasshopper during migration bearing in mind its left-handed light-compass reaction to the sun and maintaining an angle of 30-110 degrees between the direction of migration and the position of the sun.

Field experiments, using crushed Agropyron smithii, to evoke an olfactory stimulus-response reaction, showed that the reaction-time (and probably sensory receptivity of stimuli) is closely associated with development in that the higher instars had faster reaction-times.

Observations of their climbing habits disclosed that C. pellucida appeared to respond more actively to heat (thermotaxis and thermokinesis), while Melanoplus bivittatus Say. appeared to respond more pronouncedly to illumination (phototaxis and photokinesis).

The color changes, from darker to lighter pigmentation of the exoskeleton of C. pellucida, as development progresses, may be due to increased temperature as the season advances.

Partial or complete damage of the flight appendages of the females is caused by the males when hyperexcited during sexual stimulation.

INTRODUCTION

The field of insect behavior, in relation to the entire environmental complex, has received minor emphasis in past entomological studies. Only during recent years have entomologists realized the importance of knowing the fundamental behavior pattern of the insects under study.

When considering behavior it must be considered as the sum total of the responses arising as a result of stimuli received from the total environment. The total environment constitutes not only those factors which are commonly thought of as existing in nature, i.e. the external environment, but also includes the organism as part of that environment. As a result of external influences (solar radiation, heat, cold, humidity, etc.) the organism will be affected internally, either on the metabolic or on the general physiological processes. This effect in combination with the influences of the external factors on their activities initiates the characteristic type of response. Furthermore, in animal aggregations, the presence and activity of any one individual will in many instances be a stimulus for the activity of another. The individual organism will behave in accordance with such factors as optical stimuli, crowding, movement, etc., and when combined with the influence of other external factors, a specific type of behavior will result.

Since the physical environment is constantly influencing the insect, its behavior in regard to these factors may be evidenced quite readily. However, other factors must be considered. These would

include, among other things, a study of the activities of the insect as they directly relate to varying populations as well as to feeding responses. In food consumption alone there may lie a vast complex of effects.*

Therefore, it seems to be of utmost importance; first, to determine which measurable and observable factors have a direct influence upon the activities of the insect; second, what the responses are to the various stimuli; third, what modifications and conditioning effects are acquired by the organism as a result of consistent environmental influences; and fourth, how the present behavior of the insect is related to and possibly responsible for future behavior and activity. (Uvarovs 'Phase Theory' (see Uvarov, 1921) or the cyclic phenomena of grasshopper abundance seems to be evidence in support of the fourth objective mentioned above.)

It is the purpose of this study to learn and interpret in so far as possible, the behavior of Camnula pellucida Scud. and to try to correlate its activities to measurable environmental factors.

C. pellucida was chosen as the subject in this investigation because it is an active insect which will produce pronounced reactions to various stimuli. This species was suggested by Dr. B.P. Uvarov as a desirable grasshopper for this study.

* Very recently it has been demonstrated by Spiegelman (1946), that the type of material entering the cells and tissues of an organism will determine, within limits, not only the type and structure produced in that organism, but will determine the type and structure of the successive generations. This is direct evidence in favor of the theory of adaptation to a change in environment.

The project was outlined at Montana State College and the investigations were carried out in Canada during the summer of 1947 when the author was employed by the Dominion Department of Agriculture, Division of Entomology. Known infestations of C. pellucida were present in southern Saskatchewan and these offered excellent opportunities for the investigational work. The sudden increase of this roadside species of grasshopper on both sides of the international boundary in the Great Plains Region, gave the project an additional impetus due to the economic importance of this pest.

ACKNOWLEDGMENT

The writer gratefully acknowledges his indebtedness to Dr. J.H. Pepper for the proposal of the problem and for constant help and advice during its development, to Mr. Ellsworth Hastings for helpful criticism and assistance, to officials of the Dominion Entomological Laboratories at Saskatoon, Saskatchewan and Lethbridge, Alberta for the loan of equipment used in the study, and to officials of the Dominion Department of Agriculture, Division of Entomology, Ottawa, Canada, for permission to work on the project and to use the data for thesis material.

REVIEW OF LITERATURE

Studies of the factors involved in insect reactions and behavior have been of interest to entomologists for many years. To many, the influencing factors meant only temperature and humidity, and throughout the literature a vast amount of material can be found which deals with these two factors in relation to the behavior of insects.

Reamur (1736)*, although unknowingly, made a start on the investigation of temperature effects upon living systems when he constructed his thermometer. Hancock (1904) proposed that the gustatory stimulus provoked an oviposition response in the green meadow grasshopper, Orchelimum glaberrimum, Burm. From there on the bearing of physiology on economic entomology (as pointed out by Dewitz, 1912) became evident.

Sanderson and Peairs (1914) and Peairs (1914) showed a relationship between temperature and insect development, while Pierce (1916) added humidity as a possible additional influencing factor affecting cotton boll-weevil activity. Although his graphs, showing zones of development, are hypothetical to a certain extent, they illustrate the possibility of a combined influence of these two factors.

McIndoo (1922) turned his efforts towards a study of the sensory responses of insects, while Folsom (1922) studied some of the ecological aspects of insect behavior. Corkins (1922) made direct observations on the habits of the Mormon cricket, Anabrus simplex Hald., their mob reactions, and their responses to surface stimuli. Studies of the factors possibly affecting the oviposition response of certain Dipterous

* reference is made by author and year to Literature Cited.

Coleopterous, Lepidopterous, and Hymenopterous insects were outlined by Richardson (1925).

Up to this time not much attention had been given to the underlying causes for the responses of insects to environmental stimuli. Scientists were merely interested in knowing if such responses were capable of being evoked by certain stimuli.

Temperature and moisture, however, still received the greatest attention. Margulis (1924), in his studies on the effect of environmental temperature on metabolism showed that a relationship existed between this factor and the rate of metabolism. Other workers such as Peairs (1927) and Bodine (1925) showed that temperature was a directing factor in the rate of development of insects. The latter states, ".... other factors being constant, the increment in rate (of development) seems to increase in direct proportion to the increase in temperature within the normal limits of development."

In connection with humidity and water relationships, Buxton (1932) has summarized the information up to his time. Johnson (1942), concluded that water loss from insects is proportional to the saturation deficit.* Alexander et al (1944) have concluded, from their studies

* Some controversy is apparent in the opinion of workers as to whether relative humidity or saturation deficiency should be used in determining the effects of moisture on insect behavior. Kennedy (1939) states, "Thus it seems that relative humidity is more relevant to behavior than saturation deficiency, and that insects are 'equipped with special sense organs for the perception of humidity'". He proposes this working hypothesis, "Although metabolic processes may often be better related to saturation deficiency than relative humidity, the humidity receptors carried by insects are more in the nature of hygrosopes than evaporimeters."

of desiccation, that the transmission of water through the cuticle of the insect is greatly enhanced by the use of inert dusts. They state, "...according to Robinson (1928) the water content of insects of different species is directly proportional to the food on which they live, and in the case of the grain weevil he found that about half of its water exists in a free state, while the other half is 'bound' to colloids. Our experiments show 90% of the water content of the insect is given off at a constant rate. ...this evidence suggests that the proportion of their content water is 'bound' in a manner distinguishable from 'free water' cannot exceed about 10%". This therefore, seemed to indicate the interaction of physiological and physico-chemical factors as related to moisture in its effect on the behavior of insects.

C. pellucida has not received extensive investigation although the Acrididae in general have been prominent subjects of study. Ball (1915) outlined some of the migratory habits and appearances of C. pellucida nymphs and adults and also described some of his observations on the rate and method of travel. Henderson (1924) states, "The migratory habits as described by E.D. Ball are accurate as regards methods and rate of movement, but not as concerns the direction of movement as described by him." He pointed out "that movement actually occurred in nearly all directions at the same time," whereas Ball maintained that a definite relationship existed between the direction of movement and the position of the sun.

Parker (1924) and (1930), has, by detailed study in the field and in the laboratory, shown that temperature directly affects the type

of movement made by C. pellucida; that it has a marked effect upon coloration and the amount of food consumed per day; and also bears a relationship to the time of hatching and the development of the species.

Griddle (1933) made some notable observations on the food and oviposition habits of C. pellucida. He states, "..... it shows a very strong preference for a comparatively few grasses", and goes on to mention that these are Agropyron smithii Rydb., Poa pratensis L., barley grass, Hordeum jubatum L., and brome grass, Bromus inermis, Leyss.:

Some of the work done on the behavior of grasshoppers and locusts was that performed by Dr. J.S. Kennedy. His papers (1939) and (1945) give evidence of the environmental factors which influence the activity and behavior of the desert locust, Schistocerca gregaria Forsk. In his earlier paper such features of locust behavior as concentration, aggregation, and gregarization receive attention. He also offers evidence as to the cause of these activities. In his later paper he suggests that the factors involved and bearing influence upon migrant hoppers are, optical responses, gregarious inertia, light-compass-reactions to the sun, and 'the tendency to follow the line of maximum mutual visibility'.

Since Uvarov (1921) proposed the Theory of Phases, considerable investigations have been undertaken in the study of the behavior of locusts in the Middle East and Africa. Faure (1932, 1934) studied the swarming habits and phases of Schistocerca gregaria in South Africa. Maxwell-Darling (1934, 1936, 1937) made observations of the solitary

phase and outbreak centers of the same species in the Sudan and in Arabia; while Kennedy (1937) studied the humidity reactions of the gregarious phase of Locusta migratoria migratorioides R & F. Further investigations of the occurrence and phases of L. migratorioides were made in Sudan by Johnson and Maxwell-Darling (1931), while Lean (1931) studied the effect of climate on the migration and breeding of L. migratorioides in Nigeria.

These locusts of the Middle East and Africa, because of their widespread presence and international economic importance, have become the most popular insect for the investigation of insect behavior. Therefore, most of our present day knowledge of the activities of grasshoppers and locusts in respect to environmental influences, comes from the work done on the Schistocerca and Locusta species.

LOCATION AND DESCRIPTION OF WORK SITE

The observational work was carried out in the Shaunavon district, north and west of Shaunavon, Saskatchewan during the summer months of 1947. This area, lying in the Great Plains Region of western Canada, is distinctly treeless and relatively flat, lying at the base of the eastern bench of the Cypress Hills. The soil is mainly loam to sandy clay loam with an intermingling of glacial till on the western border due to its close proximity to the Cypress Hills. The average annual precipitation is 12-20 inches, most of which falls in the winter and early spring. Drought conditions in summer have prevailed during the

past four years.

Six sites were chosen in this district to serve as focal points for the observations of behavior of C. pellucida. These sites were selected bearing in mind population densities, vegetation type and accessibility.

Area I

This was located 6 miles north and 0.3 miles west of Shaunavon. This was a road allowance 120x20 feet, covered with green western wheat grass, (Agropyron smithii Rydb.), 3-6 inches high. On either end of the area was tansey mustard, (Sophia incisa (Engelm) Greene), 6-12 inches in height. The roadside ditch was 2 feet deep, V-shaped, with no vegetation on its southern exposed slope. The road allowance ran east and west with a barley field on the south side.

