NUTRITIONAL ECOLOGY OF THE CLEAR-WINGED GRASSHOPPER, *CAMNULA PELLUCIDA* (SCUDDER) (ORTHOPTERA, ACRIDIDAE)*

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(With 1 Plate, 28 Text-figures and 27 Tables)

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* This paper was submitted in August, 1956 to the Faculty of Graduate Studies of the University of Saskatchewan, (Saskatoon, Sask., Canada) in partial fulfilment of the requirements for the Degree of Doctor of Philosophy, and to the National Research Council of Canada as report of work done under their Post Doctoral Fellowship.

I—Introduction

The clear-winged grasshopper, *Camnula pellucida* (Scudder), is one of the most important grasshopper pests of cereals in the agricultural areas of Canada and the United States. In 1949, it was estimated* that grasshoppers caused an economic loss of about $23,140,000 to wheat and $5,530,000 to other crops in the province of Saskatchewan alone. At least 30 per cent. of this loss must be ascribed to *Camnula*. Apart from the losses to field crops, this grasshopper is very destructive to range areas, especially in the province of British Columbia, occasionally destroying most of the forage and thus threatening the livestock industry.

The breeding places of the grasshopper typically comprise native sod situated in close proximity to cultivated fields, where the grasshopper hatches and feeds to some extent. From these places the grasshopper attacks the adjoining cultivated fields, but, at the time of oviposition, returns to the breeding places on the sod.

Criddle (1933*a*) found that *Camnula* has a very strong preference for comparatively few grasses and that in Manitoba a majority of its eggs are to be found among the roots either of western couch-grass (*Agropyron smithii* Rybd.) or Kentucky bluegrass (*Poa pratensis* L.), and, when these grasses are not present, wild barley (*Hordeum jubatum* L.) or brome grass (*Bromus inermis* Leyss.) provide suitable substitutes. Riegert (1948, unpublished thesis) also found western couch-grass greatly favoured by *Camnula*.

A study of the nutritional ecology of *C. pellucida* is needed as a contribution to the understanding of the relationship of food factors and the grasshopper abundance. The objective of the present investigation was, therefore, to investigate food as an element in the environment of *C. pellucida* by studying (1) the preference of the grasshopper for a wide range of species of broad-leaved and grass-like plant species, (2) the effect of a small number of grasses and grass-like species on its growth and survival, and (3) utilization of food on exclusive diets.

This problem was undertaken at the suggestion of Mr. L. G. Putnam, Co-ordinator of Grasshopper Research in Western Canada, under the supervision of Dr. J. G. Rempel, Professor of Biology, University of Saskatchewan. The work was accomplished with a grant-in-aid from the Saskatchewan Research Council and, later, on a Post-Doctorate Fellowship of the National Research Council of Canada.

The work was done in the Biology Department of the University and in the Dominion Entomological Laboratory situated on the university campus. I wish to thank Dr. Rempel and Mr. Putnam for guidance and for their interest in the progress and implementation of the project. I offer my appreciation and thanks to Dr. M. L. Cameron and Dr. L. G. Saunders for assistance during Dr. Rempel's leave of absence. Thanks are extended to Drs. R. P. Knowles and J. L. Bolton of the Dominion Forage Crop Laboratory, Saskatoon and to Dr. Heinrichs of Swift Current for identifying plants and for providing seeds of grasses used in these experiments. I also wish to acknowledge the assistance of Mr. G. O. Handegord of the Division of Building Research for the electrical circuits in temperature and humidity controls of the rearing cabinet. I am much obliged to Dr. D. S. Rawson, Head of the Department of Biology, and to Dr. H. Macdonald, Chief of the Dominion Entomological Laboratory, for extending to me the facilities of their departments.

*38th Annual Report of Field Crops Commissioner, Canada, 1950, p. 123.

II—REVIEW OF LITERATURE

Basis of Differential Feeding.—The mechanism by which insects in general, and grasshoppers in particular, are able to select the food they prefer is not clear even though the problem of host specificity has attracted the attention of workers for about 50 years. From the earliest work on host specificity, as that of Grevillius (1905) on the brown-tail moth, *Euproctis chrysorrhoea* (L.) feeding on the chickweed, *Stellaria*, and the classical work of Verschaffelt (1910) on *Pieris* butterflies feeding on members of the family Cruciferae, to the recent works of Chauvin (1951) and Dethier (1941, 1953, 1954), the general belief is that the preference of plants by the insects is determined by "token stimuli" (e.g., *sinigrin*) which have no significant nutritional value to the insect. Thus Fraenkel (1951) came to the conclusion that leaves of all the plants contain the basic nutritional substances and hence the selection of food plants is not made on the basis of their nutritional content : "It is the presence or absence of odd chemical substances in which the plants differ, such as glucosides, essential oils, alkaloids, saponins or tannins, which renders the plant a suitable or unsuitable food."

On the other hand, it has also been observed that the feeding responses to token stimuli, in the absence of nutrients, are sometimes erratic and do not compare with the quantity of feeding that occurs when fresh leaves of a normal host plant are offered. Painter (1951) explained the resistance of some plants to insects as due to "the absence of necessary vitamins, amino acids or fatty acids in the part of the plant on which the insect feeds". This explanation does credit the insect with the ability to select the plant from the point of view of nutrition. Thorsteinson (1955) found in the diamond-back moth, *Plutella maculipennis*, and some other insects that feeding response to a token stimulus, in the absence of nutrients, was very low. From this as well as other such observations, it appears that nutritional needs of the insect do play a role in its differential feeding, although the token stimulus by constant association with the naturally preferred food may deceive some insects into giving a positive feeding response to mere filter paper or any neutral substrate treated with test preparations.

Among the physical factors influencing the differential feeding of grasshoppers, succulence appears to be of prime importance. Tauber *et al.* (1945), from their experiments of feeding *Melanoplus bivittatus* (Say) on dry foods, observed that dry alfalfa is unable to support life for long, whereas if access to water is provided the grasshoppers can do as well on dry food as on some foods supplied fresh from nature. Husain *et al.* (1946) and Roonwal (1953) gave a comprehensive account of the differential feeding of the desert locust *Schistocerca gregaria* (Forsk.), and found that the locust prefers succulent to papery food. Williams (1954) also reported succulence of food to be of prime importance and not so much the toughness of the blades. He failed to detect a correlation between toughness of the grass and the feeding responses of grasshoppers. However, small-sized particles of tough grass recovered from faeces showed that the grasshoppers bite off the tough grass in smaller bits than from tender grass.

Differential Feeding in Grasshoppers.—It is now freely conceded that the grasshoppers are oligophagous rather than polyphagous or omnivorous. Some of them are grass feeders ; others prefer forbs, while still others are mixed feeders. Rubtzov (1932*a*, 1932*b*), from his observations on more important Siberian grasshoppers in the field, found that their selection for feeding does not exceed 6 to 10 per cent. of the total number of species present. From his extensive studies of ecological distribution, he (1932*b*) found that every plant community has a characteristic grasshopper population, and *vice versa*. The connection between the two is so close that "indicator" plants could be found to indicate specific grasshopper populations. For example, one of the two major grasshopper pests, *Gomphocerus sibericus* L., is closely connected with localities having *Agropyron cristatum* ; another grasshopper pest, *Chorthippus albomarginatus* DeG., is associated with *Poa pratensis*. These indicators serve as indices to the microclimatic conditions most favourable to the grasshoppers.

Among the grasshopper species of economic importance in North America, *Melanoplus mexicanus* (Saussure) prefers, flourishes and produces the largest number of eggs on wheat, sunflower (*Helianthus petiolaris* Nutt.), barley, dandelion (*Taraxacum officinale* Weber), alfalfa, Kentucky bluegrass (*Poa pratensis* L.), brome (*Bromus inermis* Leyss.), Russian thistle (*Salsola pestifer* A. Nels., as small sprouts) and tansy mustard=flixweed (*Descurainia sophia* (L.) Webb.), and it is generally a forbs-feeder or perhaps a general feeder preferring forbs (Washburn, 1912 ; Hebard, 1938 ; Skoog, 1941 ; Urquhart, 1941 ; Brett, 1947 ; Pfadt, 1949*a* ; Smith, 1950 ; Smith *et al.*, 1952 ; Scharff, 1954 ; Barnes, 1955). Isely (1938, 1946) gave a comprehensive account of feeding habits of grasshoppers in Texas, indicating how the grass-feeders soon starve on forbs and forb-feeders starve in the absence of their food plants. In his later work (1946), he gave critical field observations carried out for a period of three years in a backyard area with seven distinct types of vegetations. He found that graminivorous species, which in nature thrive best in mesophytic habitats, select succulent grasses for food in cages, and those species which are more and more tolerant of xeric environment in nature refuse succulent grasses and feed on more mature native grasses typical of drier situations. Isely (1944) even correlated mandibular morphology of the grasshoppers with food specificity.

Criddle's (1933*b*, pp. 477-479) observations on differential feeding habits of grasshopper species in the Prairie Provinces of Canada are very interesting. He gave several examples of grasshoppers restricted to single host species ; e.g., *M. bowditchi canus* Hebd. is restricted to the sage, *Artemesia cana* Pursh, and the non-flying grasshopper, *Hypochlora alba* Dodge, to another sage, *Artemesia ludoviciana* Nutt. Other grasshoppers are able to differentiate between families of the plant kingdom ; e.g., *Acrolophitus hirtipes* (Say, Acridinae) subsists exclusively upon members of Boraginaceae. An oedopodine grasshopper, *Spharagemon equale* (Say), especially in the immature stages, shows a marked preference for members of the mustard family Cruciferae, while several species of *Trimerotropis* are partial to *Astragalus* spp. (Fabaceae). Regarding *Camnula*, Criddle (1933*a*) observed that it has a strong preference for *Agropyron smithii*, *Poa pratensis*, *Hordeum jubatum* and *Bromus inermis* and that green oats are not favourable food for reproduction purposes.

In some grasshopper species it has been found that the food preference changes with the growth stages of the food as also with the growth stages of the grasshopper. Thus Moore (1936) noted that *Agropyron smithii* was not fed upon to any extent by *Camnula* in the spring or fall, but, while in head, it appeared to be a favourite plant. Jacobson and Farstad (1941), Jones (1943), and McBean and Platt (1951) noted varietal resistance of wheat and barley to *M. mexicanus*. Prescott (1951) observed that the declining succulence of range grasses normal to late summer conditions in south-eastern Montana caused a separation of practically all grasshopper species on the short-grass range area into two major groups : (i) the primary range grass-feeders and (ii) forbs-feeders. The separation was so rigid that attempts to starve individuals of one group into eating the other group were unsuccessful. Newton and Esselbaugh (1952) showed the occurrence of a regular sequence of 63 species of adult grasshoppers in eastern Wyoming and divided the over-all grasshopper complex into early, intermediate, and late-developing species. Anderson and Wright (1952), from their daily observation on Montana range lands in 1949, 1950 and 1951, found that the distribution of grasshopper species on range is not random, but is dependent on vegetation and the grasshoppers are selective feeders.

Regarding the change of food preference with the growth stages of grasshoppers. Rubtzov (1932*a*) observed that the range of preference of food-plants generally increases with the development of the grasshoppers and some plants are eaten by nymphs and not by the adults ; this may be due to the hardening of the plant tissues. He (1932*b*) observed that most grasshoppers in Siberia change their habitat during their life cycle the adults living in one and migrating to another for oviposition. The difference in microclimate between the two habitats may be considerable, and the species with habitats in which this difference is greatest exhibits the greatest fluctuations in numbers, leading to outbreaks. In North American grasshoppers, Pfadt (1949*b*) noted that the first - and second-instar nymphs of *Aulocara elliotti* (Thos.) feed chiefly on Sandberg's grass (*Poa secunda* Presl.), while the older nymphs and adults feed almost exclusively on western couch-grass (*A. smithii*), although both the grasses are available in green condition early in the season. Similarly, Scharff (1954) found that all nymphal instars of *M. mexicanus* prefer downy chess (*Bromus tectorum* L.), while the adults feed on some other grasses and forbs. Perhaps this change may be due to the grass ripening very early and having little foliage left when the grasshopper becomes adult. He even contended (*loc. cit.*, p. 486) that "*M. mexicanus*, when the habitat permits, generally chooses plants favourable to its growth and vitality".

Survival, Fecundity and Growth of Grasshoppers.—A large amount of work has been done on the effect of different plants on the survival, fecundity and growth of grasshoppers. Davis (1949), from his surveys in the field, showed that the nymphs, adults and egg-pods of *M. mexicanus* and *M. differentialis* are 40 per cent. less abundant in the grassy field margins than in the weedy ones. In choice of egg-laying sites in the weedy or grassy margins, he found that the egg-pods of these grasshoppers in the grassy margins are only 58 per cent. as numerous as those in the weedy margins. Earlier, Criddle (1933*b*, p. 482) also laid stress on the accessibility of suitable food as an important consideration to oviposition in any given locality.

Pfadt (1949*a*), from his cage experiments on field-collected late-instar nymphs of *M. mexicanus*, found that at the end of a four-week period a very high percentage of mortality (up to 90 per cent.) occurs on the native grasses, *viz.*, sandgrass (*Calamovilfa longifolia* Scribn.), blue grama (*Bouteloua gracilis* Lag.), fescue (*Festuca rubra* L.) and the speargrasses (*Stipa comata* and *S. viridula* Trin.) ; on some broad-leaved plants, *viz.*, lamb's-quarters (*Chenopodium album* L.) and Russian thistle (*Salsola pestifer* A. Nels.), the mortality is also very high (75 per cent.). On the other hand, certain other grasses, *viz.*, downy chess (*Bromus tectorum* L.), crested wheat-grass (*A. cristatum* (L.)), the poas (*P. pratensis* L. and *P. arida* Vasey), wheat and certain broad-leaved plants, *viz.*, sunflower (*Helianthus petiolaris* Nutt.), alfalfa, corn and dandelion (*Taraxacum erythrospermum* Andrz.), gave very low mortality ; on wheat and the broad-leaved plants mentioned, it was even lower (10-18 per cent.). He found the following plants (in descending order of suitability) favourable from the point of view of egg production : dandelion, thistle, Kentucky bluegrass and western couch-grass, there being a high positive correlation of 0·9 between plants which are preferred and plants which afford high survival and a similarly high correlation of 0·76 between survival and production of egg-pods. On rearing *M. mexicanus* from egg to adult stage on eight different plants, Pfadt (*op. cit.*) found significant differences in the size of teneral adults and in their length of nymphal periods, the period being shortest on the most favourable diet. The plants in descending order of favourableness are : tansy mustard=flixweed (*Descurainia sophia* (L.)), dandelion, wheat, downy chess (*B. tectorum*), Kentucky bluegrass, western couch-grass, thistle and alfalfa.

Brett (1947), Smith *et al.* (1952), and Barnes (1955) also studied the effect of food on survival, fecundity and growth of *M. mexicanus* under laboratory conditions in Oklahoma, Canada and Arizona, respectively. They agreed with Pfadt that this grasshopper fares better on forbs than on grasses, and that alfalfa is not a suitable food for growth and fecundity of the grasshopper if this diet is fed to it exclusively and from the earliest stage. Barnes (1955) explained the lack of agreement between field and laboratory observations on the reactions of the grasshopper to alfalfa by pointing out that the weeds in the field supplement the alfalfa diet, and that the mixed diet produces normal to above-normal development.

Tauber *et al.* (1945) reported that wild lettuce and alfalfa effect the highest egg production in *M. bivittatus*, the other high producers being red clover, garden leaf lettuce, onion plants, soybean and sweet clover. On the other hand, caster-oil plant and ripe tomato give the lowest egg record. The interesting points in their work are as follows : (i) Alfalfa and red clover affect reproductive potential favourably, lending support to the suggestion that these, particularly alfalfa may be factors in offering an exceptionally favourable environment for building up a higher population of the grasshopper than a situation where only natural wild food plants grow. (ii) There is a lack of agreement found between egg production and preferred plants ; *e.g.*, corn silk, reported to be eagerly sought by *M. bivittatus* in the fields as well as in cage experiments, ranked seventeenth among 30 food plants tested. (iii) The necessity of abundant succulent food was demonstrated by their experiments on drying and dried foods. These experiments showed that timothy (*Phleum pratense* L.) gives the lowest number of egg pods. Earlier, Bodenheimer (1932) observed in the case of the desert locust, *Schistocerca gregaria*, that fresh, succulent vegetation growing after rainfall may exert a powerful influence in quickening the sex maturation of locusts, and his observation was confirmed in India by Karandikar (Rao, 1942).

Kozhanchikov (1950), in his study of the effect of different food plants on development and sexual maturation of the migratory locust, *Locusta migratoria migratorioides*, in Russia, arranged the food plants in six groups, *viz.*, (i) those on which the complete life cycle can be accomplished ; (ii) those on which nymphal development is completed, although with considerable mortality, but adults do not mature sexually ; (iii) those on which grasshoppers can reach the last instar, but die at the final moult or immediately after, hopper mortality being considerable ; (iv) those on which only the early hoppers survive ; (v) those which are eaten by hoppers of the first instar, which may survive upto 10 days, but are unable to moult ; and (vi) those which are not eaten by first-instar hoppers, even when starved. He concluded that more primitive groups of Acrididae feed mainly on the lower Dicotyledones, while the more advanced Oedopodinae feed mainly on Monocotyledones.

Growth Measurements.—Because of wide application of growth measurements in various fields of biology, there is a long list of very good works published on growth measurements. An exhaustive historical account, as well as methods of computing relative growth, were given by Brody (1927). Calvert (1929) summarized the rates of growth of animals and discussed criteria of growth in general, comparing the criteria in arthropods and vertebrates. The technique of measuring growth on the bases of live weights, linear growth, duration of stadia, rate of growth, fecundity and survival has been employed to test the efficiency of different diets in animals. Thus it has been found in most groups of animals that growth in live weights is continuous, while in linear dimensions it is discontinuous, occurring chiefly and more abruptly at intervals corresponding to shedding of moults. Some of the important papers on the topic of growth are : Shafer (1923), Titschank (1924, 1926), Yagi (1926), Saller (1927), Bodenheimer (1927, 1932, 1933), Schmalhausen (1928), Huxley (1932), Huxley and Teissier (1936), Hodge (1933), Key (1936), Ludwig (1934), Duarte (1938), Woodruff (1939*a*, 1939*b*), Richards (1949), Nagy (1950, 1952), and Davey (1954).

Hodge (1933) gave smoothed growth curves for *M. differentialis* on mixed as well as five exclusive diets and found the mixed diet (lettuce, wheat leaves and apple fruit) the best (82·6 per cent. transformed to adult), the exclusive diets giving the percentage transformation of the grasshopper in the descending order as follows : wheat, 72 per cent. ; barley, 44·4 per cent. ; rye, 42 per cent. ; lettuce, 21·4 per cent. and oats, 4·3 per cent. He found growth rates remarkably similar for all diets excepting those of lettuce and oat leaves, which are unsatisfactory diets.