Area II

This road allowance was located 8.5 miles north and one mile west of Shaunavon. This area was the southeast corner of a quarter section, vegetated by a mixture of Timothy grass, (Phleum pratense L.) 8-12 inches high, and Agropyron smithii, 2-4 inches in height. The latter was curly and somewhat dried out but still green at the base of the stems. Interspersed in this was tansey mustard, (Sophia incisa) 6 inches tall, which was green and flowering. Along the outer margin of the wheat field covering the quarter section of land was a single row of tumbling mustard, (Sisymbrium altissimum L.) approximately 18 inches high. The wheat was green, 6-8 inches in height and quite luxuriant.

Area III

This road allowance was located 10 miles north and 1.8 miles west of Shaunavon. Vegetation was Agropyron smithii, curly and browned at the tips, about 2-3 inches tall. About 50% of the vegetation on this east-west road allowance was Sophia incisa, which was rather defoliated 4-6 inches high, but still green. The field adjacent to the road was summerfallowed.

Area IV

This area was a north-south road allowance located 8.9 miles north and two miles west of Shaunavon, at the northeast corner of a section of summerfallow. The entire corner was about 80x20 feet and covered with a dense stand of Sophia incisa, approximately 12-18 inches high but rather defoliated by the mixed population of Melanoplus bivittatus Say. (40%) and C. pellucida (60%). Agropyron smithii, short, about 2 inches in height and still green was interspersed at the base of these weeds.

Area V

This area was located 8.1 miles north and 2 miles west of Shaunavon and was a dry slough bottom through which a road ran. The area comprised about two acres, covered with a dense growth of vegetation consisting of brome grass, (Bromus inermis Leyss.) and wild barley, (Hord-eum jubatum L.). Hardly any bare ground was visible between the grass stems for the vegetation was approximately 12-18 inches high, green and flowering.

Area VI

This area, a roadside ditch 4 feet deep and 8x50 feet in area, was located 12 miles north and 0.7 miles west of Shaunavon. The vegetation was slough sedge, (Carex spp.) 8-12 inches high, very green and succulent. The slough extended south covering an area of about two acres.

These were all roadside areas in which C. pellucida was very abundant. Only in one area was there a mixed population namely Area IV. The above descriptions are of the areas as they appeared during the latter part of June, 1947. Observations continued through July and August during which time extreme heat and drought conditions caused excessive drying of the vegetation, so that by the beginning of September no green vegetation was in evidence except in Area VI. In all the other Areas only on the lower part of the stems to about one-half inch above the ground did any green plant material remain visible.

EQUIPMENT USED

The following equipment was used to make measurements of the various physical environmental factors thought to influence grasshopper behavior:

1. A Thermocouple Potentiometer, General Electric PJ-1B, was used with constantin-copper thermocouples. Air and soil surface temperatures were measured.
2. A Bulb Aspirated Psychrometer, 'Julien P. Friez & Son Inc. Baltimore

M.D.', was used to measure the relative humidity of the air.

3. A 'Taylor' Fan Anemometer was used to measure the wind velocity in feet per minute. These readings were taken at the three feet and the six inch levels. All wind velocity data will be for the six inch level* unless otherwise specified.

4. Field Binoculars were used to observe the activity of the grasshopper from a distance, so that the observer would not influence the behavior by becoming an additional stimulus.

5. A Stop Watch was used to measure time whenever it was necessary to do so.

The one factor which was not specifically measured was that of sunlight intensity. Workers in the field have shown that light intensity is an important factor in the behavior of grasshoppers. Since no instrument was available to take these readings in this project, the only information obtained was a general description of cloudiness, hazyness, or clear skies.

* Since it was extremely difficult and at times impossible to take wind velocity readings with type of an instrument at the exact micro-habitat of the observed grasshopper, an arbitrary standard, the six inch level, was chosen for all readings. Furthermore, it was felt that differences in the measured wind velocity at specific heights within the '0-6 inch level' would not be significant in view of the accuracy of the anemometer used.

METHODS

Continuity of observation was an essential factor, therefore, the investigations were begun as soon as possible after hatching was complete. Furthermore, continuity was of importance because one object was to determine if nymphal behavior differed from adult behavior and in what respects it differed. Observations were started when most of the grasshoppers were in the third instar of development although some data was obtained concerning first and second instar nymphs. Attempts were made to make these observations at various times of the day and night and under as many climatic conditions as possible.

Observations of the behavior of C. pellucida were always accompanied by measurements of as many of the various influencing physical environmental factors as possible. When a specific type of activity, such as 'Start of Climbing' (see below), was observed, the individual specimen was regarded rather than the masses. The observer watched the individual grasshopper and when it moved or fed, started to climb weeds, etc., the air and soil surface temperatures were taken at the location where the reaction of the individual was noted. The relative humidity and wind velocity were then measured. Time of day and sunlight intensity were also recorded, together with the behavior activity observed. By observation of the behavior of the individual grasshopper, information as to the behavior of the masses was anticipated.

One objective to be gained by making observations of movement of individual grasshoppers of the various instars was to determine if

possible, what environmental factors were operating, what differences in the intensity of these factors (stimuli) were present for the various types of behavior, and in what respect the movements of the various instars differed from one another. After the first several observations it became evident that no true concept of the activity differences between instars could be obtained.

This was due to what appeared to be, and what Kennedy (1945) called "optical responses" and "compensation-reactions to fellow hoppers". These factors caused the behavior to be very complex and difficult to analyze. The movement of one individual may be the stimulus for the second one to move, and in this respect the measurement of the environmental influences would not be sufficient to warrant a basis for the second 'hoppers activity. Furthermore, these 'optical responses' and 'compensation-reactions' appeared to result in the activity of the individual instars occurring over wide ranges of temperature, relative humidity, wind velocity, etc., thereby not showing a conclusive difference in the reactions to these stimuli. The data obtained was therefore not analyzed as to the movement responses of the individual instars in relation to the measured environmental stimuli, but rather lumped showing only the variation in activity and movement of all nymphs in relation to these factors.

In making observations on the movement behavior of C. pellucida, several rather well defined types of activity could be recognized. These were "Start of Movement", "General Movement", "Maximum Movement", "Start of Climbing", "Frenzied Movement", "Heat Torpor", "Stop Move-

ment", and "No Activity". These categories of activity are closely related to those made by Parker (1930).

When migrations of C. pellucida were noticed, it was evident that these were not of great duration of movement, (usually one-half to one hour) nor was the distance travelled very great. The point of origin of the migration was usually a 'concentration center' such as the egg laying sites, and the area into which they migrated was usually more heavily vegetated or was a cropped field (except in the case of evening migrations when the reverse was noted). Air and soil surface temperatures, relative humidity, wind velocity and direction were recorded in the areas from and to which the migrations occurred. The position of the sun and the direction of these mass movements was carefully considered and recorded.

Field Experiment with Agropyron smithii

Whether or not the reactivity of all instars was similar was a doubtful question. The following experiment was conducted in an effort to determine if the reactions of the various instars were similar and if their reaction-times were the same.

The stimulus used here to evoke a response, was crushed Agropyron smithii, a grass to which this species of grasshopper seems to have a great affinity. Green, succulent leaves of this grass were crushed by hand so that the plant cells were ruptured and the vegetation became a moist mass. This 'ball' of leaves was then placed among the vegetation (in Area I), while the observer retreated to observe the reaction of the insects to this stimulus, through field binoculars.

The reaction-time was noted for the first positive response to the source of stimulation. A 'positive response' as used here, was the first orientation of a hopper to the stimulus, i.e. pointing its head in the direction of the 'ball' of A. smithii. The time interval between the first placing of the crushed grass on the ground and the first orientation of any 'hopper within an approximate three yard radius of the source, was designated as the "reaction-time for a positive response". The time interval between the first placing of the crushed grass on the ground and the complete orientation of all the grasshoppers within the above mentioned radius, was designated as the "reaction-time for a general response".

Since the tests were carried out in the same manner, from the same positions in Area I, such factors as the observers presence, optical responses, and 'compensation-reactions to fellow hoppers' remained standard influencing factors. As far as could be determined, wind velocity, temperature, humidity and sunlight were the only variable factors. The trials were executed on three consecutive days.

During the course of the observations mentioned above, notes were made on any phase of activity or behavior which seemed to be specific for C. pellucida. Some interesting observations were made and these are included in this paper.

PRESENTATION OF DATA

The data presented in Table I shows the relative population densities of C. pellucida in Areas I and V during the period June 27 to August 20, 1947. Complete data for Area V, over that period of time was not obtained.

Table II presents the air and soil surface temperatures, light, relative humidity, and wind velocity at which "Start of Movement" was noted for C. pellucida nymphs. Similarly, Tables III to IX present the measured external factors operating at which "General Movement", "Maximum Movement", "Start of Climbing", "Frenzied Movement", "Heat Torpor", "Movement Stopped", and "No Activity", respectively, was noted for C. pellucida nymphs. These categories were based principally on those established by Parker (1930). Although they are somewhat arbitrary, they nevertheless are types of activity which can most easily be recognized when observing the behavior of this species. Data listed in these tables are recorded chronologically.

The data presented in Tables X to XV show the air and soil surface temperatures, relative humidity and wind velocity at which first to sixth instar 'hoppers, respectively, were observed as starting to feed. These factors and their respective probable influence on feeding will be discussed later. Again, data listed in these tables are recorded chronologically.

Data accrued on the migration of C. pellucida are presented in Table XVI. Some of the environmental factors measured are listed and it seems to indicate that the temperature-sunlight-humidity complex may

be the major influencing factor in the migration of this species of grasshopper.

The results of the experiment conducted using crushed Agropyron smithii to evoke an olfactory stimulus-response reaction, are presented in Table XVII.

Table I - The relative population densities of C. pellucida in Areas I and V, during the period June 27 to August 20, 1947.

Date	Instar	Area I Population per sq.yd.	Area V Population per sq.yd.
June 27	3-4, some 5	200	---
June 30	3-5	200	---
July 2	3-5	50	---
July 8	5,6,3&4	10	250
July 12	6, some 4&5	5	250
July 31	6	550	600
Aug. 20	6	25	30

Table II - Air and soil surface temperatures, light, relative humidity, and wind velocity at which a 'start of movement' was noted for C. pellucida nymphs.

Observation Number	Air Temp.		Soil Temp.		Light	R.H. %	Wind m.p.h.
	°C	°F	°C	°F			
1	19.5	(67.1)	32.5	(90.5)	in sun	50	2.9
2	22.0	(71.6)	35.0	(95.0)	in sun	50	2.9
3	22.9	(73.2)	36.5	(97.5)	in sun	41	3.9
4	22.0	(71.6)	33.0	(91.4)	in sun	45	2.8
5	20.0	(68.0)	29.7	(85.5)	in sun	48	2.2
6	23.4	(74.1)	33.0	(91.4)	in sun	23	2.2
7	20.0	(68.0)	31.4	(88.5)	in sun	36	3.9
8	23.0	(73.4)	32.8	(91.0)	in sun	36	1.0
9	31.0	(87.8)	39.0	(102.2)	in sun	30	3.2
10	28.2	(82.8)	31.2	(88.2)	in sun	35	2.6
11	29.0	(84.2)	34.5	(94.1)	in sun	32	1.1
12	28.4	(83.1)	34.5	(94.1)	in shade	13	nil
Average	24.1	(75.4)	33.6	(92.5)		36.6	2.4
Minimum	19.5	(67.1)	29.7	(85.5)		13	nil
Maximum	31.0	(87.8)	39.0	(102.2)		50	3.9

Table III - Air and soil surface temperatures, light, relative humidity, and wind velocity at which a 'general movement' of C. pel-lucida nymphs was observed.

Observation Number	Air Temp.		Soil Temp.		Light	R.H. %	Wind m.p.h.
	°C	°F	°C	°F			
1	20.0	(68.0)	34.8	(95.0)	in sun	46	2.9
2	19.8	(67.6)	34.0	(93.2)	in sun	45	2.8
3	22.9	(73.2)	36.5	(97.5)	in sun	45	2.8
4	22.0	(71.6)	28.0	(82.4)	in sun	48	2.2
5	27.5	(81.5)	35.5	(95.9)	in sun	36	3.9
6	26.5	(79.7)	33.8	(92.8)	in sun	36	3.9
7	29.4	(84.9)	37.0	(98.6)	in sun	29.5	2.0
8	33.8	(92.8)	35.8	(96.4)	in sun	50	3.0
9	31.5	(88.7)	38.2	(100.8)	hazy	23	nil
10	31.0	(87.8)	33.8	(92.8)	hazy	22.5	2.6
11	34.0	(93.2)	31.0	(87.8)	in sun	35	2.6
12	30.0	(86.0)	36.5	(97.7)	in sun	22.5	2.6
13	31.5	(88.7)	33.5	(92.3)	in sun	21.5	1.0
14	32.8	(91.0)	25.5	(95.9)	in sun	27.5	1.1
Average	28.0	(82.4)	34.6	(94.3)		34.8	2.4
Minimum	19.8	(67.6)	28.0	(82.4)		21.5	nil
Maximum	34.0	(93.2)	38.2	(100.8)		50	3.9

Table IV - Air and soil surface temperatures, light, relative humidity, and wind velocity at which 'maximum movement' of C. pel-lucida nymphs was observed.

Observation Number	Air Temp.		Soil Temp.		Light	R.H. %	Wind m.p.h.
	°C	°F	°C	°F			
1	29.4	(84.9)	41.0	(105.8)	in sun	29.5	2.0
2	30.5	(86.9)	42.0	(107.6)	in sun	30	3.2
3	31.0	(87.8)	37.5	(99.5)	in sun	58	1.0
4	31.5	(88.7)	39.0	(102.2)	hazy	23	nil
5	35.5	(95.9)	42.0	(107.6)	in sun	13	nil
Average	31.6	(88.9)	40.3	(104.5)		30.7	1.2
Minimum	29.4	(84.9)	37.5	(99.5)		13	nil
Maximum	35.5	(95.9)	42.0	(107.6)		58	3.2

Table V - Air and soil surface temperatures, light, relative humidity, and wind velocity at which 'start of climbing' of C. pel-lucida nymphs was observed.

Height of Climb	Air Temp.		Soil Temp.		Light	R.H.	Wind
	°C	°F	°C	°F		%	m.p.h.
2 inches	38.5	(101.3)	42.5	(108.5)	in sun	45	2.8
$\frac{1}{2}$ "	31.0	(87.8)	42.5	(108.5)	in sun	45	2.8
$1\frac{1}{2}$ "	31.7	(89.1)	36.7	(98.1)	in sun	48	2.2
6 "	30.5	(86.9)	36.0	(96.8)	in sun	19.5	0.4
3-6 "	29.4	(84.9)	41.0	(105.8)	in sun	29.5	2.0
6 "	30.5	(86.9)	33.0	(91.4)	in sun	33	0.5
$\frac{1}{2}$ "	33.5	(92.3)	37.5	(99.5)	in sun	58	1.0
1 "	29.0	(84.2)	32.8	(91.0)	in sun	52.5	1.0
6 "	34.0	(93.2)	38.0	(100.4)	in sun	35	2.6
3-6 "	32.0	(89.6)	28.5	(83.3)	in sun	21	0.9
6 "	30.0	(86.0)	35.0	(95.0)	in sun	32	1.1
6 "	30.5	(86.9)	36.0	(96.8)	in sun	27.5	1.1
Average	31.7	(89.1)	36.6	(97.9)		37.2	1.5
Minimum	29.0	(84.2)	28.5	(83.3)		19.5	0.4
Maximum	38.5	(101.3)	42.5	(108.5)		58	2.8

Table VI - Air and soil surface temperatures, light, relative humidity, and wind velocity at which 'frenzied movement' of C. pel-lucida nymphs was observed.

Observation Number	Air Temp.		Soil Temp.		Light	R.H.	Wind
	°C	°F	°C	°F		%	m.p.h.
1	33.5	(92.3)	43.0	(109.4)	in sun	29.5	2.0
2	34.0	(93.2)	44.0	(111.2)	in sun	19.5	3.4
3	38.0	(100.4)	42.8	(109.0)	in sun	38.5	nil
4	44.0	(111.2)	49.2	(120.6)	in sun	38.5	nil
5	32.8	(91.8)	45.2	(113.4)	in sun	27.5	1.1
6	38.0	(100.4)	42.0	(107.6)	in sun	30	4.0
7	32.8	(91.8)	42.8	(109.0)	in sun	19.5	nil
8	44.0	(111.2)	49.2	(120.6)	in sun	38.5	3.4
Average	37.1	(98.8)	44.8	(112.6)		30.2	1.7
Minimum	32.8	(91.8)	42.0	(107.6)		19.5	nil
Maximum	44.0	(111.2)	49.2	(120.6)		38.5	4.0

Table VII - Air and soil surface temperatures, light, relative humidity, and wind velocity at which 'heat torpor' of C. pellucida nymphs was observed.

Observation Number	Air Temp.		Soil Temp.		Light	R.H. %	Wind m.p.h.
	°C	°F	°C	°F			
1	34.0	(93.2)	44.0	(111.2)	in sun	19.5	nil
2	38.0	(100.4)	42.8	(109.0)	in sun	38.5	nil
3	44.0	(111.2)	49.2	(120.6)	in sun	38.5	nil
4	42.5	(108.5)	46.5	(115.7)	in sun	10	3.0
Average	39.6	(103.4)	45.6	(114.1)		26.6	0.8
Minimum	34.0	(93.2)	42.8	(109.0)		10	nil
Maximum	44.0	(111.2)	49.2	(120.6)		38.5	3.0

Table VIII - Air and soil surface temperatures, light, relative humidity, and wind velocity at which 'movement stopped' in observed C. pellucida nymphs.

Observation Number	Air Temp.		Soil Temp.		Light	R.H. %	Wind m.p.h.
	°C	°F	°C	°F			
1	21.9	(71.4)	32.0	(89.6)	shade, cloud	45	2.8
2	23.0	(73.4)	29.0	(84.2)	shade, cloud	23	2.2
3	22.0	(71.6)	26.0	(78.8)	shade, cloud	45	1.1
4	20.4	(68.7)	31.8	(89.2)	shade, cloud	36	3.9
5	23.0	(73.4)	29.0	(84.2)	shade, cloud	36	1.0
6	23.8	(74.8)	30.5	(86.9)	shade, cloud	30	3.2
Average	22.4	(72.3)	29.7	(85.5)		35.8	2.4
Minimum	20.4	(68.7)	26.0	(78.8)		23	1.0
Maximum	23.8	(74.8)	32.0	(89.6)		45	3.9

Table IX - Air and soil surface temperatures, light, relative humidity, and wind velocity at which 'no activity' was observed in C. pellucida nymphs.

Time of Day	Air Temp. °C °F	Soil Temp. °C °F	Light	R.H. %	Wind m.p.h.
3:30 P.M.	19.0(66.2)	27.2(90.0)	shade	45	3.3
1:45 P.M.	16.5(61.7)	19.5(67.1)	shade	68	1.7
7:20 A.M.	16.2(61.2)	19.0(66.2)	in sun	70	3.4
8:00 A.M.	17.0(62.6)	20.0(68.0)	in sun	70	5.8
8:45 A.M.	17.5(63.5)	26.0(78.8)	shade	58	4.3
8:45 A.M.	20.0(68.0)	23.5(74.3)	shade	68	1.0
4:30 P.M.	30.5(86.9)	33.0(91.4)	hazy	20	nil
8:00 A.M.	28.5(83.3)	33.0(91.4)	in sun	33	0.5
8:30 P.M.	23.0(73.4)	25.5(77.9)	no sun	24	1.1
8:30 P.M.	23.2(73.8)	24.0(75.2)	no sun	26	1.1
3:00 A.M.	14.5(58.1)	16.0(60.8)	no sun	86	nil
3:30 A.M.	14.0(57.2)	15.2(59.4)	no sun	88	nil
4:00 A.M.	14.5(58.1)	15.2(59.4)	no sun	89	0.2
4:30 A.M.	13.5(56.3)	14.5(58.1)	no sun	92	0.7
5:00 A.M.	12.8(55.0)	14.0(57.2)	in sun	97.5	nil
5:30 A.M.	16.3(61.3)	15.0(59.0)	in sun	94	nil
6:00 A.M.	17.0(62.6)	17.8(64.0)	in sun	85	nil
7:00 A.M.	23.0(73.4)	20.1(68.2)	in sun	66	nil
4:45 P.M.	28.0(82.4)	31.5(88.7)	in sun	26	nil
8:00 A.M.	28.2(82.8)	31.2(88.2)	in sun	35	2.6
1:30 P.M.	33.2(91.8)	38.1(100.4)	hazy	38.5	nil
1:00 P.M.	30.0(86.0)	33.0(91.4)	hazy	38.5	nil
2:00 P.M.	27.0(80.6)	37.0(98.6)	shade	36	nil
4:00 P.M.	28.0(82.4)	31.0(87.8)	shade	30.5	0.5
2:00 P.M.	27.8(82.0)	30.5(86.9)	shade	28.5	3.4
3:00 P.M.	26.2(79.2)	28.0(82.4)	shade	53	nil
9:30 A.M.	23.8(74.8)	21.8(71.2)	in sun	42.5	0.9
3:00 A.M.	13.2(55.8)	14.8(58.6)	no sun	61	nil
Average	21.5(70.7)	24.1(76.3)		56	1.1
Minimum	12.8(55.0)	14.0(57.2)		20	nil
Maximum	33.2(91.8)	38.1(100.4)		97.5	5.8

Table X - Air and soil surface temperatures, relative humidity, and wind velocity at which observed first instar nymphs of C. pellucida started to feed.

Time of Day	Air Temp.		Soil Temp.		R.H. %	Wind m.p.h.	Food
	°C	°F	°C	°F			
2:30 P.M.	20.0	(68.0)	34.8	(95.0)	46	2.9	Agropyron
1:45 P.M.	29.0	(84.2)	36.2	(97.2)	36	1.0	Wheat
2:30 P.M.	27.4	(81.3)	31.8	(89.2)	33	nil	Agropyron
10:00 A.M.	24.4	(75.9)	28.0	(82.4)	38.5	nil	Agropyron
Average	25.2	(77.3)	32.7	(91.0)	38.4	1.0	
Minimum	20.0	(68.0)	28.0	(82.4)	33	nil	
Maximum	29.0	(84.2)	36.2	(97.2)	46	2.9	

Table XI - Air and soil surface temperatures, relative humidity, and wind velocity at which observed second instar nymphs of C. pellucida started to feed.