Rubtzov (1932*c*) measured the amounts of brome leaves ingested by five species of Siberian grasshoppers by means of a millimetre-squared paper and found that the adult grasshopper devours 30 to 50 per cent. of its own weight of the grass in a day, and during its whole development an individual devours 20 times its weight in the adult stage. Sirazitdinova (1935) followed the technique of Rubtzov and determined the amounts of food consumed by four Siberian grasshoppers. On wheat, he found that the amounts eaten in a day varied with the weather, decreasing to 34 to 50 per cent. on dull, cloudy days ; the females, which devoured whole leaves, ate greater amounts than the males, which ate only along the edges of the leaves.

Chauvin (1939), in his experiments on deficient diets on the desert locust, *Schistocerca gregaria*, used a mixed diet of turnips, artichokes, oyster plant, mushrooms and a mixture of wheat grains and haricot beans. He found that the locust matures on this diet, but on the separate components of this diet it develops poorly and does not mature. Later, in 1946, he published the coefficient of utilization of food in the desert locust and found that the adults retain only about 30 per cent. of the weight of food ingested. In India, Husain *et al.* (1946) found that the first instar nymphs of the desert locust absorb about 50 per cent. of the dry matter of food (fig leaves) and that this percentage decreases as the nymphs advance in age till the absorption is only about 30 per cent. in the fourth instar. This figure for the late instars and adults agrees with the figure obtained by Chauvin (1946). Husain *et al.* (*op. cit.*) found that the quality of food affects the duration of nymphal instars. Recently, Davey (1954) published a paper on the relation of food eaten to growth in the desert locust. She found that the percentages of food assimilated fall from 78 in the first to 35 in the fifth stadium. She gave measurements of live weights and lengths of males and females in the nymphal and adult stages and showed that the females become progressively heavier and larger than the males. Earlier, Key (1936) reared the migratory locust, *L. migratoria migratorioides*, at constant temperature and light intensity but in two different relative humidities. He found that famales are, on the average, 50 per cent. heavier than males even in the third instar, that the live weights he obtained at the moults do not fit the theory of doubling of weights and that the nymphs kept in a very dry atmosphere are much lighter than those kept in a moist atmosphere.

III—DIFFERENTIAL FEEDING OF *Camnula pellucida*

1. *Material and Technique*

(a) *Biological Material.*—Adult males and females of *Camnula pellucida* were collected for this experiment on August 3 and 4, 1955, south of Cypress Lake, Saskatchewan, Canada, from a road allowance, where the native vegetation consisted of speargrass (*Stipa comata*), western couch-grass (*Agropyron smithii*), pasture sage (*Artemisia frigida* Willd.) and involute-leaved sedge (*Carex eleocharis* Bail.). Some adults were caught *in copulo* and many others were seen copulating in the cages after they were captured. The grasshopper material was, therefore, sexually mature at that time. The sex ratio of the collected sample of 245 grasshoppers was close to 50:50. A large number of these grasshoppers died in a few days, apparently of disease caused by the fungus *Empusa grylli*.

(b) *Experimental Procedure.*—The grasshoppers were starved for 16 to 24 hours ; and then liberated into a cage measuring (inside) 14·5 in.×14·5 in.×10·5 in. high. In each experiment, at one time four species of plants in three replicates were placed in a circular randomized arrangement. The leaves of the plants were pointed alternately inwards and outwards (Pl. VII, fig. 1). The plants were plucked freshly either from nature or from the greenhouse. In order to keep them succulent for the duration of the experiment, they were inserted through a cork into a vial filled with water. Two light bulbs of 25 watts each were put in the cage, one in the ceiling and the other in the back wall of the cage, uniformly illuminating the cage and keeping a temperature of about 90° F. (32·2° C.). This arrangement minimized the effect of phototropism and temperature gradient. The cage was kept inside a basement room where there was no direct sunlight.

The grasshoppers, after liberation into the cage, were scattered evenly by waving a cloth or some other object. After this they were left undisturbed to settle on the food plants The number of grasshoppers was noted on each replicate of the four plant species in the experiment at intervals of 5, 10 and 20 minutes. Usually the grasshoppers were found to be most actively sampling the different food plants during the first five minutes, in which time they found the plant most palatable to them ; they ceased to show any interest in the food after 20 minutes. After this period they did not feed for several hours and their food response was then very erratic. No observations were, therefore, recorded after 20 minutes.

From other experiments, it was found that the grasshopper showed great predilection for seedlings of barley. This plant, from seedling to the stage prior to the appearance of ears, was, therefore, selected as a standard reference, with the *preference value* (abbreviated, both in singular and plural, P.V.) of 100 per cent for comparison with the other three plant species in each experiment. The total number of grasshoppers feeding on all the three replicates of a plant species was regarded as the measure of preference of the grasshopper for that plant. For comparative and quantitative assessment of the preference, this total number was converted into percentage of a similar total number of grasshoppers found on all the three replicates of barley (taken as 100 per cent). Since greenhouse-grown barley (*Hordeum vulgare* var. *vantage*) was used throughout as a constant reference in each experiment in the same relative position with the other three plant species, the preference values for the plants thus obtained are comparable among themselves with respect to barley.

This technique is similar to that used by Roonwal (1953) in his differential feeding experiments on the desert locust, *Schistocerca gregaria*, in India. The technique differs from that of Pfadt (1949*a*) in being predominantly quantitative. Pfadt, in his experiments, found that his technique, being not quantitative, presented difficulties in accurately evaluating the differential feeding of *M. mexicanus* when two plant species tested were eaten in fairly large proportions. This difficulty, is eliminated in the technique employed in the present study.

2. *Results and Discussion*

(a) Camnula *as a Grass Feeder*.—62 plant species, including 27 grasses, one sedge (*Carex eleocharis* Bail.) and the rest forbs, were tested for the preferential feeding of the clear-winged grasshopper (Table 1). The families of these plants have been arranged into a frequency distribution table (Table 2) of their preferential values with the class interval of 10. It will be seen in this table that the grass family, Poaceae, occurs in 10 out of 11 classes. In the seven classes of high preference values above 40 per cent, Poaceae is the only preferred plant family, with the exception of three families, *viz.*, Chenopodiaceae, Fabaceae and Cyperaceae. This indicates that the clear-winged grasshopper is primarily a grass feeder. Among the classes of low P.V., five families (Poaceae, Chenopodiaceae, Carduaceae, Cruciferae and Umbelliferae) are preferred in the class 31 to 40 per cent ; four families (Poaceae, Chenopodiaceae, Cichoriaceae and Cruciferae are preferred in the next lower class of 21 to 30 per cent ; six families (Poaceae, Polygonaceae, Chenopodiaceae, Rosaceae, Fabaceae and Cichoriaceae) are in the next lower class of 11 to 20 per cent, and 14 families, all forbs except one, in the lowest class of P.V. of 0 to 10 per cent.

TABLE 1

Preference Values (P.Vs) of Camnula pellucida *(Scudder) for Various Grasses and Weeds.*

N. B.—Barley (*Hordeum vulgare* var. *vantage*) was used as the standard grass (with the P. V. at 100%) for comparison with other plants.

Family	Botanical name of plant	Common name of plant	Preference Value (P.V.)
	(A). MONOCOTYLEDONES		
1. Poaceae (grass family)	*Agropyron albicans* Scribn. & Smith	Awned northern wheat-grass	71
	A. cristatum (L.) Gaertn.	Crested wheat-grass	19
	A. desertorum (Fisch.) Scribn.	Crested wheat-grass	36
	A. elongatum (Host.) Beauv.	Tall wheat-grass.	9
	A. intermedium (Host.)	Intermediate wheat-grass	57
	A. repens (L.) Beauv.	Eastern couch-grass	50
	A. riparium Scribn. & Smith	Streambank wheat-grass	30
	A. smithii Rydb.	Western couch-grass	105
	A. trachycaulum (Link) Malte	Slender wheat-grass	50
	Agrostis stolonifera L.	Redtop	55
	Avena sativa L. var. *fortune*	Oats	20
	Beckmannia syzigachne (Steud.) Fern	Sloughgrass	79
	Bouteloua gracilis (H. B. K.) Lag.	Blue grama	17
	Bromus inermis Leyss.	Smooth brome	24
	Calamagrostis inexpansa Gray	Northern reed grass	21
	Elymus junceus Fisch.	Russian wild rye	36
	E. giganteus	..	21
	Festuca rubra L.	Red fescue	35
	Hordeum jubatum L.	Wild barley	59
	H. vulgare L. var. *vantage*	Cultivated barley	100
	Lolium perennae L.	Perennial ryegrass	50
	Phalaris arundinacea L.	Reed canary-grass	131
	Poa ampla Merr.	Big bluegrass	64
	P. compressa L.	Canada bluegrass	43
	P. pratensis L.	Kentucky bluegrass	64
	Stipa viridula Trin.	Green speargrass	53
	Triticum vulgare var. *selkirk*	Selkirk wheat	80
2. Cyperaceae (Sedge family)	*Carex eleocharis* Bail.	Involute-leaved sedge	50

TABLE 1—*contd.*

Family	Botanical name of plant	Common name of plant	Preference Value (P.V.)
	(B). DICOTYLEDONES		
3. Polygonaceae (Buckwheat family).	*Polygonum* sp.		0
	P. convolvulus L.	Wild buckwheat.	17
4. Chenopodiaceae (Goosefoot family).	*Axyris amaranthoides* L.	Russian pigweed	84
	Chenopodium album L.	Lambs' quarters	16
	Kochia scoparia	....	33
	Salsola pestifer A. Nels.	Russian thistle	21
	Beta vulgaris L.	Beet	39
5. Amaranthaceae (Amaranth family)	*Amaranthus retroflexus* L.	Redroot pigweed	0
6. Portulacaceae (Purslane family)	*Portulaca* oleracea L.	Purslane	0
7. Rosaceae (Rose family).	*Rosa* sp.	Wild rose	13
	Potentilla sp.		0
8. Fabaceae (Pea family).	*Astragalus pectinatus* Dougl.	Narrow-leaved milk vetch	0
	Medicago sativa L.	Alfalfa	60
	Melilotus alba Desv.	White sweet clover	0
	Trifolium pratense L.	Red clover	17
9. Malvaceae (Mallow family).	*Malva rotundifolia* L.	Mallow	5
10. Elaeagnaceae (Oleaster family.)	*Elaeagnus commutata* Bernh.	Silverberry	0
11. Carduaceae (Thistle family).	*Artemisia frigida* Willd.	Pasture sage	0
	Cirsium arvense var. *integrifolium* (L.) Scop.	Entire-leaved Canadian thistle	35
	Grindelia perennis A. Nels.	Gumweed	0
	Solidago sp.	Goldenrod	0
12. Plantaginaceae (Plantain family).	*Plantago major* L.	Plantain	7
13. Caprifoliaceae (Honeysuckle family).	*Symphoricarpos accidentalis* Host	Snowberry	3
14. Cichoriaceae (Chicory family)	*Lactuca* sp.	Garden lettuce	0 28
	Sonchus arvensis L.	Perennial sowthistle	18
	Taraxacum officinale Web.	Dandelion	29
	Tragopogon dubius Scop.	Yellow goat's-beard	0

TABLE 1—*concld.*

Family	Botanical name of plant	Common name of plant	Preference Value (P.V.)
15. Cruciferae (Mustard family).	*Brassica oleracea* var. *gemmifera* Zenker	Brussels sprouts .	33
	Brassica oleracea var. *italica* Plenck	Broccoli	29
16. Umbelliferae (Parsley family).	*Petroselinum crispum* Nym.	Parsley	0
	Daucus carota var. *sativa*	Carrots	39
17. Solanaceae (Potato family).	*Datura* sp.	Datura	2
	Lycopersicon pimpinellifolium Mill	Tomato	0
	Petunia axillaris BSP.	Large white petunia . .	5
	Solanum tuberosum L.	Potato	30

TABLE 2

Frequency distribution of Preference Values (P. Vs.) of Camnula pellucida *(Scudder), for various plant families*

Class interval in the P.Vs.	Frequencies	Plant families
101 & above	1	Poaceae.
91—100	1	Poaceae.
81—90	1	Chenopodiaceae.
71—80	1	Poaceae.
61—70	1	Poaceae.
51—60	2	Poaceae, Fabaceae.
41—50	2	Poaceae, Cyperaceae.
31—40	5	Poaceae, Chenopodiaceae, Carduaceae, Cruciferae, Umbelliferae.
21—30	4	Poaceae, Chenopodiaceae, Cichoriaceae, Cruciferae.
11—20	6	Poaceae, Polygonaceae, Chenopodiaceae, Rosaceae, Fabaceae, Cichoriaceae.
0—10	14	Poaceae, Polygonaceae, Amaranthaceae, Portulacaceae, Rosaceae, Fabaceae Malvaceae, Elaeagnaceae, Carduaceae, Plantiganaceae, Caprifoliaceae, Cichoriaceae, Umbelliferae, Solanaceae.

Considering the mean P.V. (Table 3) for the different plant families in the descending order, it will be seen that the grass family, Poaceae, is at the top (P.V. 51·3), indicating primary preference of the grasshopper for the grasses. The goosefoot and mustard families (Chenopodiaceae and Cruciferae) have their P.V. close together (38·7 and 31·3, respectively) and may, therefore, be regarded as comprising the second category. Four families, parsley (Umbelliferae), pea (Fabaceae), chicory (Cichoriaceae) and buckwheat (Polygonaceae) also have their P. V. close to each other (19·6, 19·4, 18·6, and 17·4, respectively) ; these, therefore, may be grouped together in the third category. Another five families, potato (Solanaceae), thistle (Carduaceae), plantain (Plantaginaceae), rose (Rosaceae) and mallow (Malvaceae) have their P. V. close to each other (9·3, 8·7, 7·3, 6·5 and 4·9, respectively) and form the fourth category. The other three families (Amaranthaceae, Portulacaceae and Elaeagnaceae) show the P.V. at zero per cent and are the families which are probably shunned by the grasshopper.

TABLE 3

Mean Preference Values (P.Vs.) of the Camnula pellucida *(Scudder), for the different Plant Families*

Name of plant family	No. of sp. tested	Mean P.V. for the family	Category
1. Poaceae (Grass family) and Cyperaceae	28	51·3	I
2. Chenopodiaceae (Goosefoot family)	5	38·7	II
3. Cruciferae (Mustard family)	2	31·3	
4. Umbelliferae (Parsley family)	2	19·6	III
5. Fabaceae (Pea family)	4	19·4	
6. Cichoriaceae (Chicory family)	4	18·6	
7. Polygonaceae (Buckwheat family)	2	17·4	
8. Solanaceae (Potato family)	4	9·3	IV
9. Carduaceae (Thistle family)	4	8·7	
10. Plantaginaceae (Plantain family)	1	17·3	
11. Rosaceae (Rose family)	2	6·5	
12. Malvaceae (Mallow family)	1	4·9	
13. Amaranthaceae (Amaranth family)	1	0·0	V
14. Portulacaceae (Portulaca family)	1	0·0	
15. Elaeagnaceae (Oleaster family)	1	0·0	

Since the supply of grasshoppers was very limited and their number had decreased very much, no further tests were performed on unpreferred plant species to see if the grasshopper would feed on them under stress. It is, therefore, not possible to say at this stage if these plants (P.V. zero per cent) are avoided even under conditions of starvation. However, the broad inference from these experiments is clear, that *Camnula pellucida* is a grass feeder and that occasionally it may eat a few forbs of the second and third categories (*vide supra*). This inference is supported if Table 4 (*vide infra*) is further examined, in which all the plant species tested here are arranged in order of the frequency distribution of their P.V.

TABLE 4

Frequency Distribution of Preference Values (P.Vs.) of Camnula pellucida (*Scudder*), *for various grasses and weeds*

N. B.—The cultivated plant species have been marked with an asterisk (*).

Class interval in P.Vs.	Frequencies of P.Vs. within class interval	Species of plants	Classification by P.Vs.
101 & above	2	*Phalaris arundinacea**, *Agropyron smithii*	I
91—100	1	*Hordeum vulgare**	
81—90	1	*Axyris amaranthoides*	
71—80	3	*A. albicans*, *Beckmannia syzigachne*, *Triticum vulgare*	II
61—70	2	*Poa ampla*, *P. pratensis*	
51—60	5	*A. intermedium*,* *A. stolonifera*, *Hordeum jubatum*, *Stipa viridula*, *Medicago sativa*	III
41—50	5	*A. repens*, *A. trachycaulum*,* *Lolium perennae*, *Poa compressa*, *Carex*	
31—40	8	*A. desertorum*, *Elymus junceus*,* *Festuca rubra*,* *Kochia scoparia*, *Beta vulgaris*, *Cirsium arvense*, *Brassica oleracea* var. *gemmifera*,* *Daucus carota**.	IV
21—30	9	*A. riparium*, *Bromus inermis*,* *Calamagrostis inexpansa*, *Elymus giganteus*, *Salsola pestifer*, *Lectuca*,* *Taraxacum*, *Brassica oleracea* var. *italica**, *Solanum tuberosum**.	
11—20	8	*A. cristatum**, *Avena sativa*,* *Bouteloua gracilis*, *Polygonum convolvulus*, *Chenopodium album*, Wild rose, *Trifolium pratense*,* *Sonchus arvensis*.	
0--10	19	*A. elongatum*,* *Polygonum* sp., *Amaranthus retroflexus*, *Portulaca oleracea*, *Potentilla* sp., *Astragalus pectinatus*, *Melilotus alba*, *Malva rotundifolia*, *Elaeagnus commutata*, *Artemisia frigida*, *Solidago*, *Grindelia perennis*, *Plantago*, *Symphoricarpos*, *Tragopogon dubius*, *Petroselinum crispum*,* *Lycopersicon pimpinellifolium*, *Petunia axillaris*, *Datura* sp.	

The conclusion that *Camnula* is predominantly a grass feeder is borne out by observations of previous workers in Canada as well as in the United States. Thus, Treherne and Buckell (1924) observed in British Columbia that the food of this grasshopper both in the nymphal and adult stages consists entirely of the grasses and grains. Moore (1936) found the same situation in Manitoba. Hebard (1925, p. 76), in South Dakota, observed that "areas of short grass, best for grazing purposes, are always the most infested" with *Camnula*.

(b) *Grasses Preferred by* Camnula.—Having seen that the grasshopper is mainly a grass feeder, it would be interesting to find out which grass species are preferred by this grasshopper. Table 4 gives a frequency distribution among the P.V. of all the individual species tested in this experiment. In this table, the plant species can be broadly divided into four classes. The first three of these classes (above 40 per cent P.V.), including 16 grasses, one sedge and two forbs, are dominated by grasses, while the fourth class has 33 forbs and only 11 grasses. The classification is as follows :

Class I : This class, in order of the preference values, is composed of reed canary-grass (*Phalaris arundinacea*, P.V. 131), western couch-grass (*A. smithii*, P.V. 105), cultivated barley (*Hordeum vulgare* var. *vantage* standard reference 100 per cent) and Russian pigweed (*Axyris amaranthoides*, P.V. 84). The last-mentioned plant is a forb.