Time of Day	Air Temp.		Soil Temp.		R.H. %	Wind m.p.h.	Food
	°C	°F	°C	°F			
2:30 P.M.	20.0	(68.0)	34.8	(95.0)	46	2.9	Agropyron
1:45 P.M.	29.0	(84.2)	36.2	(97.2)	36	1.0	Wheat
3:35 P.M.	29.0	(84.2)	36.0	(96.8)	19.5	0.4	Tansey Mustard
3:55 P.M.	28.0	(82.4)	34.0	(93.2)	19.5	0.4	Tansey Mustard
9:30 A.M.	33.5	(92.3)	37.5	(99.5)	58	1.0	Barley
2:30 P.M.	27.4	(81.3)	31.8	(89.2)	33	nil	Agropyron
10:00 A.M.	24.4	(75.9)	28.0	(82.4)	38.5	nil	Agropyron
Average	27.3	(81.2)	34.0	(93.3)	35.8	0.8	
Minimum	20.0	(68.0)	28.0	(82.4)	19.5	nil	
Maximum	33.5	(92.3)	37.5	(99.5)	46	2.9	

Table XII - Air and soil surface temperatures, relative humidity, and wind velocity at which observed third instar nymphs of C. pellucida started to feed.

Time of Day	Air Temp.		Soil Temp.		R.H. %	Wind m.p.h.	Food
	°C	°F	°C	°F			
1:00 P.M.	19.5	(67.1)	32.5	(90.5)	50	2.9	Agropyron
2:00 P.M.	24.5	(76.1)	34.5	(94.1)	50	2.9	Agropyron
2:30 P.M.	20.0	(68.0)	34.8	(95.0)	46	2.9	Agropyron
10:45 A.M.	31.0	(87.8)	42.5	(108.5)	45	2.8	Agropyron
9:30 A.M.	31.7	(89.1)	36.7	(98.1)	48	2.2	Agropyron
10:30 A.M.	24.0	(75.2)	36.8	(98.2)	48	1.1	Barley
10:30 A.M.	26.0	(78.8)	34.0	(93.2)	45	1.1	Barley
1:45 P.M.	25.0	(77.0)	34.0	(93.2)	36	1.0	Wheat
3:35 P.M.	29.0	(84.2)	36.0	(96.8)	19.5	0.4	Tansey Mustard
3:55 P.M.	28.0	(82.4)	34.0	(93.2)	19.5	0.4	Tansey Mustard
8:45 A.M.	29.4	(84.9)	37.0	(98.6)	29.5	2.0	Agropyron
8:30 A.M.	30.5	(86.9)	33.0	(91.4)	33	0.5	Tansey Mustard
10:15 A.M.	29.0	(84.2)	32.8	(91.0)	52.5	1.0	Barley
9:00 A.M.	33.5	(92.3)	36.5	(97.7)	22.5	nil	Agropyron
9:00 A.M.	29.0	(84.2)	34.5	(94.1)	32	1.1	Tansey Mustard
10:00 A.M.	24.4	(75.9)	28.0	(82.4)	38.5	nil	Agropyron
Average	27.4	(81.4)	34.9	(94.9)	39	1.5	
Minimum	19.5	(67.1)	28.0	(82.4)	19.5	nil	
Maximum	33.5	(92.3)	42.5	(108.5)	52.5	2.9	

Table XIII - Air and soil surface temperatures, relative humidity, and wind velocity at which observed fourth instar nymphs of C. pellucida started to feed.

Time of Day	Air Temp.		Soil Temp.		R.H. %	Wind m.p.h.	Food
	°C	°F	°C	°F			
2:30 P.M.	20.0	(68.0)	34.8	(95.0)	46	2.9	Agropyron
9:15 A.M.	23.0	(73.4)	34.5	(94.1)	48	2.2	Agropyron
9:30 A.M.	31.7	(89.1)	36.7	(98.1)	48	2.2	Agropyron
10:30 A.M.	24.0	(75.2)	36.8	(98.2)	48	1.1	Barley
10:30 A.M.	27.5	(81.5)	34.5	(94.1)	45	1.1	Barley
10:30 A.M.	26.0	(78.8)	34.0	(93.2)	45	1.1	Barley
3:35 P.M.	30.5	(86.9)	36.0	(96.8)	19.5	0.4	Tansey Mustard
3:55 P.M.	29.0	(84.2)	34.0	(93.2)	19.5	0.4	Tansey Mustard
4:30 P.M.	30.5	(86.9)	33.0	(91.4)	20	0.4	Tansey Mustard
8:45 A.M.	29.4	(84.9)	37.0	(98.6)	29.5	2.0	Agropyron
8:30 A.M.	34.0	(93.2)	31.0	(87.8)	35	2.6	Tansey Mustard
8:30 A.M.	31.0	(87.8)	38.0	(100.4)	35	nil	Tansey Mustard
9:00 A.M.	33.5	(92.3)	36.5	(97.7)	22.5	nil	Agropyron
10:00 A.M.	32.0	(89.6)	31.8	(98.2)	21	0.9	Agropyron
1:30 P.M.	44.0	(111.2)	49.2	(120.6)	38.5	nil	Slough sedge
9:00 A.M.	29.0	(84.2)	34.5	(94.1)	32	1.1	Tansey Mustard
10:00 A.M.	24.4	(75.9)	28.0	(82.4)	38.5	nil	Agropyron
Average	29.5	(85.1)	35.4	(95.7)	35.5	1.2	
Minimum	20.0	(68.0)	28.0	(82.4)	19.5	nil	
Maximum	44.0	(111.2)	49.2	(120.6)	48	2.9	

Table XIV - Air and soil surface temperatures, relative humidity, and wind velocity at which observed fifth instar nymphs of C. pellucida started to feed.

Time of Day	Air Temp. °C °F	Soil Temp. °C °F	R.H. %	Wind m.p.h.	Food
9:30 A.M.	31.7(89.1)	36.7(98.1)	48	2.2	Agropyron
3:35 P.M.	33.2(91.8)	36.0(96.8)	19.5	0.4	Tansey Mustard
3:55 P.M.	29.0(84.2)	34.0(93.2)	19.5	0.4	Tansey Mustard
8:45 A.M.	29.4(84.9)	37.0(98.6)	29.5	2.0	Agropyron
9:30 A.M.	30.5(86.9)	33.0(91.4)	33	0.5	Tansey Mustard
10:30 A.M.	33.0(91.4)	30.2(86.4)	20.5	1.0	Wheat
9:00 A.M.	33.5(92.3)	36.5(97.7)	22.5	nil	Agropyron
10:00 A.M.	32.0(89.6)	31.8(89.2)	21	0.9	Agropyron
1:30 P.M.	44.0(111.2)	49.2(120.6)	38.5	nil	Slough sedge
9:30 A.M.	30.0(86.0)	35.0(95.0)	29	1.1	Tansey Mustard
9:30 A.M.	30.5(86.9)	36.0(96.8)	29	1.1	Tansey Mustard
10:30 A.M.	35.5(95.9)	45.2(113.4)	27.5	1.1	Agropyron
9:40 A.M.	25.2(77.4)	24.0(75.2)	42.5	0.9	Agropyron
10:00 A.M.	24.4(75.9)	28.0(82.4)	38.5	nil	Agropyron
Average	31.6(88.8)	35.3(95.5)	31.1	0.9	
Minimum	24.4(75.9)	24.0(75.2)	19.5	nil	
Maximum	44.0(111.2)	49.2(120.6)	48	2.2	

Table XV - Air and soil surface temperatures, relative humidity, and wind velocity at which observed sixth instar (adults) of C. pellucida started to feed.

Time of Day	Air Temp. °C °F	Soil Temp. °C °F	R.H. %	Wind m.p.h.	Food
9:00 A.M.	33.5(92.3)	36.5(97.7)	22.5	nil	Agropyron
9:30 A.M.	30.5(86.9)	36.0(96.8)	29	1.1	Tansey Mustard
10:30 A.M.	35.5(95.9)	45.2(113.4)	27.5	1.1	Agropyron
Average	33.2(91.7)	39.2(102.6)	26.3	0.8	
Minimum	30.5(86.9)	36.0(96.8)	22.5	nil	
Maximum	35.5(95.9)	45.2(113.4)	29	1.1	

Table XVI (a) - Conditions of wind velocity, temperature and relative humidity in areas from which migrations of C. pellucida occurred; as well as direction of migration and the time of day when observations were made.

Wind direction & velocity in m.p.h.	Time of Day	Migration from listed vegetation					Vegetation
		Air Temp. °C °F	Soil Temp. °C °F	R.H. %	Migration		
W 1.0	10:30 A.M.	33.0(91.4)	41.5(106.7)	12.5	W	Agropyron	
WNW 3.4	4:00 P.M.	36.0(96.8)	44.2(111.6)	9.0	WNW	Agropyron	
WNW 3.4	4:00 P.M.	36.0(96.8)	44.2(111.6)	9.0	WNW	Agropyron	
NNW trace	7:30 P.M.	24.8(76.6)	25.5(77.9)	19.0	N	Barley	
NNW trace	7:30 P.M.	24.8(76.6)	25.5(77.9)	19.0	N	Barley	
SW 0.5	1:00 P.M.	28.0(82.4)	40.0(104.0)	4.0	S	Agropyron	
SW 0.7	3:00 P.M.	31.5(88.7)	38.2(100.8)	23.0	nil	Agropyron	
W trace	9:00 A.M.	33.0(91.4)	42.0(107.6)	22.5	SW	Agropyron	
Average		30.9(87.6)	37.7(99.9)	14.8			
Minimum		24.8(76.6)	25.5(77.9)	4.0			
Maximum		36.0(96.8)	44.2(111.6)	23.0			

Table XVI (b) - Conditions of wind velocity, temperature and relative humidity in areas to which the above migrations of C. pellucida occurred; as well as the time of day when observations were made.

Wind direction & velocity in m.p.h.	Time of Day	Migration to listed vegetation					
		Air Temp.		Soil Temp.		R.H.	Vegetation
		C	F	C	F	%	
W 1.0	10:30 A.M.	33.0	(91.4)	30.2	(86.4)	20.5	Wheat
WNW 3.4	4:00 P.M.	34.0	(93.2)	31.6	(88.9)	17.0	Agropyron and Tansey Mustard
WNW 3.4	4:00 P.M.	35.1	(95.2)	35.0	(95.0)	13.0	Barley
NNW trace	7:30 P.M.	27.0	(80.6)	29.2	(84.6)	25.5	Agropyron
NNW trace	7:30 P.M.	26.0	(78.8)	27.8	(82.0)	25.5	Agropyron and Tansey Mustard
SW 0.5	1:00 P.M.	27.0	(80.6)	32.0	(89.6)	21.0	Wheat
SW 0.7	3:00 P.M.	31.0	(87.8)	33.8	(92.8)	22.5	Barley
W trace	9:00 A.M.	30.2	(86.4)	23.8	(74.8)	24.0	Agropyron 12"
Average		30.4	(86.7)	30.8	(87.4)	21.1	
Minimum		26.0	(78.8)	27.8	(82.0)	13.0	
Maximum		35.1	(95.2)	35.0	(95.0)	25.5	

Table XVII - Reaction time of C. pellucida nymphs to a crushed-
Agropyron stimulus under measured conditions of wind
velocity, temperature and relative humidity.

Date	Time of Day	Air Temp. °C °F	Soil Temp. °C °F	Wind m.p.h.	R.H. %	Time for positive response	Time for general response
June 27	2:30 P.M.	20.0(68.0)	34.8(95.0)	2.9	46	0:30 min.	2:00 min.
June 28	3:00 P.M.	16.5(61.7)	19.5(67.1)	1.7	68	0:35 "	2:00 "
June 29	9:30 A.M.	22.0(71.6)	35.0(95.0)	3.9	41	0:30 "	2:00 "
June 29	1:30 P.M.	22.9(73.2)	36.5(97.5)	3.9	41	0:35 "	2:15 "

DISCUSSION OF RESULTS

I. Fluctuation in Population Densities:

The natural population fluctuations of C. pellucida have been of interest and also something of a mystery to many people. Observations were made and counts of population recorded in the hope that some explanation could be forwarded for the apparent rise and fall of grasshopper populations over a period of time in a localized area.

The data presented in Table I shows the variation in population in Area I and V over a period of 55 and 44 days respectively. Both these areas are typical egg laying sites, such as described by Ball (1915) and Criddle (1933), for C. pellucida. Unfortunately observations were begun after hatching was completed and no information was obtained as to the population of the first instar nymphs in these areas. However, on the basis of the previous fall grasshopper egg survey in this area, the egg population had been well over 1000 eggs per square yard, thus the first instar population must have been within that range also. On July 12, in Area I, the 'hopper population was only 2.5% of that present on June 27. About two weeks later the population had increased tremendously but fell off again towards the end of August.

By observation of the population present at various intervals of time, a rather feasible explanation may be offered for the somewhat phenomenal variations in numbers within one localized area. The hatching site may be regarded as a focal point. As development increased, movement and distance of travel were increased also. At the same time

the amount of succulent food within the area became less as the season advanced. Consequently the 'hoppers moved out, by migration, etc., probably in search of better food, so that by the time the 'hoppers had reached the fourth to the sixth instar of development, the outward movement from the 'focal point' was at its maximum while the population within any small portion of this 'maximum occupied area' had decreased considerably in respect to the preceeding population present. This decrease, however, only represented a wider distribution of the original population.

The point of lowest population density and the largest distribution of population seems to be correlated with development of the species. In Area I, on July 12, the lowest population of 5 per square yard, coincided with the time when most of the grasshoppers had reached maturity. Criddle (1933) pointed out that there is a period of about ten days between morphological maturity and sexual maturity. He also stated that the adults which have reached sexual maturity have a tendency to return to some suitable egg laying site for copulation and oviposition. This seems to be borne out by the data in Table I, for on July 31 many mature adults had returned to the original 'focal point', thereby producing the remarkable increase in population. It may be assumed that sexual maturity enhanced a gregarious tendency and caused the 'hoppers to accumulate in such large concentrations in localized areas.

By the time oviposition had been completed, the population gradually decreased as the adults died; so that by the end of August relatively

few grasshoppers remained.

II. Movement of *C. pellucida*:

Movement of this species of grasshopper was so varied and the number of possible influencing factors so numerous and complex that considerable difficulty was experienced in explaining adequately the factors responsible. Parker (1930) recognized several behavior patterns and activities of *C. pellucida* and gave evidence in support of his statements. He correlated movement with temperature.

The data obtained in this study indicated that *C. pellucida* movements cannot adequately and accurately be linked with one factor alone, such as temperature. However, fig. I. seems to show some correlation between the activities observed and temperature. The data seems to indicate that with a steady rise in temperature activity is increased also, i.e. no activity resulted at air temperatures of 21.5 °C (70.7 °F), while movement started at 24.1 °C (75.4 °F), with a 'general movement' of the species at 28.0 °C (82.4 °F) and a 'maximum movement' at 31.6 °C (88.9 °F). Hoppers began to climb the vegetation at 31.7 °C (89.1 °F) and were greatly excited at 37.1 °C (98.8 °F) while some went into 'heat torpor' at 39.6 °C (103.3 °F). As soon as the temperatures dropped, the usual activities resumed at the above temperature but all activity ceased at 22.4 °C (72.3 °F). Therefore, from this data, (average air temperatures were quoted above) temperature appeared to be the most plausible factor to be correlated with the activity of the insect.

However, the possible influence of light and solar radiation

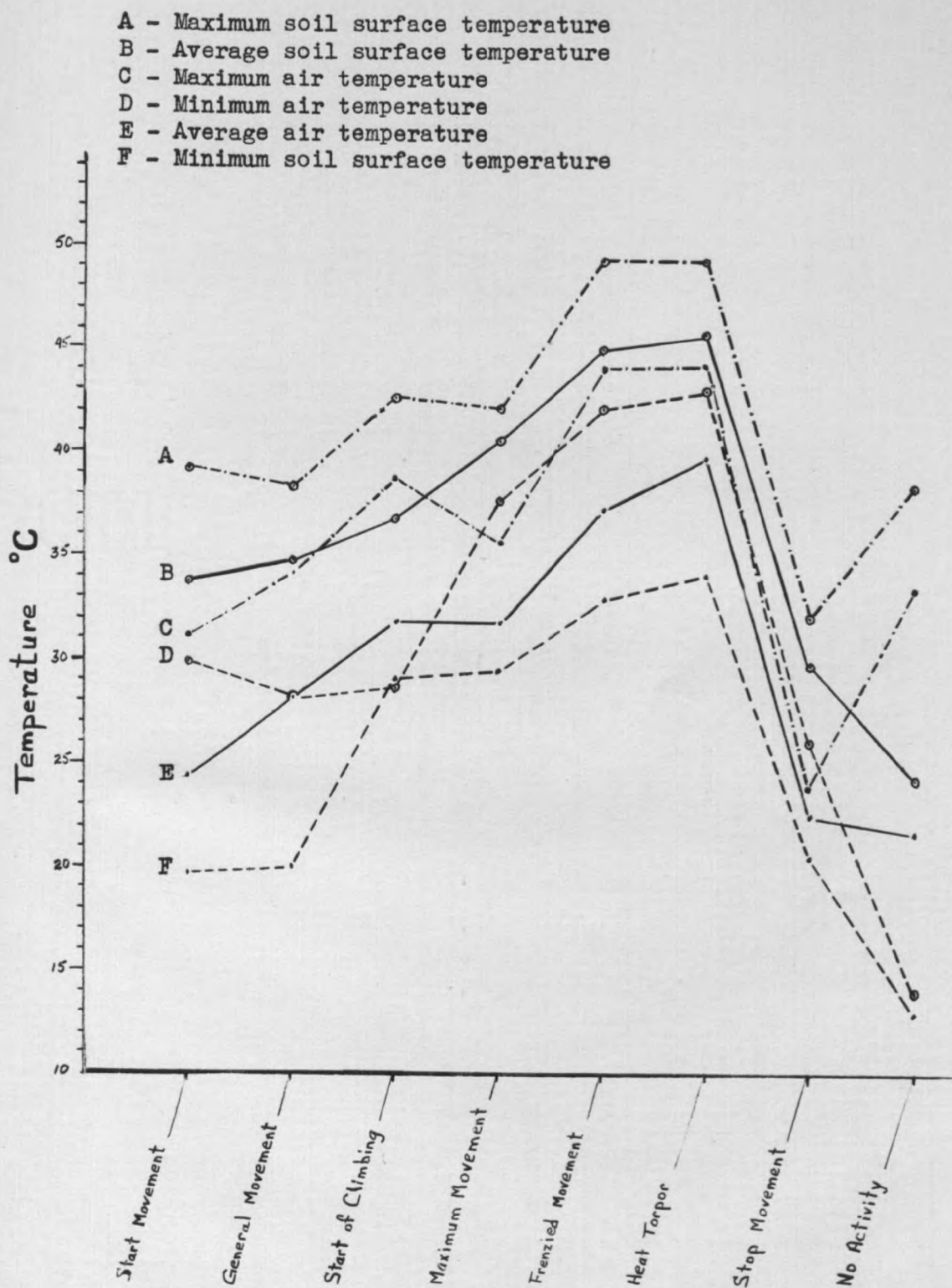


Fig. 1 - Graph showing the relationship between temperature and activity of C. pellucida.

should not be overlooked. In almost all instances where activity was observed, this action had taken place at a time when the sun was shining. Table VII, showing the various conditions of temperature, light, relative humidity and wind velocity during which movement of C. pellucida stopped, indicates that movement ceased when the sun was obscured by a cloud. Therefore a possible positive photokinesis displayed by the insect may be as vital a factor as temperature in determining the cause for certain activities. Since temperature will decrease with a decreased intensity of light, such as is produced by a cloud passing before the sun, the insect may also be caused to stop its activity due to positive thermokinesis which would produce variation of locomotion proportional to the variation in temperature.

No precise and well defined division could be attained between the influence of sunlight intensity and temperature, but from the data accrued and presented it seems evident that both these factors form a complex of which neither can be designated as being the principle factor but both being complimentary factors in the production of movement responses.

It is known that a grasshoppers internal temperature varies with the external temperature, (grasshoppers being poikilothermic), but it also varies in relation to the intensity of solar radiation. It may then be assumed that C. pellucida stopped its activities when the sun was obscured by a cloud (Table VII) because the adsorption of solar rays (heat) by the insect was not the same as that of the earth or the air. The air temperature may not have decreased as sharply due to the

decrease in sunlight intensity, as that of the insects body temperature. In this respect the intensity of sunlight seems to play a larger role in governing the activities of the insect than does temperature; in that the insect may be more photokinetic than thermokinetic.

Similarly, since air temperatures may not change much while the grasshoppers temperature may change considerably, the sunlight intensity factor may also be a cause for the overlapping of temperature ranges in which various behavior activities were observed. For example in fig. 1, the highest air temperature at which 'general movement' was observed was 34.0 °C (93.2 °F) while the lowest air temperature at which 'maximum movement' of the nymphs was noted was 29.4 °C (84.9 °F). Other measured factors were not at great variance, therefore, the sunlight intensity factor may be of importance when viewing activity as a result of a phototaxis supplemented by a thermotaxis.

Kennedy (1939) says, "In literature on diurnal behavior it is sometimes mentioned that humidity is important but, owing to the difficulty of separating humidity and temperature, proof is hard to obtain." The data obtained in this project showed that a minimum relative humidity of 10% was present when C. pellucida were observed as being in 'heat torpor', a maximum relative humidity of 97.5% was present when 'no activity' was observed, while all other movement activities were noted as taking place within a relative humidity range of 24 to 38.5%. It appears then that little evidence is present to show that relative humidity is specifically important here, and its influence on behavior of C. pellucida remains doubtful.

The effect of wind on the behavior of this species, as observed in this project, will be dealt with later.

When endeavoring to analyze the behavior of a living organism, not only must the external environmental influences be considered, but the organism itself must receive attention also. Since adaptability is a characteristic of all living matter the possibility of 'conditioning' was considered in the movement of C. pellucida. In so far as the data presented allows, some 'conditioning' seems to have occurred. Third instar nymphs, on June 27, (Observation No. 1, Table II) started moving at an air temperature of 19.5 °C (67.1 °F) and a soil surface temperature of 32.5 °C (90.5 °F). On July 8, (Observation No. 9, Table II) third instar nymphs started moving at an air temperature of 31.0 °C (87.8 °F) and a soil surface temperature of 39.0 °C (102.2 °F).

On June 29, (Observation No. 2, Table III) fourth instar nymphs were moving about freely at an air temperature of 19.8 °C (67.6 °F), while on July 8, (Observation No. 10, Table III) they were moving freely at an air temperature of 31.0 °C (87.8 °F).

On July 1, (Observation No. 1, Table IV) 'maximum movement' of fifth instar nymphs occurred at an air temperature of 29.4 °C (84.9 °F) while on July 11, (Observation No. 5, Table IV) they underwent similar movements at an air temperature of 35.5 °C (95.9 °F).