Class II : This class comprises five grasses, *viz.*, awned northern wheat-grass (*A. albicans*, P. V. 71), sloughgrass (*Beckmannia syzigachne*, P. V. 79), Selkirk wheat (*Triticum vulgare*, P. V. 80), big bluegrass (*Poa ampla*, P. V. 64) and Kentucky bluegrass (*Poa pratensis*, P. V. 64).

Class III : This class has nine grasses and a forb, *viz.*, intermediate wheat-grass (*A. intermedium*, P. V. 57), redtop grass (*A. stolonifera*, P. V. 55), wild barley (*Hordeum jubatum*, P. V. 59), green speargrass (*Stipa viridula*, P. V. 53), alfalfa (*Medicago sativa*, P. V. 60, a forb), eastern couch-grass (*A. repens*, P. V. 50), slender wheat-grass (*A. trachycaulum*, P. V. 50), perennial ryegrass (*Lolium perennae*, P. V. 50, an imported weed which is quite common in grain fields), Canada bluegrass (*Poa compressa*, P. V. 43) and involute-leaved sedge (*Carex eleocharis*, P. V. 50).

Class IV : This class comprises 33 forbs and 11 grasses. The latter are as follows : Crested wheat-grass (*A. desertorum*, P. V. 36), Russian wild rye (*Elymus junceus*, P. V. 36), red fescue (*Festuca rubra*, P. V. 35), streambank wheat-grass (*A. riparium*, P. V. 30), brome (*Bromus inermis*, P. V. 24), northern reedgrass (*Calamagrostis inexpansa*, P. V. 21), *Elymus giganteus* (P. V. 21), oats (*Avena sativa* var. *fortune* P. V. 20), crested wheat-grass (*A. cristatum*, P. V. 19), blue grama (*Bouteloua gracilis*, P. V. 17) and tall wheat-grass (*A. elongatum*, P. V. 9). Of these, four or five are the more important ones which are extensively cultivated in the Canadian Prairies as good pasture crops ; these are the two crested wheat-grasses, Russian wild rye, brome and tall wheat-grass. Most of these grasses were imported from Russia not long ago. Tall wheat-grass is being currently tried in demonstration areas and, being the lowest among the grasses tested, it appears to hold promise as a possible choice for seeding.

Among the grasses having high P. V., reed canary-grass and western couch-grass top the list. Reed canary-grass (*Phalaris arundinacea*) is a tall and leafy forage grass of the wet meadows, cultivated in Saskatchewan. It is very hardy and when once established it will tolerate occasional dry seasons. It has been known to be palatable for cattle, although it tends to become coarse. During the 1947-53 period, 26,706 pounds of seed of this grass were sold to farmers in the agricultural representative districts (Nollet, 1954). The other grass, western couch-grass (*A. smithii*), was mentioned by Criddle (1933*a*, 1933*b*, p. 479). Moore (1936) also found that western couch-grass supported the heaviest infestation of *Camnula* in Manitoba. He, however, found that this grass was eaten mainly while in head. Riegert (1948), in Montana, used crushed leaves of this grass to evoke an olfactory response in the grasshopper, which appears to indicate that the grass is highly palatable to *Camnula*.

Fraser *et al* (1954) show the distribution of this grass in Saskatchewan in the brown, dark brown and black soil zones. The brown soil zone particularly covers the area round Swift Current, Maple Creek, and the area around Cypress Lake, where *Camnula* has been found in large populations for the last several years and where the adult grasshoppers, as well as the eggs, were secured for this study.

Among the grasses of Class II (P. V. 60 to 80 per cent), the important ones are wheat and the Poas (*P. ampla* and *P. pratensis*), the two species of the latter having equal P. V. (64·3 each). Kentucky bluegrass, I was told by Mr. Putnam, grows in the province of British Columbia, and he has found the outbreak of *Camnula* often associated with areas of this grass. Criddle (1933*a*) and Moore (1936), in Manitoba, found the sod of western couch-grass and Kentucky bluegrass heavily infested with *Camnula* egg pods, and, when these grasses are not available, brome, wild barley and timothy (*Phleum pratense L.*) provide suitable substitutes.

In Saskatchewan, Putnam (1954, p. 134) has observed that "characteristically it [*Camnula*] feeds in grâin fields or other sources of succulent food supply" and Pickford (1954, unpublished) finds that *Camnula* prefers the succulent leaves of young wheat plants to the native grasses growing on field margins. In the field margins, he found involute-leaved sedge as the most preferred plant. This sedge, in the classification (Table 4), falls in class III and has the P. V. 50.0 (lower than the Poas and wheat). It is possible that, in a certain plant association, sedge might get all the attention of the grasshopper. In fact, in November, 1955, we found the *Carex* sod in the field margin of a summerfallow wheat field around Cypress Lake, near Robsart, Saskatchewan, as our richest source of *Camnula* egg pods. This would suggest that the grasshopper had concentrated on the compact sod for egg laying and was feeding on the sedge, if it was not too dry. In the same general area of Cypress Lake, observations were made on the preferential feeding of *Camnula* in a plant association consisting of *A. smithii*, *Stipa comata*, *Carex eleocharis* and *Artemisia frigida*. In this association, where *A. smithii* and *Carex* occurred together, the former was observed to be getting much greater attention.

(c) *Importance of Food Preference*.—It has been stated (Putnam, 1954, p. 134) that *Camnula* characteristically feeds in the grain fields or on other succulent food. In the fall (August-September), after feeding in the field, the adults retire in large concentrations to suitable breeding areas for egg laying, basking and feeding.

These breeding areas "may be sod or turf areas of a roadside or verge an overgrazed small pasture, the bank of a slough, creek or coulee or a barnyard" (Putnam, *op. cit.*). In close proximity to the fields, such areas may be the marginal allowances between the field and the roadside ditch, fence rows or the road allowances. These situations, besides providing suitable places for oviposition, must have succulent and palatable vegetation for the adults and the young nymphs when they emerge in the spring. Criddle (1933*a*) observed, in Manitoba, both in the fields as well as in cage experiments that a large number of natural egg beds were abandoned by the grasshopper because of the lack of succulent vegetation even after the insects had begun to oviposit. He was convinced that "in every case the absence of succulent food, or moisture resulted in a marked reduction in breeding activity and at times in death". The grasshopper thus shows preference both for *site* as well as *food* (Criddle, *loc. cit.*, p. 100).

Succulence, or moisture content, of the grass is one of the important prerequisites for its palatability. The highest P. V. for reed canary-grass (131) in the differential feeding experiments is perhaps due to this factor. Williams (1954) has reported that, of all the physical factors affecting the feeding response of grasshoppers, moisture content of the grass is the most important. Toughness of the grass in itself does not make it unacceptable, excepting perhaps in the case of young nymphs. However, there must be other factors of a chemical nature involved too, because the grasshopper shows a low preference for perennial sowthistle (P.V. 18) and tall wheat-grass (P. V. 9), although they are very succulent food. That toughness is of little consideration in the choice of food is noticeable in *Camnula*, for it shows high preference for western couch-grass and involute-leaved sedge.

The grasshopper does exercise some kind of choice among the reasonably succulent and green vegetation also. A study of the preference values of the grasses is thus of great importance in understanding the ecology of the breeding places of *Camnula*. Criddle (1933*a*) found in Manitoba that "a majority of its eggs are to be found among the roots either of *Agropyron smithii* Rydb. or *Poa pratensis* L." and, in the absence of these grasses, *Hordeum jubatum* or *Bromus inermis* is the next choice. *Carex* sod in the field margin near Robsart (*vide supra*), found to be full of *Camnula* eggs, is another such example.

The study of food preference of *Camnula* is important in another aspect also. The eggs laid in the summer and fall (August-September) commonly reach about 50 per cent of total embryonic development in the fields before the diapause sets in ; in this stage, they pass the winter months. The nymphs emerge in the spring (about May-June), which is also the time the grains are emerging in the fields. Depending on the weather conditions governing the time of sowing of the grains, the seedlings will appear either at the same time as the emergence of the nymphs or earlier or later. The nymphs naturally sample the grasses around the place of their emergence first. If the grasses were of a high enough preference value, but low in promoting growth and egg production, they could keep the nymphs from invading the distant crop and also discourage or retard egg production. In this way, such grasses could possibly form a trap, as Brett (1947) regarded alfalfa for *M. mexicanus*. Although there is a high positive correlation between highly preferred plants and their nutritional adequacy to the grasshopper (Pfadt, 1949*a*), an inverse ratio between the two is possible for plants which do not rank very high in preferability. The nutritional requirements of the grasshopper change with its development, resulting in a lack of agreement between the food plants preferred during the growth period and those preferred during the development of the gonads. In situations where the nymphs are forced to eat the grasses for a while before they have the choice to attack the crop in the field, the low P. V. grasses might be able to starve them.

The observations of several authors on the change of preference for food-plants of the grasshopper with their growth are interesting (Pfadt, 1949*b* ; Scharff, 1954). This raises the important question as to whether the grasshoppers are able to select the food most beneficial to them in their current stage of growth. Scharff (1954) has answered the question in the affirmative : "when the habitat permits". This qualification perhaps implies that the most beneficial food is also the most palatable, and the grasshopper will give first preference to such a food, if it is available. But there are also a few observations which are contradictory to this theory. Thus, Brett (1947), Smith *et al* (1952), and Barnes (1955) have found in the case of *M. mexicanus* that alfalfa is not a satisfactory diet for the growth of the nymphs, although it is preferred as the *third* or *fourth* choice (Pfadt, 1949*a*). The first two choices of this grasshopper are dandelion and wheat, which are undoubtedly the most beneficial to it (upholding the theory that preferability and favourability are correlated). Smith *et al* (1952) have reported 65 per cent survival on dandelion and only 20 per cent on alfalfa (which is, after all, the fourth choice). They found that the duration of nymphal life on dandelion is 46·5 days and on alfalfa, 58·5 days, and that the average number of eggs laid on wheat diet is 116·9 and only 12·9 on alfalfa.

In the absence of highly preferred food-plants in the field, the third or fourth choice, taken under stress, may actually be harmful, as alfalfa has proved in the case of *M. mexicanus*. To use Scharff's (1954) expression, the grasshopper will eat dandelion and wheat every time if the "habitat permits". This raises our hopes that careful quantitative investigations of food preference will enable us to discover a grass or forb which will be reasonably palatable to the grasshopper but at the same time will discourage its breeding.

IV—EFFECT OF FOOD ON SURVIVAL AND DEVELOPMENT OF *CAMNULA PELLUCIDA*

Food is one of the important elements in the environment controlling the chances of an animal to abound in nature. The quality and, to some extent, the quantity of food greatly modify the speed of the development, survival and longevity of the animal. In this chapter, three experiments are reported using 22 grasses and a sedge for noting the survival and development of the grasshoppers reared on them.

1. Material and Technique

(a) *Biological Material*

(i) *Grasshoppers.*—The grasshopper nymphs for these experiments were obtained in the laboratory from eggs collected near Cypress Lake in south-western Saskatchewan in the fall of 1954 and the spring of 1955. The eggs were stored in the refrigerator until they were needed. The chilling ensured the breaking of diapause in the eggs collected in the fall and did not harm the eggs collected in the spring, in which development had progressed up to the diapause stage in the field. The eggs, when incubated, hatched in five to seven days.

(ii) *Host Plants.*—Twenty-two grasses and a sedge were used ; these consisted of both native and introduced cultivated grasses, and four cereals. Excepting for the sedge and eastern couch-grass, all others were grown from seeds either purchased or received from the Dominion Forage Laboratory at Saskatoon or the Dominion Experimental Station at Swift Current. Eastern couch-grass and the sedge were dug out as sod in the field and transplanted into pots. The grasses and the sedge offered to the grasshoppers in cages were in early leaf stage.

(b) *Rearing*

(i) *Greenhouse.*—The experiments were conducted in a compartment of the Science Service greenhouse at the University of Saskatchewan, Saskatoon. The temperature of the compartment was maintained at 90° F. (32.2° C.) by a controlled steam-heating arrangement. The relative humidity and temperature were recorded on a hygrothermograph for the duration of one of the experiments and an occasional check was kept on the temperature and humidity for the rest of the experiments. The temperature of the greenhouse, at the level of the cages, was fairly steady at 90° F. (32·2° C.) with a daily rise up to 100° F. (37·8° C.) during the noon for a couple of hours on sunny days. The relative humidity, on the other hand, fluctuated between 30 and 50 per cent. A table fan kept the air in the compartment and the cages in proper motion for good ventilation.

(ii) *Growing of Grasses.*—In the second and the third experiments at least 20 pots of each grass were kept in reserve to ensure that the grasses eaten down in the experimental pots could be replaced. Insufficient provision was made for this in the first experiment ; on this account, a few grasses had to be withdrawn from the experiment in the third week. The cereals were grown within a fortnight of their requirement in the experiment because they grew the quickest of all grasses. During the experiment, each pot was put in a clay saucer and the grass was watered every morning and afternoon from beneath. At almost every weekly examination, the grass on which the nymphs had fed for the week was replaced by a fresh pot of grass so that the nymphs always had more than sufficient grass to eat and the grass in the experiment also stayed in good condition.

(iii) *Rearing of Grasshoppers.*—Each cage for rearing was made of a wire-gauze cylindrical design, 12 in. high and $7\frac{3}{4}$ in. in diameter. It was fitted into the grass pot on the soil enclosing the grass and was covered on the top by a piece of nylon netting held on by a rubber band cut from a used tyre tube. A layer of sand was put on the top soil in the pot before introducing the nymphs. This prevented the salts in the soil from efflorescing on the surface and reduced the humidity in the cage. Twenty-five freshly hatched nymphs were introduced in every cage at the start of the experiment.

(c) *Experimental Design and Procedure*

Three experiments were performed over a period of two years. The first experiment was started on March 22, 1955, the second on March 21, 1956, and the third experiment was begun on May 1, 1956. Six grasses used in the first experiment were repeated in the second experiment along with six new ones, and seven of the first experiment were repeated in the third experiment along with five new ones. Thus all the grasses of the first experiment, with the exception of oats, were repeated in the second or the third experiment to check the results.

Each experiment consisted of 12 treatments in a randomized block design, using 12 species of grasses, and each treatment consisted of four replicates. Thus, there were 100 nymphs in a treatment at the start of the experiment and the total number of nymphs found alive in a treatment at weekly intervals was regarded as the percentage survival for that week. Two grasses, *viz.*, wheat and barley (cultural varieties *selkirk* and *vantage*, respectively), were used in each experiment to serve as controls.

The cages in all the three experiments were examined at the end of weekly intervals and the number of surviving nymphs along with the data of their developmental stages were recorded. The tested food-plants of the grasshopper, therefore, can be judged from the standpoint of (i) survival alone and (ii) survival and development. The latter is expressed by the *survival and development index** (abbreviated, both in singular and plural, S.D.I.), which is the sum of the products of the number in each instar by the number of the instar. For example, if, out of the original population of 100, the cage population was found to consist of six fifth instar nymphs and eight adults, the S.D.I. would be $(6\times5)+(8\times6)=78$, while the percentage survival would be 14.

The weekly mean S.D.I. of the grasshopper for the replicates and treatments of food-plants (varieties or species of plants) were analyzed for *variance* in a random block design. A series of tables was prepared for each experiment, arranging the mean S.D.I. in descending order for each week and giving the differences between mean values of the best (maximum S.D.I.) individual grass and the remainder on one hand and that between the worst (minimum S.D.I.) and the remainder on the other. These differences were then judged against the *least significant difference* (L.S.D.) at 0·05 and 0·01 levels of significance to make groups of plants which (i) do not differ from the best grass at either the 0·05 or the 0·01 level ; (ii) do not differ from the best at the 0·01 level only, but differ at the 0·05 level ; (iii) do not differ from the poorest grass (minimum S.D.I.) at both the levels.

If the difference between two mean values is found to be as great or greater than the L.S.D. at 0·05 level of significance, the inference is that the odds are 19:1 against such a difference being due to chance alone and that two grasses, therefore, are inherently different so far as the S.D.I. are concerned ; the mean value being compared is, then, called "significantly different" from the mean with which, the comparison is made. Setting a higher level of significance, at 0·01 makes the discrimination of differences even more critical ; at this level the odds are 99:1 against such a difference being due to chance alone. If the mean value is significantly different at both the levels, it is called "very significantly different" or "highly significantly different".

*This method of quantitatively estimating the survival and development of the grasshopper was suggested by Mr. L. G. Putnam.

Wheat and barley gave very good survival in the first experiment, while in the second and third experiments they proved to be relatively poor supporters. This trend was consistently observed throughout the winter and spring of 1955-56, whenever an experiment was conducted. In order that seed-borne disease might not be a cause of deterioration of the cereal seedlings, these seeds were dusted with a fungicide before sowing in the second and third experiments. Watering the pots from the saucers beneath was regulated, fertilizer was put in the soil for all the grasses to improve growth and a layer of sand at the top was provided to decrease the humidity. Notwithstanding all these precautions, the survival of the grasshopper on the cereals was consistently poor this year, *i.e.*, 1956.

2. Results and Discussion

(a) *Survival on Different Grasses.*—Table 5 gives the percentage survival of the grasshopper at the end of weekly intervals in the three experiments. In the first experiment during the first week, big bluegrass (*Poa ampla*), fescue and barley gave the highest survival (85 per cent in each case), while six other grasses, *viz.*, slender wheat-grass (*Agropyron trachycaulum*), northern wheat-grass (*A. dasystachyum*), Canada bluegrass (*P. compressa*), Selkirk wheat (*Triticum vulgare*), brome (*Bromus inermis*) and crested wheat-grass (*A. cristatum*), gave more than 80 per cent survival. During the second week, big bluegrass, wheat, fescue and barley continued to sustain the grasshopper at a steady high level of survival. In the third week, the nymphs showed steady high survival on fescue, barley and wheat, while in the fourth week fescue emerged to be the only grass which gave survival close to 80 per cent.

TABLE 5

Percentage survival of Camnula pellucida (*Scudder*) *on different grasses*

N.B.—The following data sum up the observations of three experiments performed over a period of two years. I, March, 1955; II, March, 1956; and III, May, 1956. The results of these experiments can be identified by the Roman numerals. The first experiment did not last as long as the other two because the supply of plants was exhausted.