These observations were made in the same area (Area I). The increase in temperature (6.1 - 24.5 °C (11.0 - 46.1 °F)), over a period of 9-11 days, at which these specific activities occurred, seems to indicate that the 'hoppers may have become conditioned to heat.

Movements such as mentioned above occurred at specific temperatures during the period June 27-July 1, but considerably higher temperatures were noted during the period July 8-11, at which these same types of activity were seen.

In each of the above mentioned instances, the relative humidity was 16.5 - 22.5% higher during June 27-July 1 than during July 8-11. It seems probable that this variation in relative humidity is merely the natural relationship which temperature bears to relative humidity, i.e., an inverse proportionality. Whether this is the case or not is still a matter of conjecture, but the probable factor of adaptability and conditioning should not be deemed negligible.

III. Feeding of *C. pellucida*.

Observations were made on the initial feeding responses of *C. pellucida* nymphs and adults. It seems reasonable to assume that the desire for food is the major factor involved in a feeding response, consequently, most feeding would take place after an interval of fasting. This assumption seems to be borne out by the data presented in Tables X - XV, for feeding was observed more frequently during the forenoon than during the afternoon.

The feeding response, in relation to the stage of development of *C. pellucida*, seems to be largely dependent upon temperature effects. The lowest air temperature at which feeding of first instar nymphs was noted was 20.0 °C (68.0 °F) and the highest 29.0 °C (84.2 °F), the average being 25.2 °C (77.3 °F). The lowest soil surface temperature was 28.0 °C (82.4 °F) and the highest 36.2 °C (97.2 °F), the average

being 32.7 °C (82.4 °F). See Table X.

Second instar nymphs were noted feeding at a minimum air temperature of 20.0 °C (68.0 °F) and a maximum of 33.5 °C (92.3 °F), the average being 27.3 °C (81.2 °F). The lowest soil surface temperature was 28.0 °C (82.4 °F) and the highest 37.5 °C (99.5 °F), the average being 34.0 °C (93.3 °F). See Table XI.

The lowest air temperature at which feeding of third instar nymphs was noted was 19.5 °C (67.1 °F) and the highest 33.5 °C (92.3 °F), the average being 27.3 °C (81.2 °F). The lowest soil surface temperature was 28.0 °C (82.4 °F) and the highest 42.5 °C (108.5 °F), the average being 34.9 °C (94.9 °F). See Table XII.

Fourth instar nymphs were noted feeding at a minimum air temperature of 20.0 °C (68.0 °F) and a maximum of 44.0 °C (111.2 °F), the average being 29.5 °C (85.1 °F). The lowest soil surface temperature was 28.0 °C (82.4 °F) and the highest 49.2 °C (120.6 °F), the average being 35.4 °C (95.7 °F). See Table XIII.

The lowest air temperature at which fifth instar nymphs were noted feeding was 24.4 °C (75.9 °F) and the highest was 44.0 °C (111.2 °F), the average being 31.6 °C (88.8 °F). The lowest soil surface temperature was 24.0 °C (75.2 °F) and the highest 49.2 °C (120.6 °F), the average being 35.3 °C (95.5 °F). See Table XIV.

Sixth instar (adults) were noted feeding at a minimum air temperature of 30.5 °C (86.9 °F) and a maximum of 35.5 °C (95.9 °F), the average being 33.2 °C (91.7 °F). The lowest soil surface temperature was 36.0 °C (96.8 °F) and the highest 45.2 °C (113.4 °F), the average be-

ing 39.2 °C (102.6 °F). See Table XV.

These same data are presented in fig. 2, showing the comparative increase in temperature at which the various instars started feeding.

Thus it appears as if the higher the stage of development of the insect the higher must be the temperature in order to evoke a feeding response. However, this may be due to first, a 'conditioning' of the organism to temperature; and second, it may be 'coincidental' with the natural increase of temperature as the season (and the development of the insect), progresses. Both of these possibilities will be dealt with briefly.

One might theorize that as development increased, the 'hoppers may have become more and more adapted to the higher temperatures. A range of temperature, (20.0 - 29.0 °C (69.0 - 84.2 °F)), at which first instar grasshoppers were seen feeding appeared to be insufficiently high to allow feeding of sixth instar adults, for they fed at temperatures ranging from 30.5 - 35.5 °C (86.9 - 95.9 °F). Whether or not the sixth instar grasshoppers would refuse to feed at lower temperatures, if subjected to them over a period of time, is not known. It can be assumed, however, that if a 'conditioning' to higher temperatures took place over a period of time, a similar 'conditioning' to lower temperatures over a period of time could result in a feeding response at that lower temperature also. Therefore, the possibility of a 'conditioning' action of temperature should not be overlooked as negligible in respect to the feeding response of C. pellucida.

Although the data in Tables X - XV seem to indicate a relationship

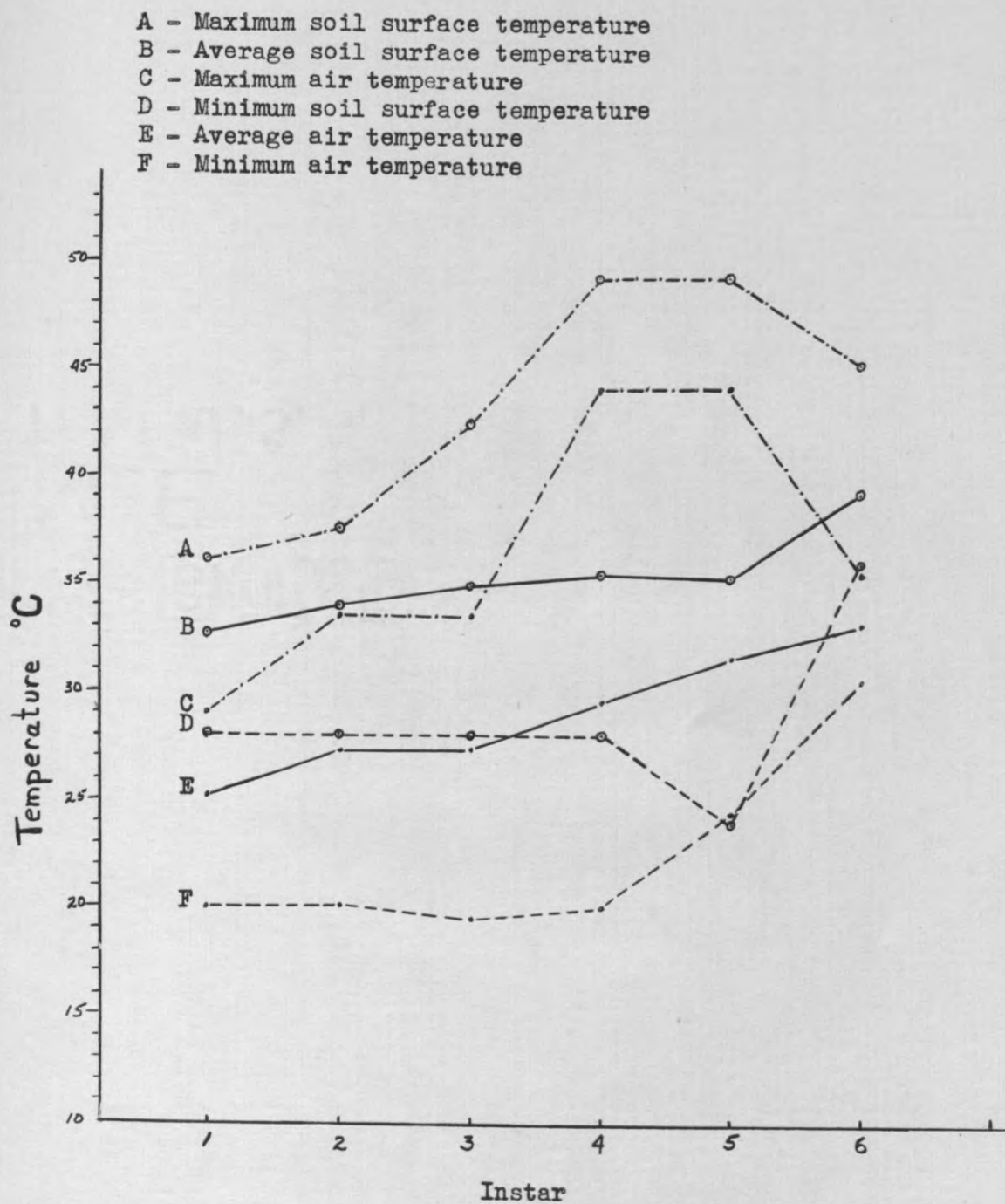


Fig. 2 - Graph showing the relationship between temperature and the start of feeding of first to sixth instar C. pellucida

between increased temperature and increased development, another possible explanation can be brought forward. Since the temperature increases as the season progresses it may be assumed that feeding at increased temperature was coincidental with this natural increase in heat and the stage of development. Feeding would then be a natural reaction under these parallel conditions of increased temperature and development (in relation to time) and would appear to be not so dependent upon temperature factors alone.

In so far as the data allows, it seems reasonable to assume that both the 'conditioning' of the hopper and the possibility of 'coincidence' (as pointed out above), are operating here and the feeding behavior of C. pellucida may be a result of one or both of these possibilities.

IV. The Effect of Wind on the Behavior of C. pellucida:

Moving air causes greater evaporation than does air which is stationary. Warm air moving over a surface will absorb more moisture than will cool air because of the increase of the saturation deficiency with an increased temperature. This might result in an increased metabolism to restore the water equilibrium, or increased feeding which in turn may result in an attempt to restore the water balance.

A cool breeze would cause a more rapid loss of heat from the organism. This, according to Chapman (1931), would decrease the metabolism of poikilothermic organisms. Such a decrease would result in a minimized activity and may explain why grasshoppers remain more or less inactive during windy days.

Observations were made on C. pellucida in an effort to confirm some of these speculations. A few examples of the effect of wind on nymphs and adults will be cited.

1. Third and fourth instar nymphs were feeding at a height of 6 inches above ground level where the air temperature was 24.0 °C (75.2 °F). The soil surface temperature was 36.0 °C (98.2 °F), the relative humidity, 48%, and the wind velocity of approximately 1 m.p.h. When a slight increase in wind to approximately 2 m.p.h. occurred, feeding stopped immediately.

2. A fourth instar nymph was feeding at a level of 6 inches above the ground where the air temperature was 25.0 °C (77.0 °F), the soil surface temperature was 34.5 °C (94.1 °F), with an air movement of approximately 1 m.p.h. When the air movement increased to 2.5 m.p.h. feeding stopped immediately.

3. Fourth and fifth instar nymphs were sitting on the vegetation at a height of 3 inches above ground level where the air temperature was 33.0 °C (91.4 °F), the soil surface temperature was 41.0 °C (105.8 °F), the relative humidity 19.5 % and a wind velocity of 3.4 m.p.h. When the wind suddenly died down to 'nil' the air temperature rose to 34.0 °C (93.2 °F) and the soil surface temperature went up to 44.0 °C (111.2 °F). The grasshoppers became quite agitated in their movements, under these changed conditions. The sun remained bright with no clouds in the sky during this observation.