Serial No.	Botanical name of grass	Experiment No.	Percentage survival				
			First week	Second week	Third week	Fourth week	Fifth week
1.	*Agropyron albicans*	I	72	65	43	..	..
		III	23	20	20	17	16
2.	*A. cristatum*	I	81	71	66	..	..
		III	26	26	25	23	23
3.	*A. elongatum*	II	67	57	56	39	20
4.	*A. dasystachyum*	I	82	61	36	..	..
		III	23	20	19	17	17
5.	*A. intermedium*	I	78	74	51	..	..
		III	19	18	18	18	18
6.	*A. repens*	III	20	17	17	17	17
7.	*A. riparium*	III	24	21	19	18	17
8.	*A. trachycaulum*	I	83	61	24	..	..
		II	79	63	58	48	15
9.	*Bromus inermis*	I	81	69	44	26	..
		II	80	59	54	44	14

TABLE 5—*concld.*

Serial No.	Botanical name of grass	Experiment No.	Percentage survival: First week	Second week	Third week	Fourth week	Fifth week
10.	*B. tectorum*	II	60	30	21	13	12
11.	*Elymus canadensis*	II	59	35	23	20	14
12.	*E. junceus*	II	66	33	17	7	3
13.	*Festuca rubra*	I	85	82	79	79	..
		III	43	39	37	37	37
14.	*Poa ampla*	I	85	85	50	27	..
		II	79	72	69	45	20
15.	*P. compressa*	I	82	63	26	..	..
		II	81	66	62	52	20
16.	*P. pratensis*	II	69	66	57	42	19
17.	*Stipa spartea*	III	2	2	2	2	2
18.	*S. viridula*	II	68	36	32	29	23
19.	*Avena sativa* var. *fortune*	I	71	34	31	9	..
20.	*Hordeum vulgare* var. *vantage*	I	85	81	79	29	..
		II	65	40	31	25	18
		III	25	24	23	22	20
21.	*Triticum vulgare* var. *selkirk*	I	82	82	78	54	..
		II	51	20	10	6	3
		III	16	12	9	6	6
22.	*Secale cereale*	III	28	26	25	25	23
23.	*Carex eleocharis*	III	22	18	16	16	16

In the second experiment, started about the same time the following year, six of the grasses used in the first were repeated. Apart from the cereals (barley and wheat), all the other grasses repeated in this experiment, *viz.*, slender wheat-grass, brome, big bluegrass, Canada bluegrass, gave in the first week the percentage survival figures more or less of the same magnitude as before. In the second week, all these grasses, excepting the cereals, continued to give better survival than the other new grasses tested in this experiment and big bluegrass stood out as the best, giving 72 per cent survival. This grass was the best in the second week of the first experiment also. In the third week, big bluegrass remained the best grass and slender wheat-grass was the second best. In the fourth week, Canada bluegrass, big bluegrass and slender wheat-grass gave a high percentage of survival. Finally, in the fifth week, the grass that gave the highest survival turned out to be speargrass (*Stipa viridula*). A set of next-best grasses was Canada bluegrass and tall wheat-grass (*A. elongatum*).

In the third experiment, seven of the grasses used in the first experiment were repeated. Here again, excepting the cereals used in the first experiment, all the grasses common in the two experiments gave good survival. In the first week, 43 per cent of the nymphs survived on fescue, 26 per cent on crested wheat-grass and 28 per cent survived on rye (*Secale cereale*), and all these three grasses maintained their relatively high position throughout the period of five weeks of the experiment.

(b) *Survival and Development on Different Grasses.*—Table 6 gives the survival and developmental indices of the grasshopper for 22 grasses and a grass-like plant in the three experiments. The information in this table is condensed from five weekly tables for each of the three experiments. The S.D.I. of one experiment are comparable with the S.D.I. of the other experiments only qualitatively, and the L.S.D. for each of the 15 tables of the three experiments are different.

TABLE 6

Survival and Developmental Index of Camnula pellucida *(Scudder), on different Grasses at the end of weekly Intervals in three experiments (I, II, III)*

Serial No.	Botanical name of grass	Experiment No.	Survival and Development Index				
			First week	Second week	Third week	Fourth week	Fifth week
1.	*Agropyron albicans*	I	34	44	42	..	..
		II	10	14	19	19	21
2.	*A. cristatum*	I	34	53	64	..	..
		III	12	18	24	27	32
3.	*A. dasystachyum*	I	37	45	30	..	..
		III	9	13	17	19	22
4.	*A. elongatum*	II	26	42	66	54	29
5.	*A. intermedium*	I	32	57	68	66	65
		III	9	13	18	22	26
6.	*A. repens*	III	8	12	17	21	24
7.	*A. riparium*	III	10	14	16	20	22
8.	*A. trachycaulum*	I	33	44	20	15	15
		II	37	56	70	70	22
9.	*Bromus inermis*	I	32	40	41	29	27
		II	30	42	59	56	19
10.	*B. tectorum*	II	23	23	23	21	17
11.	*Elymus canadensis*	II	23	23	22	29	17
12.	*E. junceus*	II	26	20	15	9	4
13.	*Festuca rubra*	I	43	72	94	109	113
		III	21	28	38	46	54
14.	*Poa ampla*	I	44	64	43	20	19
		II	29	53	75	59	28

TABLE 6—*concld.*

Serial No.	Botanical name of grass	Experiment No.	Survival and Development Index: First week	Second week	Third week	Fourth week	Fifth week
15.	*P. compressa*	I	39	51	28	19	23
		II	39	62	78	78	30
16.	*P. pratensis*	II	34	63	65	62	29
17.	*Stipa spartea*	III	1	1	2	2	3
18.	*S. viridula*	II	22	23	30	33	30
19.	*Avena sativa* var. *fortune*	I	23	24	29	37	33
20.	*Hordeum vulgare* var. *vantage*	I	40	76	80	38	33
		II	26	29	32	33	25
		III	12	18	23	27	27
21.	*Triticum vulgare* var. *selkirk*	I	41	68	79	85	87
		II	24	15	11	8	4
		III	6	7	8	6	7
22.	*Secale cereale*	III	13	21	27	31	32
23.	*Carex eleocharis*	III	7	10	12	16	19

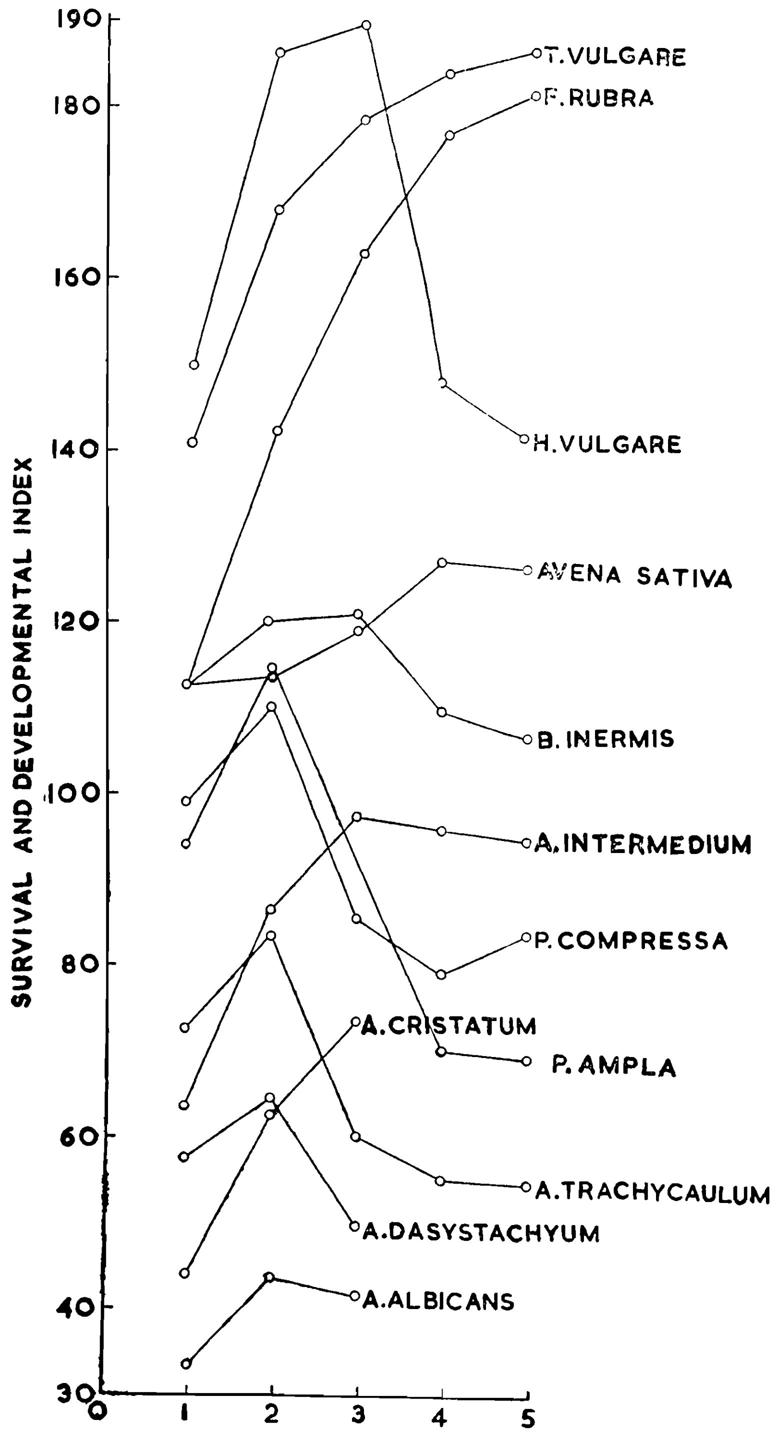
In the first experiment, at the end of the first week, big bluegrass showed the highest mean S.D.I. of 44 and is, therefore, the best grass for the first week, while oats showed the lowest S.D.I. of 23 and is, therefore, the worst. Since the difference of mean S.D.I. of this grass and that of any other grass is higher than the L.S.D. at the 0·01 level of significance, this grass is very significantly different from any other grass and may be regarded as *development retarding*. There are five grasses, *viz*., fescue (S.D.I. 43), wheat (S.D.I. 41), barley (S.D.I. 40), Canada bluegrass (S.D.I. 39) and northern wheat-grass (S.D.I. 37), in which the mean indices do not differ from the best grass (big bluegrass) at the 0·01 level ; each of these, therefore, may possibly be as good as the best grass and the whole group may be regarded as the group of grasses promoting fastest development, or briefly, *development promoting grasses*. The remaining five grasses, *viz.*, crested wheat-grass (S.D.I. 34), awned northern wheat-grass (S.D.I. 34), slender wheat-grass (S.D.I. 33), intermediate wheat-grass (S.D.I. 32) and brome (S.D.I. 32), are very significantly different from the best as well as from the worst grass ; these, therefore, may be regarded as the *borderland grasses*, which are neither particularly good nor bad.

In the second week, the best grass was no longer big bluegrass (S.D.I. 64) ; its place was taken by barley, having its S.D.I. as 76, while big bluegrass was relegated to the fourth among the promoting grasses, the other two next to barley being fescue (S.D.I. 72) and wheat (S.D.I. 68). Fescue, wheat and big bluegrass do not differ from the best grass (barley) at the 0·01 level and are, therefore, regarded here as development promoting grasses in the second week. Oats had the least S.D.I. (24), and the difference of this mean from the mean value of any other grass being very significant, it stays as the only development retarding grass in the second week also. There are seven other grasses, *viz.*, intermediate wheat-grass (S.D.I. 57), crested wheat-grass (S.D.I. 53), Canada bluegrass (S.D.I. 51), northern wheat-grass (S.D.I. 45), slender wheat-grass (S.D.I. 44), awned northern wheat-grass (S.D.I. 44) and brome (S.D.I. 40), which are very significantly different from the best as well as from the worst. These seven grasses, therefore, belong to the borderland group. In a general way, it may be noted that among the development promoting grasses, the position of fescue remains unchanged, and similarly among the borderland group and the development retarding grasses, the position of brome and oats remains at the bottom of the scale.

In the third week, the highest mean S.D.I. was for fescue (S.D.I. 94). Two other grasses, *viz.*, barley (S.D.I. 80) and wheat (S.D.I. 79), do not differ from the best at the 0·01 level. In fact, as the S.D.I. show, fescue is by far the best grass and the two cereals are inferior to it, although the three may be regarded as development promoting grasses. The S.D.I. for slender wheat-grass was the least, being 20. If the difference from this mean index and that of any other grass is reckoned, three other grasses, *viz.*, northern wheat-grass (S.D.I. 30), oats (S.D.I. 30) and Canada bluegrass (S.D.I. 28), do not differ from it at the 0·01 level ; all the four of these grasses, therefore, may be regarded as development retarding grasses. The thing to note here is the promotion of brome and oats in the scale and degradation of the others.

In the fourth and fifth weeks, fescue had the highest S. D. I. (109 in the fourth and 113 in the fifth week) and slender wheat-grass the lowest S. D. I. (15 in the fourth and 15 in the fifth week). During these two weeks, the positions of the best and the worst grasses were unchanged on the scale of S. D. I. and so also the position of the next best (wheat), which had a S. D. I. of 85 for the fourth week and 87 for the fifth week. In both of these weeks, wheat did not differ from the best (fescue) at the 0·01 level. There was a small amount of reshuffling in positions between and within the borderland and the retarding grasses ; this is, perhaps, a matter of detail only. In a general way, it may be said that the remaining seven grasses, *viz.*, intermediate wheat-grass, oats, barley, brome, Canada bluegrass, big bluegrass and slender wheat-grass, are more or less development retarding if the later instars and adults are fed on them exclusively.

The curves of survival and developmental indices of the grasshopper on 12 grasses tested in the first experiment are given in Text-Fig. 1. Each curve, from the bottom has been displaced upward by 10 degrees to accommodate all the curves in one figure. These curves are intended to show the shape of the curves rather than the quantitative fluctuations in values. Three of the grasses, *viz.*, awned northern wheat-grass (*A. albicans*), northern wheat-grass (*A. dasystachyum*) and crested wheat-grass (*A. cristatum*), were exhausted earlier and had to be discontinued after three weeks ; these, therefore, also stop earlier in the graph.



TEXT-FIG. 1.—Survival and developmental indices of *Camnula pellucida* on various grasses. Each subsequent curve from bottom has been displaced upward by 10° to relieve congestion. The index denotes surviving number of hoppers in the different instars × the weightage assigned for that instar : 1, 2, 3, 4, 5, 6, for 1st, 2nd, 3rd, 4th, 5th and 6th adult, respectively. For values of S.D.I. see table 6.

In Text-Fig. 1, it will be seen that four of the grasses, *viz.*, fescue, wheat, oats and intermediate wheat-grass, show a more or less steeply rising trend throughout their course and are, therefore, the best grasses taken as a whole. On the other hand, barley, brome, Canada bluegrass, big bluegrass and slender wheat-grass show a declining tendency during most of their course.

Among the best four grasses, the curve of fescue shows the steepest rise during the second week ; that of wheat is less steep, of intermediate wheat-grass even less, while that of oats is almost horizontal, showing very poor survival and development of the grasshopper. In fact, during this time, oats, being the worst of all, is the only grass whose curve is horizontal, while the curves of all the other eleven grasses show a rising slope to varying degrees. During the third week, the curves of these four grasses show the steepness relative to each other in the same order as in the second week. However, the curve of wheat shows a tendency to flatten, which represents a widening difference in the S. D. I. of fescue and wheat ; the curve of intermediate wheat-grass shows the flattening tendency to a lesser extent than that of wheat, because this grass showed an improvement in its S. D. I.; the curve of oats, on the other hand, shows the greatest swing upward from its horizontal position to an obtuse angle, showing that this cereal grass, though injurious to the early instar nymphs, is comparatively better for them in their later development. During the fourth week, the curve of oats keeps on rising in a straight line much like the curve of fescue, and that of wheat becomes more flat than it was in the third week, while that of intermediate wheat-grass actually bends down. This shows a great improvement in the status of oats, but it still remains in the category of development retarding grasses ; wheat, although it retains its second-best position among the two development promoting grasses, diverges in its S. D. I. from the best grass in a steady manner, while intermediate wheat-grass goes down from the borderland group to the retarding group of grasses.

If the results of the three experiments are compared (Table 7), the general conclusions of the first experiment are confirmed except in the case of wheat, barley and slender wheat-grass. In these three cases, the results of the three experiments are inconsistent : the two cereals deteriorated in the second and third experiments, while slender wheat-grass showed an improvement up to the first four weeks on its results of the first experiment in the previous year. Regarding the fifth week, there is a close agreement in the two experiments when the grass falls into the group of retarding grasses.

TABLE 7

Weekly ranking of the host grasses with respect to the survival and development of Camnula pellucida (*Scudder*) *in the three experiments* (vide *Table 6*).

N.B.—The grasses are designated by numbers used in Table 5 and arranged in descending order of their Survival and Development Indices (S.D.I.) within the category.

Category	experiment	First week	Second week	Third week	Fourth week	Fifth week
Development promoting grasses.	I	14, 13, 21, 20, 15, 3.	20, 13, 21, 14	13, 20, 21	13, 21	13, 21
	II	15, 8	16, 15, 8, 14	15, 14, 8, 4, 16, 9	15, 8, 16, 14, 9	15, 18, 4, 16, 14, 20.
	III	13	13, 22	13	13	13
"Borderland" grasses	I	2, 1, 8, 5, 9	5, 2, 15, 3, 8, 1, 9	5, 2, 14, 1, 9	5, 20	—
	II	16, 9, 14, 4, 20, 12	9, 4	20, 18	4, 20, 18	—
	III	22, 2, 20, 1, 7, 5, 6, 3, 23, 21.	2, 20, 1, 7, 5, 3, 6, 23, 21.	22, 2, 20, 1, 5, 3, 6, 7, 23, 21	22, 2, 20, 5, 6, 7, 1, 3, 23.	2, 22, 20, 5, 6, 7, 3, 1, 23.
Development retarding grasses.	I	19	19	3, 19, 15, 8	19, 9, 14, 15, 8	5, 19, 20, 9, 15, 14, 8.
	II	21, 10, 11, 18	20, 18, 11, 10, 12, 21.	10, 11, 12, 21	11, 10, 12, 21	8, 9, 10, 11, 21, 12.
	III	17	17	17	21, 17	21, 17

Fescue, by common agreement in the first and third experiments, is the best grass, giving the grasshopper steadily high survival and rapid development. It would be difficult to say what the status of the cereals is because of the inconsistent results. Perhaps wheat is a little better than barley ; the latter seems to be good for the early instars but not quite so good for the later instars (Text-Fig. 1). The three Poas seem to form a group of second-best grasses ; they are good for the grasshopper for the first three or four weeks, after which the S. D. I. of all these three fall steeply. Perhaps Canada bluegrass and big bluegrass are better than Kentucky bluegrass because of higher peaks of S. D. I. reached by them (Table 6, Experiment II : 78, 75 and 65, respectively). Canada bluegrass and Kentucky bluegrass seem to have the merit of keeping the grasshopper at a high, flat top of the peak for a period of two weeks, the S. D. I. in the second, third and fourth weeks for Canada bluegrass being 62, 78 and 78 and that for Kentucky bluegrass being 63, 65 and 62, respectively. Brome, crested wheat-grass, the two northern wheat-grasses (*A. albicans* and *A. dasystachyum*), intermediate wheat-grass and sedge belong to the borderland group of grasses, which are very important in the ecology of breeding places of *Camnula.* These are the grasses that keep up populations of the grasshopper at a steady level till better food plants become available. No one grass, excepting, to some extent, fescue, seems to be good enough for the grasshopper for its entire life. This may be due to changes in the nutritive value of the grasses (Heinrichs and Carson, 1956) and also to changes in the needs of the grasshopper, as it grows from instar to instar.