4. At an air temperature of 28.2 °C (82.8 °F), a soil surface temperature of 31.2 °C (88.2 °F), a relative humidity of 35% and a wind

velocity of 2.6 m.p.h., a fourth instar nymph sat in an open patch of ground sunning himself in the bright sunlight. (9:30 A.M.) When the air movement suddenly died down to 'nil' the air temperature rose to 34.0 °C (93.2 °F) and the soil surface temperature went up to 38.0 °C (100.4 °F). The 'hopper ascended a plant to a height of 6 inches above ground level where the air temperature was 31.0 °C (87.8 °F), and started to feed. Within several minutes the wind rose to 2.6 m.p.h. again and the grasshopper stopped feeding and descended to ground level where the soil surface temperature was 34.0 °C (93.2 °F).

5. At an air temperature of 40.0 °C (104.0 °F), a soil surface temperature of 46.4 °C (115.5 °F), a relative humidity of 10% and a wind blowing at 8 m.p.h., the grasshoppers were moving about very restlessly but no flight was evident. As soon as the wind velocity decreased to 2-3 m.p.h. local sporadic flight ensued.

6. In an area where most of the grasshoppers had reached the adult stage of development, no flight was evident at wind velocities of 12 m.p.h. Air and soil surface temperatures were 28.6 °C (83.5 °F) and 43.8 °C (110.8 °F), respectively, while the relative humidity was 11%. Not only was flight arrested but even the movement of the population on the ground was very limited.

7. At an air temperature of 33.5 °C (92.3 °F), a soil surface temperature of 40.5 °C (104.8 °F), a relative humidity of 19% and a wind velocity of 7.2 m.p.h., no adults of C. pellucida were seen in flight. After several minutes the sun came out from behind some hazy clouds and the wind dropped to 4.4 m.p.h. At that point flying started.

The wind velocity increased again and flight decreased proportionately until a wind velocity of about 6.5 m.p.h. was reached. All flight stopped at this point even though the sun was out bright and temperatures like those mentioned above, were present. The whole observation was made over a period of about ten minutes.

These examples show that wind may be a factor in the regulation of grasshopper behavior. In all the above cited observations, as many of the variable environmental factors, which could be of influence, were measured.

The above observations indicated that feeding did not take place until wind velocities had fallen below 2 m.p.h. Since these feedings occurred at air temperatures ranging from 24.0 - 31.0 °C (75.2 - 87.8 °F), the range of temperature at which feeding of third and fourth instar occurred, (see Tables XII and XIII), it may be said that the temperature factor was more responsible for the feeding than was the wind velocity. However, since wind seems to bear an inverse relationship to temperature, (as indicated in Observation 3 and 4 above where variation in wind velocities of 2-3 m.p.h. caused a corresponding variation of 1-3 °C (1.8 - 5.4 °F) in air temperature and 3-7 °C (5.4 - 12.6 °F) in soil surface temperature), it would seem to have an indirect effect on feeding through its effect on temperature. Furthermore, it seems probable that the mechanical force of increased wind velocity on the 'hopper may also be responsible for the interruption of feeding.

Parker (1930) says, "Flights do not depend upon high temperatures

alone but are greatly influenced by wind. A light breeze combined with high temperatures offers optimum conditions for flight." He indicated that flights of C. pellucida took place at average air and soil surface temperatures of 23.9 °C (75.0 °F) and 38.9 °C (102.0 °F), respectively. From the above observations, flights of adults were prevented by wind velocities over 5-6 m.p.h. even though temperatures were above the range indicated by Parker. Thus it appears as if wind can be a limiting factor in the flight of C. pellucida.

V. Migration of C. pellucida:

A migration may be defined here as a movement of an insect, caused by an unfavorable relationship between the organism and its immediate environment. This 'unfavorable relationship' may be created in either one of two ways, namely, by a change in the physiological make-up of the insect, i.e., a change in the internal environment, or by a change in the immediate external environment. The migration would then be a result of the insects endeavor to make adjustments and adaptations to the changed conditions. Therefore, it should be kept in mind that the cause of a migration must be regarded as being independent of the migration itself. After migration has been initiated, the direction and duration of movement will be the result of the influence of entirely new or modified conditions.

The migration proper, as dealt with here, refers to the movement of the insects in a rather unified body, in a directional manner. The distance travelled was usually short, approximately 100 to 200 yards, and not comparable to the mass migrations of such species as Schisto-

cerca gregaria.

Observations were made on the movement of C. pellucida in the hope that some information might be obtained as to why this species migrates back and forth from roadside into adjacent cropped fields. The desire for food may be an influencing factor but it does not explain why mass movements occurred. Visual acuity is very poor in insects, (Snodgrass 1931) and thus would not facilitate their finding more succulent food.

A study of some of the environmental factors which seem to have a bearing on the migration behavior of C. pellucida are temperature, relative humidity, wind and sunshine. The conclusions which may be drawn as a result of a study of Table XVI are:

1. Air temperatures of 24.8 - 36.0 °C (76.6 - 96.8 °F) were present in the area from which the migrations started; these temperatures being in a range at which 'general movement' of the species occurred, as pointed out above.

2. Soil surface temperatures of 25.5 - 44.2 °C (77.9 - 111.6 °F) in the areas from which migrations started, are also within a range of temperatures at which 'general' and 'maximum movement' occurred; thereby probably causing a search for lower temperatures.

3. The average air and soil surface temperatures in the areas from which migrations started was 30.9 °C (87.6 °F) and 37.7 °C (99.9 °F), respectively. The air and soil surface temperatures in the areas in which the migrations terminated was 30.4 °C (86.7 °F) and 30.8 °C (87.4 °F), respectively. This would seem to indicate a migration from higher to lower temperatures.

4. Migrations occurred from areas having an average relative humidity of 14.8%, to areas having an average relative humidity of 21.1%. This would seem to indicate a migration into areas having higher relative humidities; which areas were usually more heavily vegetated.

5. A wind was usually present and the direction of the migrations was into the wind or into some component part of it, but never with the wind.

6. Migrations took place when the sun was not obscured by clouds.

7. Migrations took place at an angle to the sun, i.e., in this series of observations the hoppers were usually keeping their left sides turned towards the sun. (Except in Observation No. 6, in which the right side was exposed to the sun.) The angle between the direction of migration and the position of the sun was 30-110 degrees.

Although all observed migrations occurred as movements into the wind or into some component part of it, it seems doubtful whether wind is much of a directing factor in migration. Observation No. 7, Table XVI, indicated that no migration took place and no wind was in evidence. Since the prevailing winds in southern Saskatchewan are 'westerlies', it may be assumed that the migrations, as observed in this series of observations, were coincidental with the prevailing winds. If such were the case then the migrations which were directed at various angles between 180 degrees north and south, may be due, not to the wind (which varied 45 degrees north and south of due west), but to some other factor. Such other factor might be relative humidity, for in

the above mentioned observation the difference in relative humidity between the two areas was very slight, (0.5%), and no migration was observed. In all other instances the difference or variation in relative humidity was from 1.5 - 17%.

All migrations which were observed as taking place in the forenoon and in the afternoon were from areas having higher temperatures and lower relative humidities, into areas having lower temperatures and higher relative humidities. The migrations observed in the evening, (Observation No. 4 and 5, Table XVI), took place from areas having lower temperatures and lower relative humidities than the areas into which the 'hoppers migrated. Therefore, it appears as if the grass-hoppers were moving more in respect to temperature than either relative humidity or wind. Fig. 2 indicates that the average air temperature at which 'general movement' occurred was 28.0 °C (82.4 °F). In the above two evening observations of migration it appeared as if they were seeking this area which had air temperatures within the above range, namely 26 -27 °C (78.8 - 80.6 °F). Although they moved into what may be termed a 'temperature preferendum area', they also migrated into an area which had an increased relative humidity of 6.5% over that of the area which they had left. Hence, it may be assumed that the temperature factor coupled with that of relative humidity is responsible for much of the movement of C. pellucida.

The migration of the 'hoppers in respect to their orientation to the sun should not be overlooked. Kennedy (1945) indicates that it is not uncommon for S. gregaria to be 'left handed' in respect to its

orientation to the sun. He goes on to say that "a light-compass-reaction to the sun" is supplementary to other factors (gregarious inertia) in maintaining a "constant common direction" of migration.

The observations made here seem to be in agreement with the views held by Kennedy. C. pellucida showed a left-handed light-compass-reaction to the sun, for their left sides were exposed to the sun's rays in almost all instances.

In so far as the observations made here allow, it may be assumed that C. pellucida orient themselves with respect to the sun while migrating, maintaining an angle of 30-110 degrees between their direction of movement and the position of the sun.

The initiating stimuli for a migration response remains speculative. Orientation in respect to the sun, temperature and relative humidity conditions may be directing factors for a directional movement, but the underlying causes for a migration initiation, are unknown. As pointed out above, the soil surface temperatures of 25.5 - 44.2 °C (77.9 - 111.6 °F) may be a partial initiating cause for movement. This movement would then probably lead to a migration in order to reach a zone which would minimize or eliminate 'unfavorable relationships' between the insect and its environment. Gregarious inertia and optical responses may keep the whole band moving simultaneously while temperature, a positive phototaxis and relative humidity form the complex of influencing factors which guide the grasshoppers during their migrations.

VI. Moulting of *C. pellucida*:

In Area IV, *Melanoplus bivittatus* Say. comprised approximately 40% of the population, while *C. pellucida* comprised the remaining 60%. On July 2, 'hoppers in the third to the fifth instar of development, were abundant and moulting was general. Moulded skins or exoskeletons were evident almost everywhere in the area but these were all *M. bivittatus*. Only after a prolonged search was a cast skin of *C. pellucida* found. This shed skin was partly devoured.

Moulting scenes were frequently observed and in almost all instances *M. bivittatus* left the shed exoskeleton and crawled away to dry. *C. pellucida*, on the other hand, remained and started to feed on the skin which had been cast off. Whether or not it is a requirement on the part of this species, to eat their cast exoskeletons, is not known. It may be reasonable to assume that *C. pellucida* is more carnivorous than *M. bivittatus*.

However, it was of interest to note that in all areas there was a decided lack of these cast exoskeletons of *C. pellucida*, while those of *M. bivittatus* could be seen wherever this species was or had been present.

VII. Climbing Habits of *C. pellucida* as compared to *M. bivittatus*:

While observing the behavior of *C. pellucida* it was noted that one peculiar characteristic of this species was its non-perching habit. *M. bivittatus* was noted as having a strong tendency to climb to the top of weeds and grasses prior to sunset while the former was rarely seen climbing the vegetation at that time of the day, but seemed to prefer

cracks and debris on the ground for night shelter. In a mixed population, such as existed in Area IV, the two species were almost completely segregated just before sundown. Most of the M. bivittatus would be up on the vegetation while the majority of the C. pellucida would be on the ground.

On several occasions all night observations were made in order to determine if 'hoppers remain at the top of the vegetation all night. It was found that only a few individuals (of M. bivittatus) remain in that position all night while the rest of the 'hoppers descend after sunset to seek shelter on the ground.

In the morning a marked difference between the behavior of these two species was again evident. Both species would be on the ground, hidden in cracks and under debris, (except for those few individuals of M. bivittatus which remained up on the vegetation), just before sun-rise. Immediately after the sun had risen and the first rays of sunshine reached the earth, it was noted that a majority of the M. bivittatus would move up onto the vegetation. C. pellucida would remain in seclusion on the ground for as long as two hours after sun-rise or until such time as the temperature of the air and soil surface had risen to about 24.1°C (75.4°F) and 33.6°C (92.5°F) respectively. (At this temperature range 'movement started', see Table II). Then the 'hoppers were seen moving into open patches to bask in the sun.