V—GROWTH OF *CAMNULA PELLUCIDA* ON EXCLUSIVE DIETS

Growth has two aspects, *viz.*, the course of growth and the rate of growth. The course of growth is studied by cumulative, or summation curves, which integrate all the successive magnitudes of gains added from time to time (as the age advances) into a continuous whole picture. The slope of the curve tells the magnitude of these gains in growth, which may be by rapid or by slow degrees. The slope, however, does not show directly the fluctuations in the rate by which the gains were attained. This information is revealed by plotting the successive differences in grains from time to time, which gives the curve of first differences, or increments, or rate of growth, or simply the velocity curve (Brody, 1927 ; D'Arcy Thompson, 1942).

Growth is the result of utilization of food, which, in turn, takes into account the amounts of food eaten and faeces voided. The more nutritive the food is, the larger is the quantity utilized in the body for the production of live weight. The quality of food, therefore, largely influences the growth of the animal, its speed of development, its longevity and fecundity.

1. *Material and Technique*

(a) *Biological Material*

(i) *Grasshoppers.*—The grasshopper nymphs used in this experiment were reared in the laboratory from eggs collected near Cypress Lake in south-western Saskatchewan in the fall of 1954 and the spring of 1955. The newly emerged nymphs, soon after their "intermediate", or "embryonic", moult (Nelson, 1931, p. 478 ; Uvarov, 1928, p. 42), were weighed and put on exclusive diets in the cages, their average weight ranging from 5·24 to 6·52 mgm.

(b) *Equipment*

(i) *Cages.*—The cages used in the earlier experiments were of glass cylinders, 6 in. × 1½ in. in dimensions. The two ends of the cages were closed by nylon netting held on by rubber bands. In the later experiments, the cages used were made of Sealright ice cream boxes (Pl. VII, Fig. 5) about 5½ in. high and 4½ in. in diameter. Three windows, 3¼ in. × 3 in. each, were cut in the wall and Saran plastic screen 20 meshes to an inch, was fixed all along the inner wall of the box. The design of this cage was suggested by Mr. Roy Pickford of the Dominion Entomology Laboratory, Saskatoon and it proved excellent, being very simple in design, easy to make, providing very good ventilation, and affording a foothold for the moulting nymphs.

(ii) *Incubation and other equipment.*—In the earlier experiments, on *Agropyron intermedium* and *Triticum vulgare*, the glass cages were put in an incubator, the temperature of which was thermostatically maintained at 90° F. (32·2° C.). A fan, forcing air over an open surface of water, maintained the relative humidity at 40 to 50 per cent. In the later experiments, a large wooden cabinet (Pl. VII, Fig. 6) was set up and adjusted to give a constant temperature of 90° F. (32·2° C.) and a relative humidity in the range of 50 to 55 per cent. The required range of humidity was achieved by putting a limited-range Aminco-Dunmore electric hygrometer sensing element in a circuit with a baby-bottle warmer. The latter was connected to a relay and was filled with distilled water which, under the control of the hygrometer sensing element and the relay evaporated and supplied the required humidity. When the relative humidity rose above the range of the sensing element the relay disconnected the current to the bottle warmer thereby reducing the evaporation to the minimum. A feeding device was used to keep the level of water constant. An electric fan kept the air in the cabinet in circulation and maintained good ventilation in the cages.

For drying the grasses and faeces a Precision-Thelco vacuum oven Model 19A (Pl. VII, Fig. 7) was used. The grasses and the faeces were dried at 100° C. and at 25 inches of mercury pressure for two days.

(c) *Experimental Procedure*

Nymphs from the same lot which had emerged during the night were collected in the morning by means of an aspirator and were placed in a flask so that each sample was randomized. Only the nymphs emerging within two days of the first wave of emergence were used. Six experiments were conducted at different times each on a different kind of grass or sedge. Four experiments using involute-leaved sedge, brome, fescue and Kentucky bluegrass had four replicate cages in each experiment. One of the other two experiments using intermediate wheat-grass had only two replicates while the experiment on Selkirk wheat used no replicates. In the first four experiments each cage had 25 nymphs thus giving the total of 100 nymphs in the experiment ; in the fifth experiment the total used was 50, while in the last experiment it was 40. In the experiment on wheat, when the nymphs had moulted to the second instar in large numbers on one day, they were inactivated by chilling and were quickly sorted into males and females under a binocular microscope. They were then reared separately in two cages. The data collected from this experiment were used to study the pattern of growth in live weights in the developmental stages of males and females.

The nymphs were reared collectively, each 'culture' being regarded as a representative population of males and females found in the field.

Determinations of food ingested, faeces voided and percentage of food utilized are based on oven-dry matter and are calculated as per milligram of body weight of the grasshopper before that food was utilized. This gives a uniform basis for comparison of the data on different grasses.

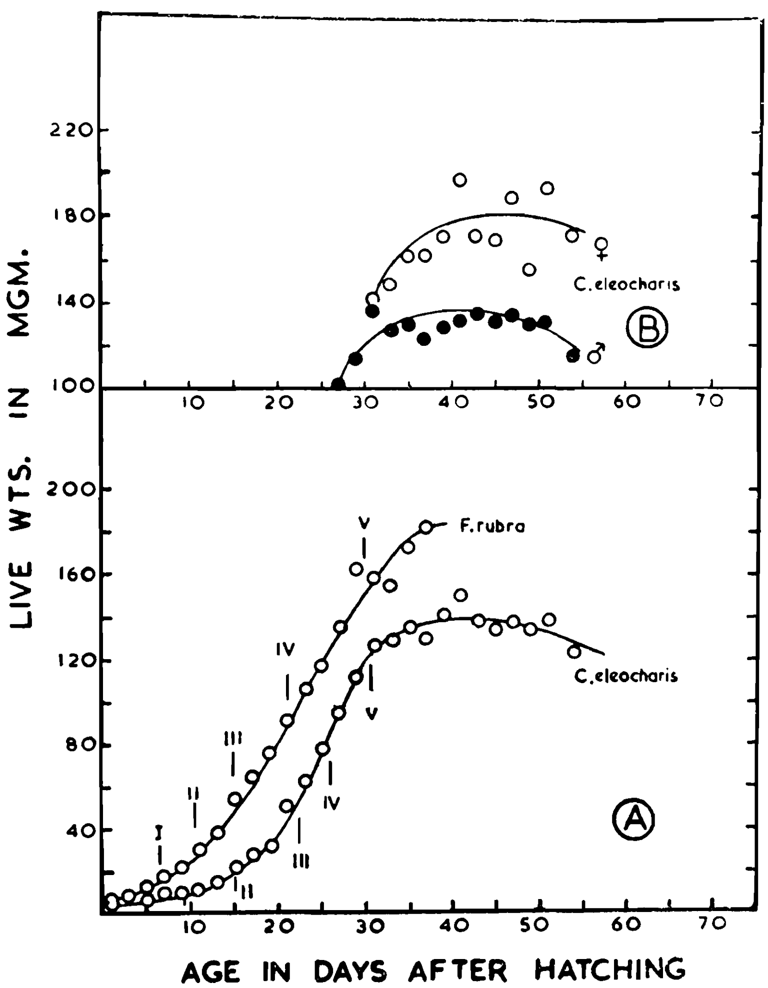
Weighed amounts of food were supplied to the population in each cage. The food was changed on alternate days and the residual food removed for drying. A parallel sample of fresh food taken from the same pot and weighed was put in the vacuum oven to determine the dry to green-weight ratio. On the basis of this oven-dry to green-weight ratio the total amount of dry matter in the fresh food offered to the nymphs was calculated. From this amount, the oven-dry weight of the residual food was deducted to give the total dry matter eaten by all the nymphs in the cage. This quantity, divided by an average number of nymphs found alive at the time of offering fresh food and at the time of removing the residual food, gives the amount of dry matter ingested by an average nymph during the two-day period. The faeces were removed at the same time as the residual food and were also oven dried. Cumulative weight of oven-dry faeces deducted from the cumulative weight of oven-dry food ingested (per mgm. body weight in both cases) gives the progressive utilization of food. This quantity, divided by the amount ingested and multiplied by 100, gives the percentage utilization of food. The rate of growth in live weights of the grasshopper on each grass has been determined by taking an average of increase in live weight for three successive observations involving four or more days. The next determination includes the weight increase on the second and the third observations with the fourth. This *running average* has uniformly smoothed the graph.

2. *The Course of Growth*

(a) *Duration of Stadia and Live Weights Attained on Exclusive Diets*

It is well-known that the quality and quantities of food eaten by insects have a great effect on the length of stadia and the live weights attained by them. An attempt has been made here to compare the length of stadia and live weights attained by the grasshopper on some of the grasses. These grasses vary in texture and water content and some of them figure prominently in the habitat of the grasshopper and others could do so.

(i) *Involute-leaved sedge* (Carex eleocharis).—Of all the plants used in this section, the sedge has the highest oven-dry to green-weight ratio (0·355). The mid-rib of the sedge is very stiff and the nymphs of early stages nibbled the leaves only along the



TEXT-FIG. 2.—Cumulative live weights (A) and sexual dimorphism in live weights (B) attained by *Camnula pellucida* fed on *Carex eleocharis* during the course of development. The live weight curve of *Camnula* fed on *Festuca rubra* is also given for comparison.

edges, leaving the mid-rib untouched. The nymphs feeding on this sedge were very irritable and difficult to handle. The moment the lid of the cage was opened even a little, they tended to jump in all directions and great care had to be exercised in handling them. On the 11th day of their life, when the mortality had become very high, water was provided in each cage by inverting a glass vial full of water on a Petri dish lined with filter paper. In comparison, the nymphs on other grasses were very docile and could be handled without difficulty. Tauber *et al* (1944) reported a similar phenomenon of nervous behaviour in the two-striped grasshopper (*Melanoplus bivittatus*) reared on dried grasses.

The nymphs moulted to second instar, on the average, at 9·6 days after hatching, to third instar at 15·4 days, to fourth instar at 22·4 days, to fifth instar at 26·0 days and to the adult stage at 30·8 days after hatching (Table 8). On the observed day (31st day), closely following the average final moult, the actual population from the four replicates consisted of five adult males, two adult females, three fifth instar nymphs, one third instar and another fourth instar nymph (Table 14).

TABLE 8

Course of growth of Camnula pellucida (*Scudder*), *on an exclusive diet of Involute-leaved sedge* (Carex eleocharis *Bail.*)

Instar	Average live weight at beginning of instar (mgm.)	Age at beginning of instar (days after hatching)	Progression growth factor
I	5·92	..	..
II	9·57	9·57	1·62
III	22·43	15·35	2·34
IV	57·76	22·43	2·58
V	86·08	25·97	1·49
Adult	124·06	30·80	1·44

It is interesting to note that on the last average day of their pre-adult life, the population had an individual as much physiologically retarded as the third instar and another one as the fourth instar nymph. If the live weights of these stragglers are compared with the average live weights of nymphs at the beginning of the instars (Table 8), it will be seen that the third instar nymph was an oversized individual, weighing 59·8 mgm. (average weight of early fourth instar being 57·76 mgm.). Since the difference in the two weights is not large, this nymph could be a female. It moulted to the fourth instar on the 32nd day and died in that stage on the 39th day.

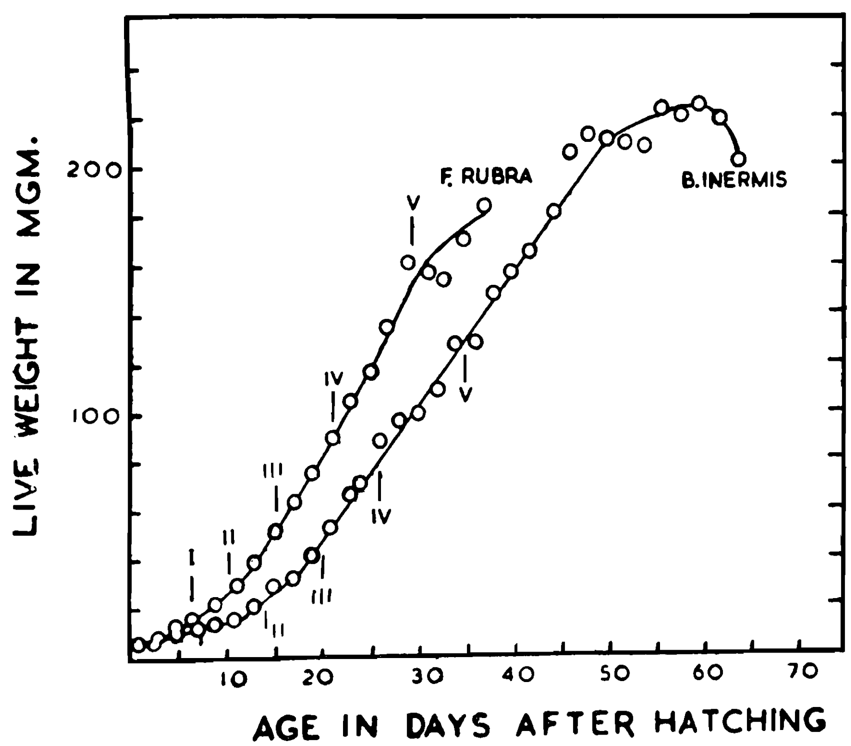
It is difficult to place much reliance on the relative weights attained by the males and females on *Carex* diet, since the numbers of teneral males and females were five and two, respectively, and of mature males and females at the termination of the experiment were six and one, respectively. However, the weights attained by the males and females on the average final moult were 136·86 and 140·75 mgm., showing the superiority of the female in weight by only three per cent : $\left[\left(\frac{\text{Mean wt. female}}{\text{Mean wt. male}} - 1\right) \times 100\right]$. At the termination of the experiment on the 54th day, the female weighed 171·2 mgm. and the male, 114·98 mgm., the sexual-dimorphism percentage of the female being 49 per cent (Text-fig. 2B) more than the male.

The course of growth of the grasshopper in live weights on sedge diet is shown in Text-fig. 2A ; the graph has the characteristic sigmoid form. It shows a slow growth in the initial stages followed by at first gradual and then rapid increase in live weight till the point of inflection of the curve is reached about the 25th day, when the curve starts swinging horizontally, indicating declining rate of growth. This phenomenon is brought out more vividly in the velocity curve (Text-fig. 9) showing average rate of growth in live weights.

The progression growth factor in live weights is shown in Table 8 as 1·62 from first to second instar, 2·34 from second instar to the third, 2·58 from third to fourth, 1·49 from fourth to fifth and 1·44 from fifth to the adult stage, the pattern of growth being low, higher, highest, respectively, from first to fourth instar and declining in the next two stages. There is more than doubling of live weights between second and third and third and fourth instars and the growth factor is at its peak in the third to fourth moult. The average for all of these five stages is 1·89, which is below Przibram's (1912) growth factor, although quite close to it.

(ii) *Smooth brome grass* (Bromus inermis).—This is a succulent grass, its oven-dry to green-weight ratio being 0·198. It is extensively cultivated on the prairies.

On this grass the nymphs moulted, on the average, to second instar at 7·4 days, to third instar at 13·6 days, to fourth instar at 20·2 days, to fifth instar at 25·3 days and to the adult stage at 35·0 days after hatching (Table 9). The observation, closely



TEXT-FIG. 3.—Cumulative live weights attained by *Camnula pellucida* fed on *Bromus inermis* (during the course of its development). The live weight curve of *Camnula* fed on *Festuca* is also given for comparison.

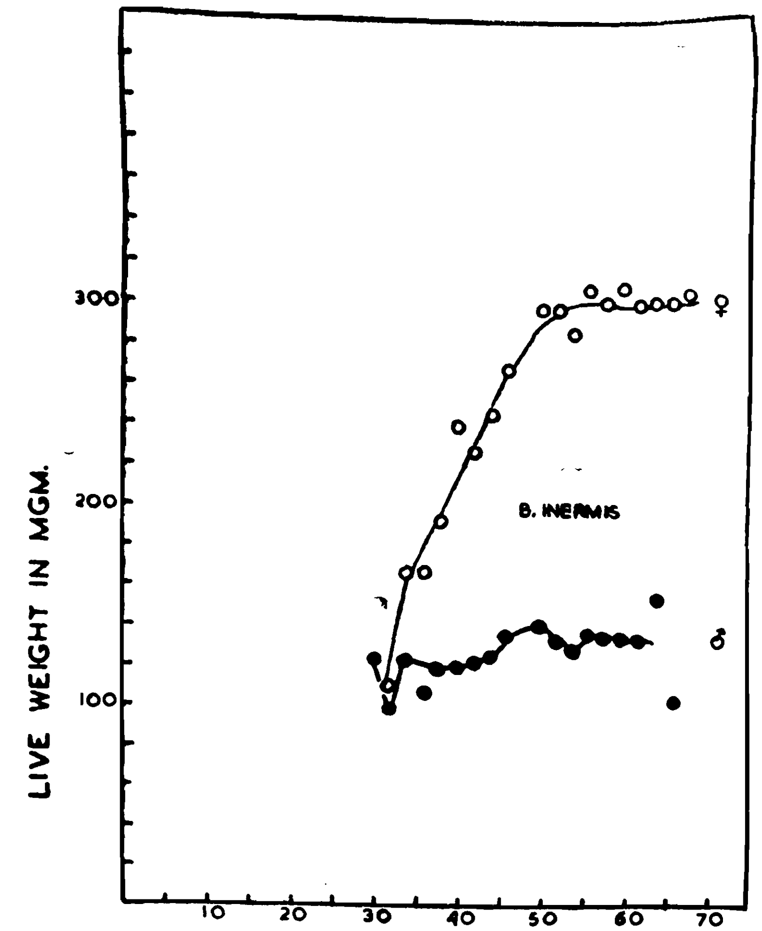
after the average final moult, was on the 36th day on which the population consisted of 23 individuals out of the original population of 100. These consisted of four adult females and 11 adult males, besides one nymph in the fourth instar and seven in the fifth (Table 17). Thus on brome diet, unlike on sedge diet, all the nymphs except one were close to the final moult. The fifth instar nymphs on this day weighed, on the average, 143·11 mgm., which, considering the average live weight of teneral adults as 136·36 mgm., appears to be excessive. All of these fifth instar nymphs were, however, females, which would account for their heavy average weight. The straggling fourth instar nymph looked a weakling for its live weight of only 40·1 mgm. on the 36th day. If it was nearing the fifth moult, it would have still to put on double its weight to make an average for the fifth instar nymph. However, this retarded nymph did not do well, as the subsequent observations would show : it weighed 49·5 mgm. on the 38th day, 40·0 mgm. on the 40th day, 54·2 mgm. on the 42nd day, 46·19 mgm. on the 44th day, 61·8 mgm. on the 46th day and ultimately died on the 50th day, still a fourth instar nymph.

TABLE 9

Course of growth of Camnula pellucida (*Scudder*), *on an exclusive diet of Smooth Brome Grass* (Bromus inermis *Leyss.*)

Instar	Average live weight at beginning of instar (mgm.)	Age at beginning of instar (days after hatching)	Progression growth factor
I	5·98	..	..
II	12·16	7·43	2·03
III	22·20	13·62	1·83
IV	48·34	20·19	2·28
V	81·86	25·25	1·69
Adult	128·67	35·02	1·57

The sexual dimorphism percentage (Text-fig. 4) of the grasshopper on brome diet is higher than on sedge diet. The teneral males and females on the average day (36th day) of final moulting weighed 107·88 mgm. and 164·0 mgm., respectively, the female being 52 per cent heavier than the male. At the termination of the experiment on the 66th day there were eight males and seven females. This is quite



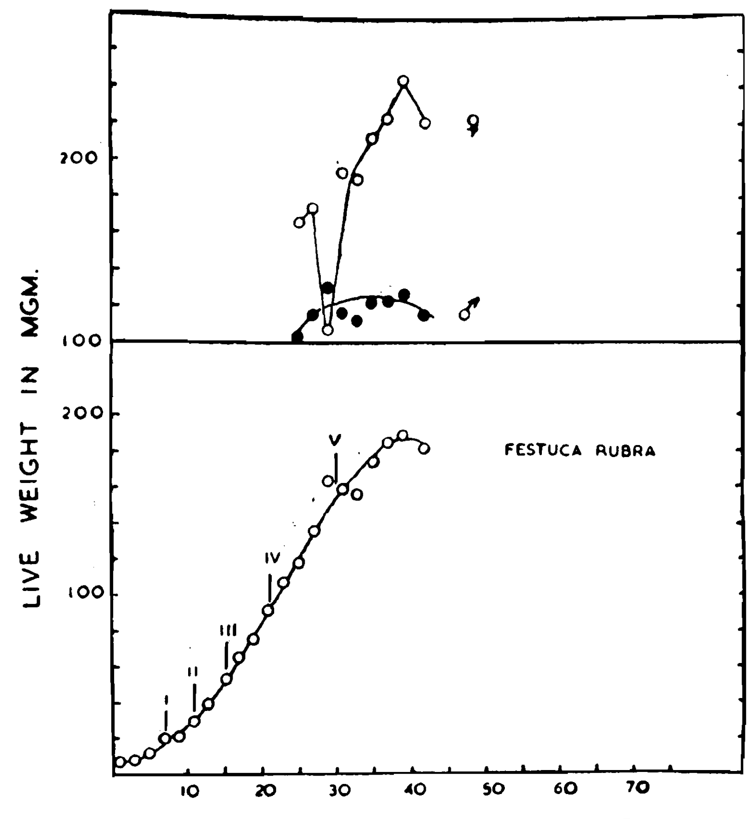
TEXT-FIG. 4.—Sexual dimorphism in live weights attained by *Camnula pellucida* fed on *Bromus inermis*.

a balanced sex ratio in the population and would give a good idea of the sexual dimorphism in live weights of the grasshopper on brome diet. The males and females on this day weighed, on the average, 102·45 mgm. and 287·47 mgm., respectively, the females being 180·6 per cent heavier than the males.

The course of growth of the grasshopper on brome is seen as a very slant sigmoid curve indicative of slow rate of growth (Text-fig. 3). The point of inflection in this curve is reached rather early on the 24th day when 69 per cent of the pre-adult life was covered, while in grasshoppers on sedge diet, this point was reached on the 25th day when about 80 per cent of their pre-adult life was covered. The nymphs on brome at this time weighed 68 mgm., while those on sedge at this point weighed 81·17 mgm.

The progression growth factor in live weight is 2·03 from first instar to the second, 1·83 from second instar to the third, 2·28 from third instar to the fourth, 1·69 from fourth to the fifth and 1·57 from fifth instar to the adult stage (Table 9). The doubling of live weights as envisaged by Przibram and Megusar (1912) occurs twice, the first time from first instar to the second and the second time from third to the fourth instar. The change from second to third instar is close to the doubling ratio. The whole pattern shows a proportionately quick growth in live weight up to the fourth instar and then a slow growth up to the end of the pre-adult life. The average of the five stages is only 1·86, which is less than the average of the sedge-fed grasshopper and far below Przibram's growth factor.

(iii) *Red fescue* (Festuca rubra).—This grass is less succulent than brome, having its oven-dry to green-weight ratio as 0·275. In appearance, however, it looks more tender and the grasshoppers ate it with greater avidity than brome.



TEXT-FIG. 5.—Cumulative live weights (lower fig.) and sexual dimorphism in live weights (upper fig.) attained by *Camnula pellucida* fed on *Festuca rubra* during the course of its development.

On the average, the nymphs moulted to second instar at 6·8 days, to third instar at 10·7 days, to fourth instar at 15·3 days, to fifth instar at 21·4 days and to the adult at 30 days after hatching (Table 10). In observation, closely after the average final moult, *i.e.*, on the 31st day, the population consisted of 21 males, 20 females and 14 fifth instar nymphs (Table 15). Thus, on this day most of the nymphs had transformed to the adult stage and those that did not were close to their final moult ;

the fifth instar nymphs attained on this day an average weight of 157·42 mgm. as compared to the average live weights of the tenerals as 159·38. This is indicative of uniform and quicker growth of the grasshopper on fescue diet than on sedge and brome diets.

TABLE 10

Course of growth of Camnula pellucida (*Scudder*), *on an exclusive diet of Red Fescue* (Festuca rubra *L.*)

Instar	Average live weight at beginning of instar (mgm.)	Age at beginning of instar (days after hatching)	Progression growth factor
I	6·52	..	..
II	15·55	6·83	2·38
III	28·33	10·65	1·82
IV	54·28	15·26	1·92
V	93·45	21·43	1·72
Adult	159·38	29·97	1·71

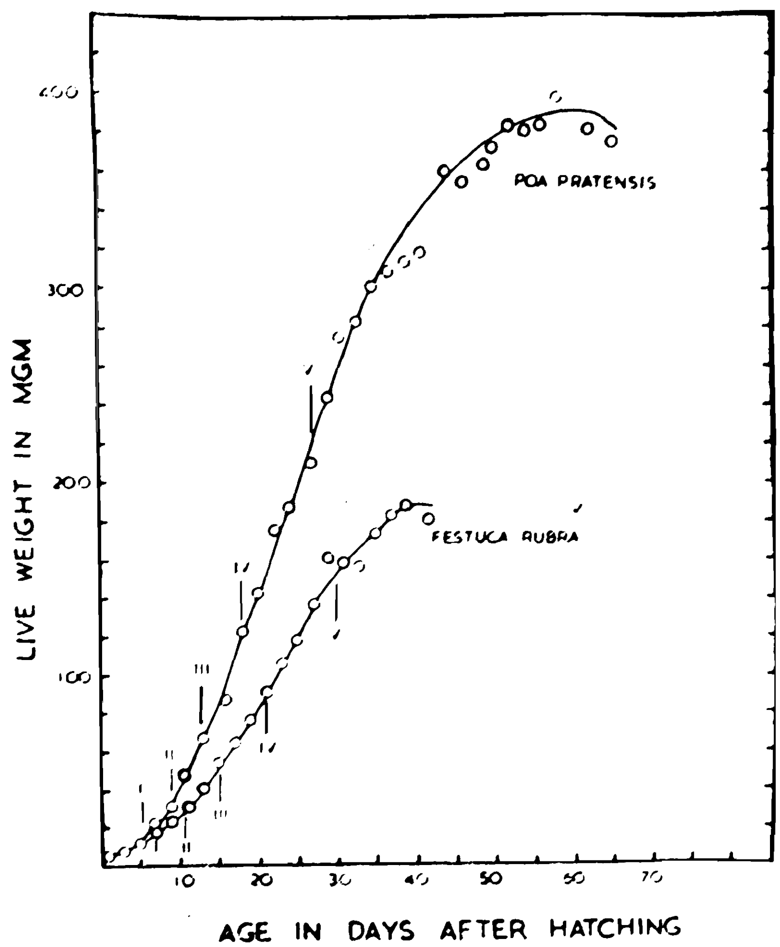
The population composition of fescue-fed grasshoppers at the average final moult was 21 males and 20 females. This ratio is even better than the ratio observed in brome-fed grasshoppers at their average final moult. The fescue-fed males on the 31st day weighed, on the average, 120·06 mgm. and the females, 195·88 mgm., their sexual dimorphism percentage being 63·15. At the termination of the experiment on the 42nd day, the sex ratio in the population had become more uneven, there being 17 males and 29 females, or 37 per cent males and 63 per cent females. In live weights, the females had acquired proportionately more body weight than the males, as would be apparent from the sexual dimorphism percentage at this stage. The males now weighed 115·28 mgm. and the females, 216·72 mgm., the latter being 87·99 per cent heavier than the males. If the grasshoppers reared on fescue and brome are compared for their sexual dimorphism for this day (42nd day), it would be found that the fescue-fed female is heavier than the brome-fed one, the former being 79·53 per cent heavier.

The course of growth of a fescue-fed grasshopper is seen as a more upright curve than that of a brome-fed grasshopper (Text-fig. 5), indicating a higher level of live weight attained on fescue diet. The point of inflection of the curve is reached on the 27th day, when the average live weight of the grasshopper population was 134·77 mgm. as against the average weight of 68·0 mgm. attained by the brome-fed grasshoppers on their point of inflection on the 24th day.

The progression growth factor in live weight is 2·38 from first instar to the second, 1·82 from second to the third, 1·92 from third to the fourth, 1·72 from fourth to the fifth instar and 1·71 from fifth instar to the adult stage (Table 10). The weights are more than doubled from first instar to the second, and keep close to the doubling ratio from second instar to the third and from third to the fourth instar. In the later instars, the growth keeps a high level, too. On the average, the progression growth factor for all the five stages is 1·9, which is close to Przibram's growth factor.

(iv) *Kentucky bluegrass* (Poa pratensis).—This grass is less succulent than fescue, its oven-dry weight to green-weight being 0·295. However, in appearance it looks very tender.

On the average, the nymphs moulted to second instar at 5·4 days, to third instar at 9·1 days, to fourth instar at 13 days, to fifth instar at 18 days and to adult stage at 27·3 days after hatching (Table 11). In observation on the 29th day, closely following the last moult, there were only eight females left in the experiment, weighing, on the average, 243·68 mgm. (Table 16). In live weight, the average teneral female was about 24 per cent heavier than a similar fescue-fed female and was the heaviest of all teneral females reared on the six grasses and the sedge. It is interesting to note in this experiment that, although equal numbers of males and females (10 of each) crossed the fifth moult, 50 per cent of the males died with the loose moult on them and the remaining males died within four days after moulting. One of the females, which moulted on the 24th day, was much deformed, having a big blister on her right hind wing. Most of the dying individuals, both adults and nymphs in the fourth



TEXT-FIG. 6.—Cumulative live weights attained by *Camnula pellucida* fed on *Poa pratensis* during the course of its development. Live weight curve of *Camnula* fed on *Festuca* is also given for comparison.

and fifth instar, gave out a red viscous fluid from the rectum. Quite a portion of the faecal pellets were seen coloured red. This fluid is perhaps some broken down product of chlorophyll digestion. A similar red pigment was reported in the gut of *Vanessa* (Linden, 1905), although its chemical nature is not clearly understood.

TABLE II

Course of growth of Camnula pellucida *(Scudder), on an exclusive diet of Kentucky Bluegrass* (Poa pratensis *L.*)

Instar	Average live weight at beginning of instar (mgm.)	Age at beginning of instar (days after hatching)	Progression growth factor
I	6·17	..	
II	14·13	5·41	2·29
III	32·16	9·10	2·24
IV	66·03	13·08	2·05
V	120·84	17·94	1·83
Adult	208·07	27·30	1·72

The course of growth curve of the grasshopper on Kentucky bluegrass is a great deal more upright than the curve on fescue (Text-fig. 6). A good deal of this divergence in the adult life, showing higher live weights attained, is no doubt due to the population consisting entirely of the females, particularly in the adult life. However, since the curve diverges from the curve on fescue consistently from the very beginning, it is clear that the weights attained by the grasshopper on this food are much higher than weights attained by the grasshopper on other diets.

The progression growth factor in live weights is 2·29 from first instar to the second, 2·28 from second to the third, 2·05 from third to the fourth, 1·83 from fourth to the fifth and 1·72 from fifth to the adult stage (Table 11). There is more than doubling of weights between the first and the fourth instars, and in the next two stages also the progression growth factor is close to two, as envisaged by Przibram (1912).

(v) *Intermediate wheat-grass* (Agropyron intermedium).—In succulence, this grass is between brome and fescue, its oven-dry to green-weight ratio being 0·249. This ratio is, however, from one sample only.

The grasshopper moulted, on the average, to second instar at 7·9 days, to third instar at 13·0 days, to fourth instar at 18·8 days, to fifth instar at 27·3 days and to adult stage at 37·3 days after hatching (Table 12). Of the two replicate cages in the experiment, in one, a single fifth instar nymph was all that survived ; it moulted to adult stage on the 30th day. In the other replicate there were two fifth instar female nymphs which moulted on widely different days. Thus, one nymph moulted to adult stage on the 38th day, while the other moulted on the 44th day.

TABLE 12

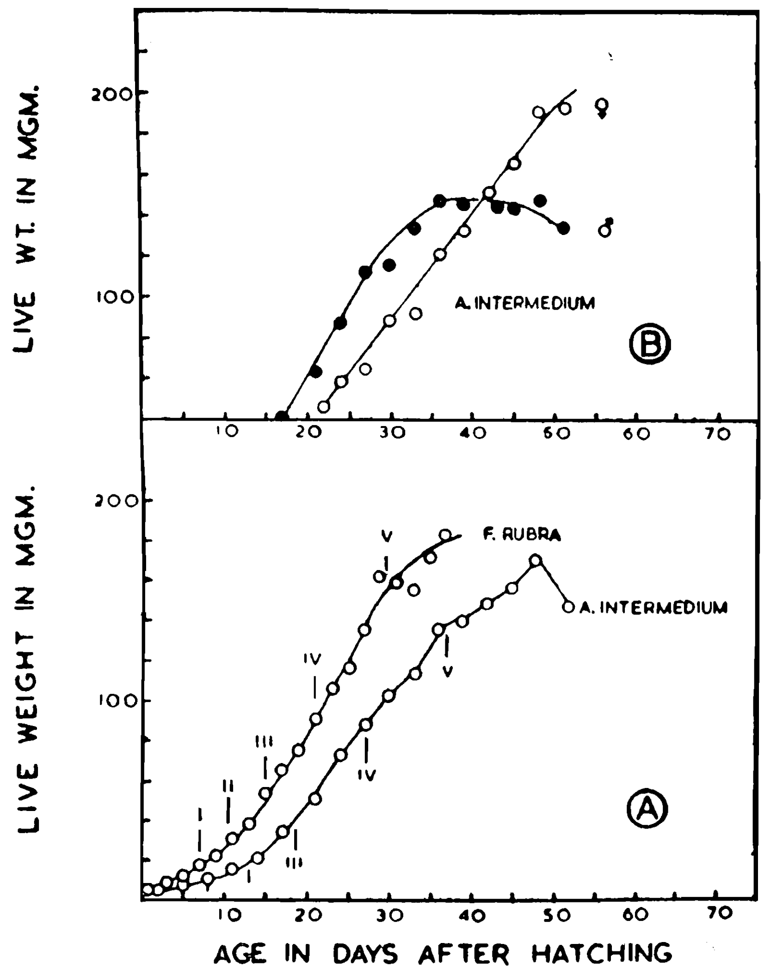
Course of growth of Camnula pellucida (*Scudder*), *on an exclusive diet of Intermediate Wheat-grass* (Agropyron intermedium *Beauv.*)

Instar	Average live weight at beginning of instar (mgm.)	Age at beginning of instar (days after hatching)	Progression growth factor
I	5·87	..	..
II	9·58	7·90	1·69
III	16·96	13·00	1·77
IV	41·45	18·80	2·44
V	91·78	27·30	2·21
Adult	137·25	37·30	1·50

On account of wide differences in the days of moulting of males and females and also the two females themselves, it is difficult to estimate the sexual dimorphism between the two sexes. However, if the differences in times of moultings are disregarded and the live weights attained by the two sexes are to be judged soon after adulthood was attained and at the termination of the experiment, it is possible to get a rough idea of the female superiority in live weights over the male fed on this diet. Thus, the male on its final moult on the 30th day weighed 116·0 mgm., while the deformed female at transformation on the 38th day weighed only 95·5 mgm. and the other normal one on the 44th day weighed 133·3 mgm. The sexual-dimorphism percentage for the second female is, therefore, 14·9. This ratio is better than what was obtained on sedge diet (three per cent in the case of teneral adults). On this diet, the experiment was continued till all the adults died. The male lived 60 days and weighed 147·6 mgm. on the last day, while the deformed female* lived 49 days, weighing 202·7 mgm. and the normal female lived 52 days, weighing 193·9 mgm. on that day. The former female was, thus, 37·33 per cent heavier than the male and the latter one, 31·4 per cent, the average of the two being 34·4 per cent, which is much lower than that obtained on sedge (49 per cent).

*The deformity in the female was due to the loss of both the hind legs and the tarsi of the right middle and the right front legs. On the 43rd day after hatching, this female was accidentally left in the weighing tube with the solitary male. The two immediately copulated, notwithstanding the severe deformity of the female. The mating had commenced at 4·40 p.m. and continued till 6·35 p.m. On the 57th day, this female died after laying an egg mass containing only five eggs.