From these observations it appears as if the photokinetic and phototactic tendencies are at variance in the two species. A pos-

itive phototaxis, possibly aided by thermokinesis and a negative geotaxis may be responsible for keeping M. bivittatus in exposed positions on the vegetation at sunset. Activity and vertical light intensity are still fairly low in the morning and positive phototaxis and negative geotaxis appeared to give greatest assistance in the ascent of the vegetation. The descent of M. bivittatus may be partly assisted by positive thermotopotaxis for it seems evident that activity proceeds along rather defined temperature gradients.

In the case of C. pellucida it seemed as if they did not climb at sunset because of the seemingly predominant influence of positive geotaxis over that of phototaxis, and assisted by positive thermokinesis, since the ground (solid) usually retains heat longer than air (gas). In the early morning their photokinetic tendencies appear to remain in the minority until thermokinesis starts activity. A positive geotaxis seems to keep them on the ground, hence their remaining hidden even after sunrise. After temperatures have gone up (as indicated above) a positive thermokinesis assisted by positive phototaxis and possibly thermophobotaxis (avoidance of cooler) may be the cause for the 'hoppers collecting in open patches for basking.

It also appears as if group formation and aggregation of C. pellucida takes place towards evening as soon as the soil surface temperatures fall to a level of about 30-35 °C (86-95 °F). At these temperatures climbing is not warranted (see Table V). At this time negative thermokinesis can take effect and the ground is sought phototactically.

Therefore, it may be assumed that C. pellucida reacts more decis-

ively due to its thermokinetic and thermotactic tendencies, than does M. bivittatus which seems to respond more as a result of photokinesis and phototaxis. However, both factors are involved in the activity of each of the species but the responses to illumination are more pronounced and seem to have a greater bearing on the behavior of the latter than on C. pellucida.

VIII. Responses and Reaction-Time of C. pellucida to a known Stimulus:

The results obtained from the experiment conducted using crushed Agropyron smithii to evoke an olfactory stimulus-response reaction, are summarized in Table XVII. The first positive response came within about 30 seconds after the application of the stimulus, and interestingly enough the response was made by a fourth instar nymph in all instances. Third instar 'hoppers responded a few seconds later, followed by second instar nymphs and last by the first instar 'hoppers. In almost all instances the 'reaction-time for a general response' was about 2 minutes.

Since the more advanced instars were the first to respond to the stimulus, and the first instar 'hoppers responded last, it may be assumed that the greater the development, the greater the response and the faster the reaction-time. It would also seem to indicate that sensory development (sensitivity or receptivity of stimuli) runs parallel with morphological development.

Therefore, one would expect that the behavior of C. pellucida is not general but rather specific and each instar may react in a different manner to a given stimulus or require varying degrees of

intensity of stimuli to evoke similar reactions. This was verified above under 'Movement' and 'Feeding'.

IX. Color Changes with Development of *C. pellucida*:

Descriptions of the external morphological characteristics of the immature and adult forms of *C. pellucida* can be found in papers published by Ball (1915), Bruner (1891), Henderson (1924), and Pettit and McDaniel (1918); hence no further mention will be made of them here.

The adult when newly emerged from the shed exoskeleton of the fifth instar, is distinctly greenish in color. Tegmina and wings, light green in color, are soft and transparent with translucent spots on the former which will later turn dark to form the typical Oedipodinae wing pattern. The two stripes running down the anterior margin of the tegmina from the base to the apex, are fairly well discernable although not creamy yellow but rather yellowish green in contrast to the pale green of the disc of the wing.

As development progresses and the grasshoppers reach sexual maturity, distinct color changes occur. The individuals lose their dark coloration, as described by Henderson (1924), and become much yellower in appearance. The ventral part of the abdomen of the males becomes almost bright yellow while the femurs and tibia, especially of the metathoracic legs, assume distinct yellow colors. The color change in females is not quite as decisive as that of the males, although some decrease in pigment intensity is noticeable.

This color change may be the result of the effects of increased temperatures as the season progresses, for workers have shown that

color intensity decreases, and other morphological characteristics change also, as the temperature increases.

X. Copulation and Oviposition:

Of all the descriptions made on the oviposition and copulation habits of C. pellucida perhaps Ball (1915), sums up the whole situation quite well in that publication. Observations made on this species by the author corroborate Ball's statements.

One interesting incident which puzzled the writer was why many of the adults, especially the females, had badly damaged tegmina and wings by the time oviposition had started. Observations of their copulatory habits revealed that the males were mainly responsible for the damage. During the period of copulation the sexual impulse or sexual actuation seems to cause the males to become very excited. One to a dozen males will crowd around one female, tear at her with their tarsal claws and spined hind legs, and during the struggle the female flight appendages will suffer severe damage. Often one of the males, in the struggle for the possession of the female, will suffer the same abuse as that of the female.

SUMMARY and CONCLUSIONS

The literature on grasshopper behavior is reviewed and discussed and certain criticisms and suggestions are added.

Field equipment used in the study and the work site are described in detail.

Populations of C. pellucida within localized areas decrease as morphological development increases, because of a wider distribution of the grasshoppers from a focal point such as the egg laying site. The maximum distribution of the species seems to coincide fairly well with the time when development has reached its peak, namely the sixth instar. Increase of population within localized areas may be correlated with sexual maturity for at that time the species aggregates for copulation and oviposition.

The activities of C. pellucida under natural conditions seems to be controlled to a large extent by temperature. Another factor which seems to show some influence upon the behavior of this species is solar radiation (sunlight). Activity was usually stopped when the sun was obscured by a cloud, but this may be due to temperature effects for the temperature varied directly with the light intensity.

Activities such as 'start of movement', 'general movement', 'maximum movement', 'start of climbing', 'frenzied movement', 'heat torpor', 'movement stopped', and 'no activity' were correlated with temperature effects. It was found that activity seemed to increase as the temperature increased.

The influence of relative humidity upon the activity of C. pel-

lucida remains doubtful.

Similar activities such as 'start of movement', 'general movement' and 'maximum movement' took place only after temperatures had increased 6.1 - 24.5 °C (11.0 - 46.1 °F) after a period of 9-11 days. This would seem to indicate the possibility of an adaptation and conditioning of the grasshopper to temperature.

From data presented it appears as if the feeding response, in relation to the stage of development of C. pellucida, seems to be largely dependent upon temperature, in that, as development increased feeding was observed at increased temperatures. First instar nymphs fed at average air and soil surface temperatures of 25.2 °C (77.3 °F) and 32.7 °C (82.4 °F), respectively; second instar nymphs, at 27.3 °C (81.2 °F) and 34.0 °C (93.3 °F), respectively; third instar nymphs, at 27.4 °C (81.4 °F) and 34.9 °C (94.9 °F), respectively; fourth instar nymphs, at 29.5 °C (85.1 °F) and 35.4 °C (95.7 °F), respectively; fifth instar nymphs, at 31.6 °C (88.8 °F) and 35.3 °C (95.5 °F), respectively; and adults, at 33.2 °C (91.7 °F) and 39.2 °C (102.6 °F), respectively.

The influence of wind on the behavior of C. pellucida seemed evident from observations made, in that feeding was interrupted by winds over 2 m.p.h. at air temperatures ranging from 24.0 - 31.0 °C (75.2 - 87.8 °F). Whether this is due to decreased temperatures as wind velocity increased, or by mere mechanical force of the wind, is unknown although both possibilities are probable.

Flights of adults were prevented by wind velocities over 5-6

m.p.h., even though temperatures were above the normal range at which activity was general, i.e., over 28 °C (82.4 °F).

Although all migrations observed were directed into the wind, or into some component part of it, the exact influence of wind on migration remains unknown.

Migrations took place only when air and soil surface temperature ranges of 24.8 - 36.0 °C (76.6 - 96.8 °F) and 25.5 - 44.2 °C (77.9 - 111.6 °F), respectively, were present. These temperature ranges are in the range at which 'general movement' of the species was noted.

Direction of grasshopper migration varied during the day and towards evening. 'Hoppers moved from areas having average air and soil surface temperatures of 30.9 °C (87.6 °F) and 37.7 °C (99.9 °F), respectively, into areas having air and soil surface temperatures of 30.4 °C (86.7 °F) and 30.8 °C (87.4 °F), respectively. It may be assumed that temperature effects influence migration in that they create the 'unfavorable relationship' which is the cause of migration.

C. pellucida showed a left-handed light-compass-reaction to the sun in that the migrating grasshoppers, in almost all instances, kept their left sides exposed to the sun. The angle between the direction of migration and the position of the sun was 30-110 degrees.

Gregarious inertia and optical responses may keep a band migrating simultaneously, while temperature, a positive phototaxis and relative humidity may guide the 'hopper during migration, bearing in mind its light-compass-reaction to the sun. The exact initial cause of migration can only be regarded in a speculative manner.

C. pellucida feed on their shed exoskeletons after moulting, while M. bivittatus rarely does. The reason for this has been assumed to be its carnivorous habits or the metabolic requirement of the insect.

The results of an experiment using crushed Agropyron smithii to evoke an olfactory stimulus-response reaction seems to indicate that the reaction-time (and hence the reactions or the responses of the insect) is closely associated with development, in that, the greater the development the faster will be the reaction-time.

Observations of the climbing habits of C. pellucida and M. bivittatus seem to indicate that the former is more strongly motivated by thermokinetic and thermotactic tendencies and positive geotaxis, which keeps them on the ground at sunset and sunrise. The latter climbs vegetation at these two periods of the day possibly because of the stronger motivation due to photokinesis, phototaxis and a negative geotaxis. Heat, light and the force of gravity seem to be in evidence in the behavior of these two species but responses to illumination apparently supercede that of heat in respect to M. bivittatus while the reverse is true of C. pellucida.

As development increases the darker pigments decrease in the exoskeleton of C. pellucida. This is especially evident in the males which assume a distinct yellowish coloration by the time they have reached sexual maturity. The color change may be due to the effects of increased temperature as the season progresses.

The intense excitement caused by sexual stimulation leads to

hyperactivity of the males, resulting in the laceration and at times the complete destruction of the female flight appendages.

APPENDIX

The term 'tropism' has lead to confusion in many publications in the past. Instead of this term, several other terms have come into use and these will be briefly outlined here. They have been taken from Kennedy (1939) pp. 533-534.

"Kinesis:

Variations in the intensity of the stimulus produce variations in the rate of random locomotion. The direction of locomotion bears no relation to the direction of a stimulus gradient or of a radiant source. In a positive kinesis locomotion rate increases with intensity of stimulus, and vice versa. Thus in a positive photokinesis animals become more active in brighter light, and consequently collect in a region of dimmer light.

"Taxis:

The stimulus affects the direction taken by the animal, apart from the latter's locomotion rate. A taxis is positive when it results in movement into a region where the stimulus is stronger

"Phobotaxis:

'Orientation in an undirected path'. ...a phobotaxis cannot be described as positive or negative.

"Topotaxis:

'the movement is directed in respect to the source of stimulation. The following varieties of directed reaction are to be distinguished':

1. Tropotaxis:

Resultant position taken up in relation to more than one source of stimulation.

2. Telotaxis:

'These vary with the strength and direction of the stimuli. The resultant movement is either directly towards or away from the source of stimulation'. No resultant position in relation to more than one source of stimulation; one source is dominant to the exclusion of others.

3. Menotaxis:

'Maintaining a definite angle between the direction of motion and the line joining the source of stimulation with the sense organ'.

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