An interesting view of the sexual dimorphism of the grasshopper on intermediate wheat-grass diet is presented in Text-fig. 7B. The nymphs could be identified by their sexes on the 16th and 17th days in the two replicate cages, respectively, when they



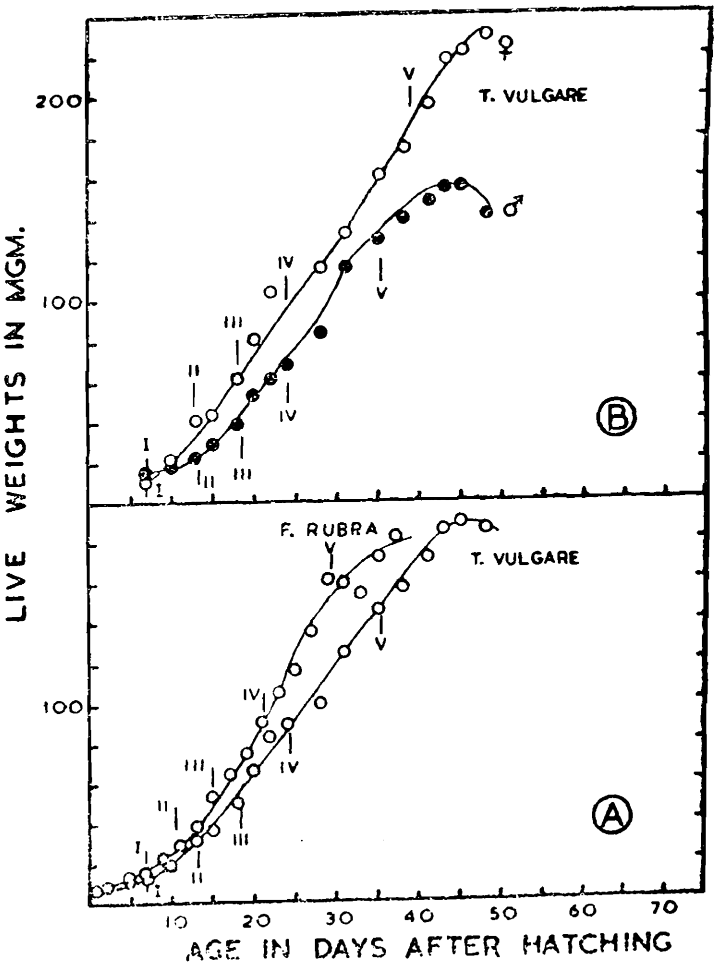
TEXT-FIG. 7.—Cumulative live weights (A) and sexual dimorphism in live weights (B) attained by *Camnula pellucida* fed on *Agropyron intermedium* during the course of its development. The live weight curve of *Camnula* fed on *Festuca* is also given for comparison.

had moulted to third instar. It was found that the first replicate had two third instar male nymphs, while the second replicate on the same day had six third instar nymphs and one second instar nymph, perhaps all females, at least so they turned out to be on the 22nd day. The interesting point was that the males, on the average, were heavier than the females. If the curves of the two sexes are examined, it would be found that the male maintains its advantage of live weight in a straight line relationship up to about 25 days and then its graph swings horizontally showing a downward trend after 35 days. The female, on the other hand, keeps on adding weight at a steady pace right up to the last few days of her life. She catches up with the male when his weight starts declining and goes ahead of him at a steady rate.

The progression growth factor for the first to second instar is 1·69, for the second to third instar is 1·77, for the third to fourth is 2·44, for the fourth to fifth instar is 2·21 and for the final stage is 1·50, the average of all the five stages being 1·92, which is close to two, as envisaged by Przibram (1912).

(vi) *Selkirk wheat* (Triticum vulgare).—This is a very succulent grass, its oven-dry to green-weight ratio being 0·195.

The nymphs reared on this grass were separated into males and females on the seventh day, when there was a large-scale moulting of the original population into the second instar. The average figures for live weights and moulting days have been



TEXT-FIG. 8.—Cumulative live weights (A) and sexual dimorphism in live weights (B) attained by *Camnula pellucida* fed on *Triticum vulgare* (var. *selkirk*) during the course of its development. The live weight curve of *Camnula* fed on *Festuca* is also given for comparison.

recombined for the purpose of comparison with results obtained on other grasses. The original observations on males and females separately have also been given in the table for comparison between the two sexes.

That there is no marked difference in the days on which first, second, third and fourth moults of the two sexes occurred is shown by Table 13. The difference in days of the fifth moult is, however, quite noticeable. The fifth instar is much longer in the female than in the male. This enables her to continue the wave of growth to a higher peak than the male. Thus three out of four fifth instar males moulted to become adults on the 35th day and the average weight of these teneral males was 126·5 mgm. In the case of the females, four out of five fifth instar nymphs moulted to become teneral adults on the 38th day, when the average live weight of the teneral female was 171·3 mgm., the sexual-dimorphism percentage in live weights being 35·4. At the termination of the experiment, on the 48th day, there were four males having their average live weight as 141·5 mgm. and four females having their average live weight as 228·9 mgm., the sexual-dimorphism percentage in their weights being 61·76

The progression growth factor of the males and females is different (Table 13). In the females, the average live weight was almost tripled from second instar to the third, after which the growth factor was 1·47 from third to the fourth, 1·69 from fourth to the fifth and 1·65 from fifth to the adult stage. In the males, however, the growth was somewhat even, the factor being 1·52 from second to the third, 1·92 from third to the fourth, 1·53 from fourth to the fifth and 1·93 from fifth to the adult stage. If the average of all the five stages is considered in the combined weights and those of males and females separately, there is an actual doubling of weights in the females, while in the case of males the ratio approaches the doubling of weights quite closely ; in the combined weights for the two sexes, the approach to doubling ratio is even closer.

TABLE 13

Course of growth of Camnula pellucida (*Scudder*) *on an exclusive diet of Selkirk Wheat* (Triticum vulgare *L.*)

N.B.—Data here are given as recombined for the two sexes as well as separately for the sexes.

Instar	Data recombined for both sexes			Data separately for the sexes as observed					
				Males			Females		
	Av. live wt.* (mgm.)	Days*	Prog. growth factor	Av. live wt.* (mgm.)	Days*	Prog. growth factor	Av. live wt.* (mgm.)	Days*	Prog. growth factor
I	6·10	..	..	..	..	..	..	..	..
II	15·41	7·0	2·53	..	..	..	..	..	..
III	32·10	13·4	2·08	23·36	13·5	1·52	43·25	13·2	2·81
IV	55·20	18·6	1·72	44·84	18·8	1·92	63·70	18·3	1·47
V	88·15	24·2	1·60	68·77	24·3	1·53	107·95	24·0	1·69
Adult	154·26	37·3	1·75	132·71	35·8	1·93	177·64	38·6	1·65

*At beginning of instar.

3. *Rate of Growth in Live Weights on Exclusive Diets*

The rates of growth in live weights (Text-figs. 9-15) further elucidate the information on growth contained in graphs illustrating the cumulative course of growth, (Text-figs. 2-8). These *curves of first differences* bring into sharp relief the slope, or steepness, of the cumulative growth graphs ; the change in slope, caused by the succession of varying increments (or decrements), creates a pattern in the course of growth. Each host grass differs from the others in nutritional values and is utilized by the grasshopper to varying extent ; therefore, the pattern of growth of the grasshopper feeding exclusively on single grasses differs within the framework of a general pattern.

The pattern of average rate of growth of the grasshopper, fed on exclusive diets, can be divided into four epochs as follows :

(*a*) *The first epoch* generally shows a steady rate of growth with little or no acceleration.

(*b*) *The second epoch* is characterized by a rapid acceleration of growth which reaches a climax at the point of inflection of the curve, generally at the end of the fourth or in the fifth instar ; it shares many features in common with "puberty" of higher animals (Brody, 1927) and is the most dynamic component of the growth pattern.

(*c*) *The third epoch* shows a rapid deceleration.

(*d*) *The fourth epoch* consists of another peak in the adult life ; this peak, generally speaking, is lower than the first peak and is followed by a fluctuating decline during the remaining part of the life. This deceleration results in negative growth when the animal loses weight consistently, indicating that the metabolism of the body is impaired and the tissues no longer keep pace with senile wastage and decay (D'Arcy Thompson, 1942).

The two peaks, one in the pre-adult life and the other in the adult life, seem to be fairly consistent features in the growth of *Camnula* and perhaps represent growth in two waves, the vegetative or somatic growth, reaching its climax in the fourth or early fifth instar, and the reproductive growth having its climax in early adult life.

On the basis of the pattern of growth they produce, the six grasses tested here fall into three categories as follows :

(A) Grasses giving fast rate of growth to the grasshopper :
  (i) Involute-leaved sedge (*Carex eleocharis*)
  (ii) Red fescue (*Festuca rubra*)
  (iii) Kentucky bluegrass (*Poa pratensis*)

(B) Grasses giving slow rate of growth to the grasshopper :
  (i) Smooth brome grass (*Bromus inermis*)
  (ii) Intermediate wheat-grass (*Agropyron intermedium*)

(C) Grass giving very slow rate of growth to the grasshopper :
  (i) Selkirk wheat (*Triticum vulgare*)

(*a*) *Grasses Giving Fast Rate of Growth*

(i) *Rate of growth on involute-leaved sedge* (Carex eleocharis).—The live weights and the average rates of growth of the grasshopper during the course of development on involute-leaved sedge are given in Table 14. The pattern of average rates of growth (Text-fig. 9) is divisible into four epochs as follows :

TABLE 14

Live weights and rate of growth of Camnula pellucida (*Scudder*) *on an exclusive diet of Sedge* (Carex eleocharis *Bail.*)

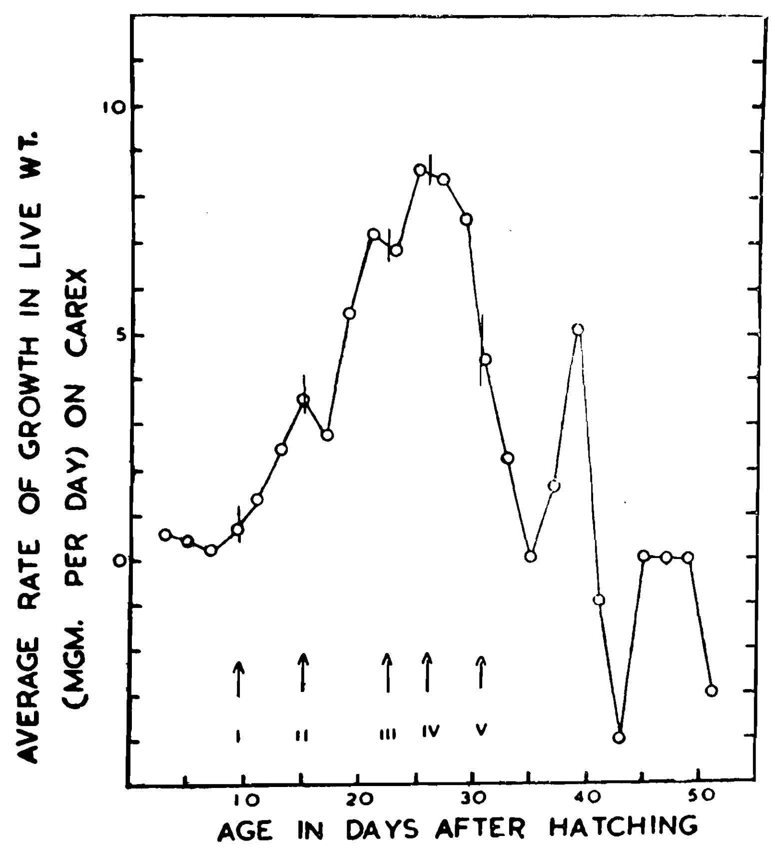
N.B.—The number of individuals in a stage is given in Arabic numerals and the instars in Roman. M. males ; F. females. Average duration of instars are delineated by horizontal lines.

	Age		Body weight			
	Days after hatching	Per cent of pre-adult life (30·80 days)	Live wt. (mgm.)	Per cent of transforming weight (124·06 mgm.)	Population composition	Rate of growth (running av. mgm. per day)
I instar	1	3·25	5·92	4·77	100 I . . .	..
	2	6·49	6·68	5·38	100 I . . .	0·51 (on 3rd day)
	5	16·23	7·97	6·42	64 I . . .	0·42
	7	22·73	8·79	7·09	44 I . . .	0·23
	9	29·22	8·87	7·15	16 II, 12 I . .	..
	9·57	31·07	9·57	7·71	....	..
II instar	11	35·71	11·31	9·12	13 II, 5 I . .	1·28
	13	42·31	14·00	11·28	1 III, 14 II . .	2·43
	15	48·70	21·03	16·95	10 III, 3 II . .	3·55
	15·35	49·84	22·43	18·08	....	..
III instar	17	55·19	28·18	22·71	11 III, 1 II . .	2·72
	19	61·69	31·91	25·72	6 IV, 3 III, 3 II .	5·49
	21	68·18	50·15	40·42	1 V, 6 IV, 5 III .	7·22
	22·43	72·82	57·76	46·56	....	..

TABLE 14—*concld.*

Age	Days after hatching	Body weight: Per cent of pre-adult life (30·80 days)	Live wt. (mgm.)	Per cent of transforming weight (124·06 mgm.)	Population composition	Rate of growth (running av. mgm. per day)
IV instar	23	74·67	60·80	49·01	5 V, 3 IV, 4 III	6·80
	25	81·97	77·34	62·34	7 V, 1 IV, 4 III	8·64
	25·97	84·32	86·08	69·39	....	..
V instar	27	87·66	95·37	76·87	1 M, 6 V, 4 IV, 1 III . .	8·41
	29	94·16	110·98	89·46	5 M, 3 V, 3 IV, 1 III . .	7·53
	30·80	100·00	124·06	100·00	....	..
Adult	31	100·65	125·50	101·16	5 M, 2 F, 3 V, 1 IV, 1 III .	4·36
	33	107·14	128·41	103·51	5 M, 2 F, 4 V, 1 IV . .	2·25
	35	113·64	134·50	108·42	6 M, 2 F, 3 V, 1 IV . .	0·09
	37	120·13	128·76	103·79	7 M, 2 F, 2 V, 1 IV . .	1·59
	39	126·62	140·85	113·53	7 M, 2 F, 2 V . . .	5·14
	41	133·12	149·33	120·37	7 M, 2 F, 2 V . . .	—0·90
	43	139·61	137·27	110·65	6 M, 1 F, 1 V . . .	—4·09
	45	146·10	132·98	107·19	6 M, 1 F, 1 V . . .	0·02
	47	152·60	137·35	110·71	6 M, 1 F, 1 V . . .	0·32
	49	159·09	134·25	108·21	6 M, 1 F, 1 V . . .	0·23
	51	165·58	138·26	111·45	6 M, 1 F	—2·99
	54	175·32	122·30	98·58	6 M, 1 F	..

(*a*) The first epoch (Text-fig. 9) consists of about seven days, or a little more than one-fourth of the pre-adult life, when the rates of growth show a decline from 0·5 mgm. to 0·23 mgm. per day. This deceleration ends just before the first moult.



TEXT-FIG. 9.—Average rate of growth in live weights of *Camnula pellucida* fed on *Carex eleocharis*. The average age at the time of moults is indicated above the X-axis by vertical strokes on the curve itself.

(*b*) The second epoch starts about the time of the first moult on the ninth day and consists of a steep rise in the rate of growth, interrupted by two troughs in the curve during which moults occur. The first moult occurs very early in the epoch on its rising slope ; the second moult coincides with a deceleration in growth which makes the first trough on the curve (on the 17th day), after which growth accelerates again and becomes much more rapid than before. The third moult occurs during a similar second trough (about the 21st day). The climax in rate of growth is reached about the 25th day, when the nymph is growing at the rate of 8·64 mgm. live weight per day. Hereafter the growth rate falls off ; this is the point of inflection, which indicates "puberty" in higher animals (Brody, 1927).

(*c*) The third epoch follows the point of inflection and consists of a rapid and steady fall in acceleration. The fall begins slowly and becomes more rapid, making the peak look a bit like a truncated cone. The fourth moult occurs early, and the fifth moult occurs about the middle of the epoch when the declining acceleration is becoming less abrupt. This decline in acceleration lasts till about the age of 35 days.

(*d*) The fourth epoch begins when the adult grasshopper again starts putting on weight rapidly to form another peak of growth rate about the 39th day. This peak in the adult life may be called the *reproductive peak* (as distinct from the previous peak in the fourth instar, which may be called the *vegetative peak*, or peak of vegetative or somatic growth). In the present study, the cage population at this stage had a preponderance of males (seven males, two females and two fifth instar nymphs—the two nymphs ultimately died without transforming). This suggests that the reproductive peak could be higher if the sex ratio in the cage population was more even. The acceleration in growth after attaining the peak falls rapidly towards negative growth as the grasshopper heads towards senility. There are a few bursts of acceleration but they are irregular and show a tendency to progressive decline.

(ii) *Rate of growth on red fescue* (Festuca rubra).—The live weights and the average rates of growth of the grasshopper during the course of development on fescue are given in Table 15. The pattern of average rates of growth (Text-fig. 10) is divisible into four epochs as follows :

TABLE 15

Live weights and rate of growth of Camnula pellucida (*Scudder*) *on an exclusive diet of Red Fescue* (Festuca rubra *L.*)

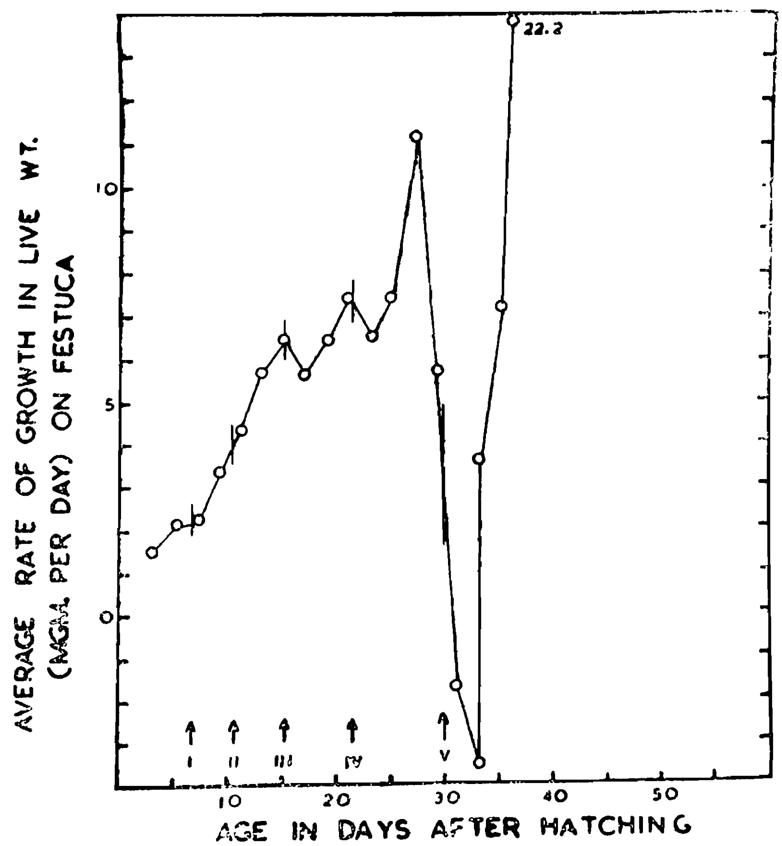
N.B.—The number of individuals in a stage is given in Arabic numerals and the instars in Roman. M, males ; F, females.

	Age		Body weight			
	Days after hatching	Per cent of pre-adult life (29·97 days)	Live wt. (mgm.)	Per cent of transforming weight (159·38 mgm.)	Population composition	Rate of growth (running av. mgm. per day)
I instar	1	3·34	6·52	4·09	100 I	..
	3	10·01	7·94	4·98	94 I	1·46
	5	16·68	12·37	7·76	8 II, 85 I . . .	2·15
	6·83	22·79	15·55	9·76	....	..
II instar	7	23·36	16·55	10·38	91 II	2·24
	9	30·03	21·33	13·38	20 III, 68 II . .	3·32
	10·65	35·53	28·33	17·78	....	..
III instar	11	36·70	29·81	18·70	76 III, 8 II . . .	4·35
	13	43·38	38·72	24·29	11 IV, 71 III . .	5·74
	15	50·05	52·76	33·10	55 IV, 24 III . .	6·43
	15·26	50·92	54·28	34·06	....	..

TABLE 15—*concld.*

	Age: Days after hatching	Age: Per cent of pre-adult life (29·97 days)	Body weight: Live wt. (mgm.)	Body weight: Per cent of transforming weight (159·38 mgm.)	Population composition	Rate of growth (running av. mgm. per day)
IV instar	17	56·72	64·42	40·42	74 IV, 3 III	5·67
	19	63·40	75·43	47·33	21 V, 53 IV	6·47
	21	70·07	90·28	56·64	43 V, 26 IV	7·40
	21·43	71·50	93·45	58·63	....	..
V instar	23	76·74	105·04	65·91	55 V, 11 IV	6·50
	25	83·42	116·26	72·95	4 M, 1 F, 57 V, 1 IV	7·43
	27	90·09	134·77	84·56	11 M, 6 F, 44 V	11·19
	29	96·76	161·02	101·03	12 M, 12 F, 33 V	5·72
	29·97	100·00	100·00	159·38	....	..
Adult	31	103·44	157·63	98·90	21 M, 20 F, 14 V	—1·75
	33	110·11	154·01	96·63	23 M, 28 F, 4 V	—3·54
	35	116·78	171·78	107·78	23 M, 31 F, 1 V	7·22
	37	123·46	182·88	114·74	21 M, 32 F	22·72
	39	130·13	262·22	164·53	21 M, 32 F	26·22
	42	140·14	239·22	150·09	17 M, 29 F	..

(*a*) The first epoch (Text-fig. 10) lasts for about seven days, covering a little less than one-fourth of the pre-adult life. During this time the rate of growth is slow, showing slight rise in acceleration. This slow tempo comes to an end at the second instar.



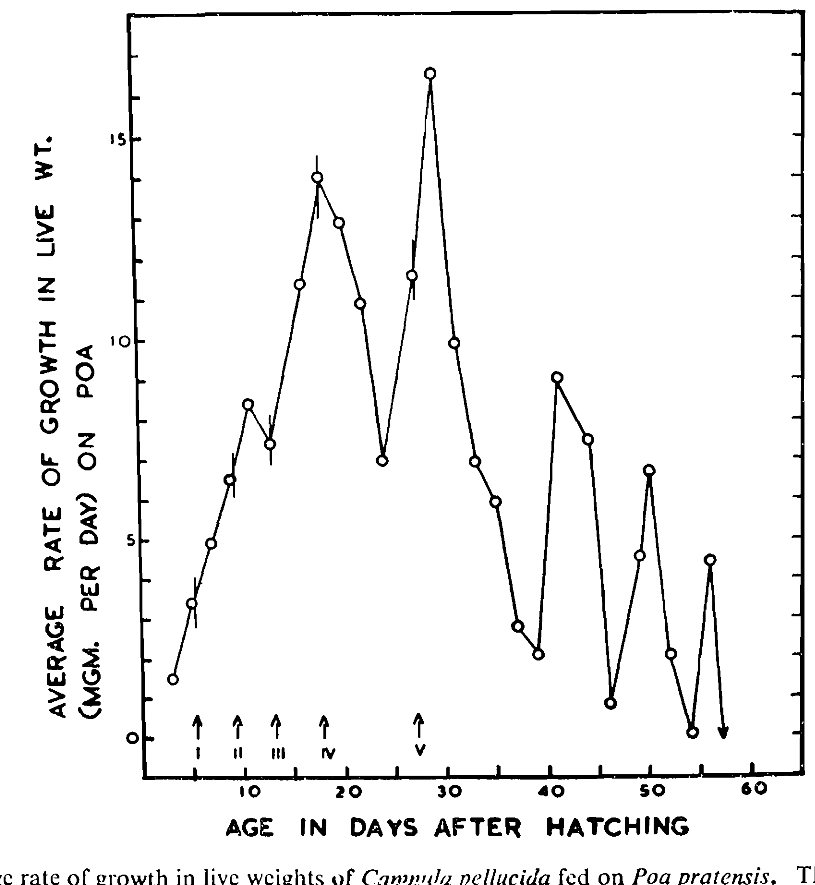
TEXT-FIG. 10.—Average rate of growth in live weights of *Camnula pellucida* fed on *Festuca rubra*. The average age at the time of moults is indicated above the X-axis by vertical strokes on the curve itself.

(*b*) The second epoch consists of a rapid rise in growth rate. During this time the nymph moults to third instar without interrupting the acceleration. About the 15th day the rate drops, showing the first trough in the curve when the nymph moults to the fourth instar. The acceleration is resumed until another drop occurs forming the second trough about the 23rd day when the nymph moults to the fifth instar. After this, the growth rate is very rapid, heading to the vegetative or somatic peak on the 27th day at the rate of 11·19 mgm. live weight per day, when 90 per cent of pre-adult life has been completed.

(*c*) The third epoch occupies the declining slope following the second epoch ; it consists of a rapid fall from the rate of 11·19 mgm. per day to a negative growth (—1·75 and —3·54 mgm. per day), when the nymph loses weight. During this period, when the fifth instar nymph is putting on weight less and less rapidly, it moults to become adult and continues in its deceleration. About the 33rd day, this fall is arrested and the fourth epoch begins.

(*d*) The fourth epoch shows spectacular acceleration from the negative growth. Between the 37th to 39th days the grasshopper was putting on weight at the rate of 22·72 to 26·22 mgm. live weight per day. Unfortunately, the experiment was terminated due to shortage of time and further points in the curve are not available to show the amplitude in fluctuations of the fourth epoch. Since the cage population at this time consisted of more females than males (males, 37 per cent ; females, 63 per cent), the spectacular rate of growth may be due largely to the greater proportion of females. Nevertheless, the disparity in the sex ratio is not large enough to account for the enormously high acceleration in growth at this time, and the reproductive peak must be very high.

(iii) *Rate of growth on Kentucky bluegrass* (Poa pratensis).—The live weights and the average rates of growth on an exclusive diet of Kentucky bluegrass are given in Table 16. The pattern of average rates of growth (Text-fig. 11) can be divided into three epochs only, the first two of the general pattern (*a* and *b*) having been merged together.



TEXT-FIG 11.—Average rate of growth in live weights of *Cannula pellucida* fed on *Poa pratensis*. The average age at the time of moults is indicated above the X-axis by vertical strokes on the curve itself.

TABLE 16

Live weights and rate of growth of Camnula pellucida (*Scudder*) *on an exclusive diet of Kentucky Bluegrass* (Poa pratensis *L.*)

N.B.—The number of individuals in a stage is given in Arabic numerals and the instars in Roman. M, males ; F, females.

	Age: Days after hatching	Age: Per cent of pre-adult life (27·30 days)	Body weight: Live wt. (mgm.)	Body weight: Per cent of transforming weight (208·07 mgm.)	Population composition	Rate of growth (running av. mgm. per day)
I instar	1	3·66	6·17	2·97	100 I	—
	3	10·99	8·16	3·92	84 I	1·50 (on 4th day)
	5	18·32	12·15	5·84	51 II, 25 I . . .	3·42
	5·41	19·82	14·13	6·79	——	—
II instar	7	25·64	21·83	10·49	70 II, 1 I . . .	4·80
	9	32·97	31·34	15·06	61 III, 4 II . . .	6·50
	9·10	33·33	32·16	15·46	——	—
III instar	11	40·29	47·83	22·99	51 IV, 13 III . .	8·46
	13	47·62	65·19	31·33	8 IV, 56 III . . .	7·67
	13·08	47·91	66·03	31·73	——	—
IV instar	16	58·61	86·19	41·42	15 V, 40 IV, 1 III . .	11·35
	17·94	65·71	120·84	58·08	——	—
V instar	18	65·93	121·91	58·59	28 V, 13 IV . . .	14·06
	20	73·26	142·45	68·46	31 V, 6 IV . . .	12·81
	22	80·59	173·15	83·22	4 M, 1 F, 27 V . .	10·87
	24	87·91	185·91	89·35	4 M, 4 F, 17 V . .	6·93
	27	98·90	207·78	99·86	9 F, 6 V . .	11·55
	27·30	100·00	208·07	100·00	——	—
Adult	29	106·23	243·68	117·11	8 F	16·58
	31	113·55	274·09	131·73	8 F	9·86
	33	120·88	283·13	136·07	6 F	6·97
	35	128·21	301·96	145·12	6 F	5·95
	37	135·53	306·91	147·53	6 F	2·73
	39	142·86	312·72	150·30	6 F	2·09
	41	150·18	315·35	151·56	6 F	9·07
	44	161·17	358·35	172·23	2 F	7·49
	46	168·50	352·80	169·56	I F	0·77
	49	179·48	362·20	174·08	1 F	4·53
	50	183·15	370·90	178·26	1 F	6·70
	52	190·48	382·30	183·74	1 F	2·13
	54	197·80	379·40	182·34	1 F	0·08
	56	205·12	382·60	183·88	1 F	4·35
	58	212·45	396·80	190·71	1 F . . .	−2·00
	62	227·11	380·60	182·92	1 F	—3·40
	65	238·10	373·10	179·31	1 F	

(*a & b*) The first epoch (Text-fig. 11) cannot be made out on this grass diet and seems to have been merged into the second, because the growth rate up to the 11th day bears almost a straight line relationship to age with no interruption from the first and second moults at all. After this day the rate accelerates from 7·67 to 8·46 mg. per day, making the first trough in the curve when the nymph moults into third instar. The rate of growth accelerates rapidly after the moult till it reaches 14·06 mgm. live weight per day on the 18th day, almost synchronously with the fourth moult. About 66 per cent of the pre-adult life is completed by this time. After this, the rate falls rapidly from 14·06 to 6·93 mgm. live weight per day in six days, forming a deep, second trough in the curve. The rate of growth rises very rapidly after the second trough and is uninterrupted by the final moult, reaching the climax of vegetative growth on the 29th day. On this day, the grasshopper is putting on 16·58 mgm. live weight per day. Thus the peak of vegetative growth on Kentucky bluegrass is formed when the grasshopper has attained adulthood.

(*c*) The third epoch consists of a rapid decline in the rate of growth from 16·58 to 2·09 mgm. live weight per day in 10 days.

(*d*) The fourth epoch consists of a wide fluctuation in the rate of growth. The over-all tendency is a decline, leading to senility. For all the diets examined, the grasshopper attained the greatest live weights on Kentucky bluegrass, because the vegetative climax is prolonged into adult life.

(iv) *Comparison of growth rates on sedge, fescue and Kentucky bluegrass.*—The growth rates on fescue and Kentucky bluegrass show the following modifications on the sedge pattern (Tables 14, 15, 16 and 22) :

First epoch.—On fescue and Kentucky bluegrass, the first epoch occupies the entire first stadium, which comprises about seven days in duration on the former and about five days on the latter grass diet. On the other hand, the epoch on sedge diet occupies seven out of nine days of the first stadium. The initial slow decline in growth rate seen on sedge corresponds to a slow rise on fescue and a fast rate on Kentucky bluegrass, thus showing a gradation in rates of growth from sedge to Kentucky bluegrass. Because of the fast rate of growth, the first and second epochs on Kentucky bluegrass combine into a single rapidly rising growth rate.

Second epoch.—The largest duration of the epoch is on Kentucky bluegrass (24 days) and the shortest on-sedge (18 days). The nymph feeding on the former grass, therefore, continues to gain live weight at an accelerating rate for the longest period, thus attaining the greatest weight at the somatic climax. Apart from the consideration of the duration, the rate of growth at the somatic climax is also the highest on Kentucky bluegrass (16·58 mgm. live weight per day) and next lower on fescue (11·19 mgm.), which ensures a heavier grasshopper on fescue and Kentucky bluegrass than on sedge.

In point of development, the nymph on fescue is the fastest. An examination of Text-figs. 9, 10 and 11 will show that, at the ' landmark ' of the first trough on the curve, the fescue-fed nymph is in the fourth instar, while the nymph on sedge is in early third instar and that on Kentucky bluegrass at the end of the third instar. Thus the fescue-fed nymph is, at this time, a whole stadium ahead of the nymph feeding on sedge and a little ahead of that feeding on Kentucky bluegrass.

Third and fourth epochs.—The sedge and fescue-fed grasshoppers attained the final moult during the third epoch, whereas the nymphs fed on Kentucky bluegrass attained this stage in the second epoch. This indicates that the grasshopper, towards the final moult, is faster in development on Kentucky bluegrass than on sedge or fescue. The growth rate becomes negative on fescue during this epoch, but on sedge and Kentucky bluegrass it remains positive. Because of the delay in the climax of somatic growth into the adult stage, there is an overlapping in the waves of somatic and reproductive growths in the grasshopper reared on Kentucky bluegrass and the two component curves of the pattern, therefore, meet at a higher level on this grass than they do on sedge and fescue. It appears that there is a small amount of overlapping of the two component curves on sedge diet as well, but the two are well separated on fescue. This would account for growth rate falling to negative values on fescue and remaining positive on the other two diets.

In the fourth epoch, the fescue-fed grasshopper shows a tremendous velocity of growth compared to the grasshoppers reared on the other two grasses; next in order of velocity are the grasshoppers reared on Kentucky bluegrass. It remains to be tested by rearing experiments, whether this high reproductive peak has a positive correlation with egg production in the grasshoppers.

(b) *Grasses Giving Slow Rate of Growth*

(i) *Rate of growth on brome grass* (Bromus inermis).—The live weight and the rate of growth in live weights of *Camnula* are given in Table 17. The pattern of average rates of growth (Text-fig. 12) is divisible into the following four epochs :

TABLE 17

Live weights and rate of growth of Camnula pellucida *(Scudder) on an exclusive diet of Brome Grass* (Bromus inermis *Leyss*)

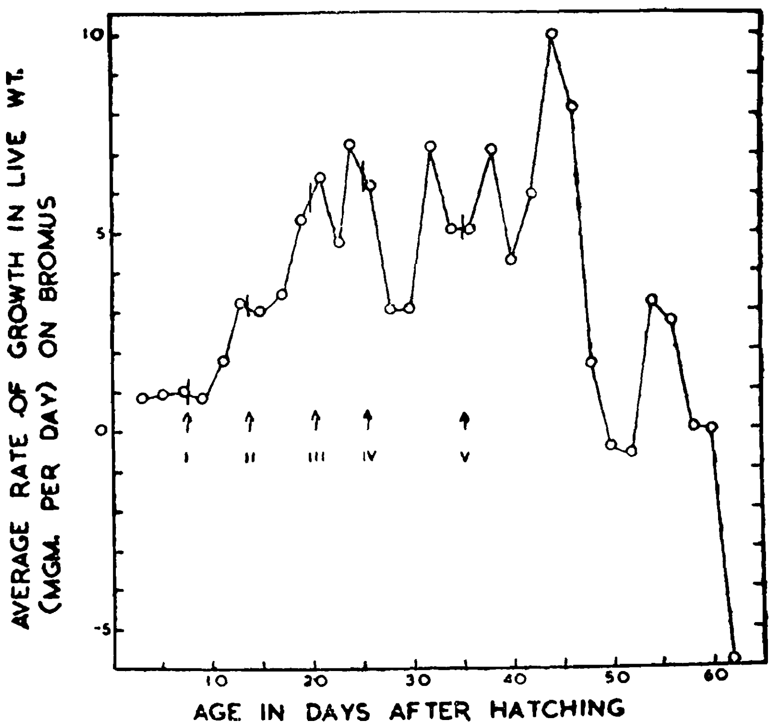
N.B.—The number of individuals in a stage is given in Arabic numerals and the instars in Roman. M, males ; F, females.

	Age		Body weight			
	Days after hatching	Per cent of pre-adult life (35·02 days)	Live wt. (mgm.)	Per cent of transforming weight (128·67 mgm.)	Population composition	Rate of growth (running av. mgm. per day)
I instar	1	2·86	5·98	4·65	100 I	—
	3	8·57	7·93	6·16	99 I	0·85
	5	14·28	9·36	7·27	2 II, 89 I . . .	0·91
	7	19·19	11·56	8·98	61 II, 8 I . . .	0·998
	7·43	21·22	12·16	9·45	——	—
II instar	9	25·70	13·35	10·38	1 III, 53 II, 3 I . .	0·84
	11	31·41	14·91	11·59	19 III, 32 II . . .	1·76
	13	37·12	20·39	15·85	32 III, 15 II . . .	3·21
	13·62	38·89	22·20	17·25	——	—
III instar	15	42·83	27·73	21·55	3 IV, 30 III, 7 II . .	2·94
	17	84·54	32·13	24·97	11 IV, 16 III, 7 II . .	3·39
	19	54·25	41·29	32·09	20 IV, 9 III, 2 II . .	5·25
	20·19	57·65	48·34	37·57	——	—
IV instar	21	59·97	53·14	41·30	1 V, 18 IV, 10 III, 1 II	6·27
	23	65·68	66·36	51·57	10 V, 14 IV, 4 III .	4·62
	24	68·53	71·63	55·67	17 V, 7 IV, 4 III . .	7·21
	25·25	72·10	81·86	63·62	——	—
V instar	26	74·24	88·00	68·39	18 V, 6 IV, 3 III . .	6·16
	28	79·95	96·28	74·83	1 M, 17 V, 7 IV, 2 III .	2·99
	30	85·67	99·96	77·69	2 M, 17 V, 6 IV, 1 III .	3·07
	32	91·38	108·55	84·36	6 M, 1F, 14 V, 4 IV, 1 III	7·14
	34	97·09	128·51	99·88	7 M, 4 F, 11 V, 2 IV .	5·07
	35·02	100·00	128·67	100·00	——	—

TABLE 17—*concld.*

Age		Body weight			
Days after hatching	Per cent of pre-adult life (35·02 days)	Live wt. (mgm.)	Per cent of transforming weight (128·67 mgm.)	Population composition	Rate of growth (running av. mgm. per day)
Adult 36	102·80	128·83	100·12	11 M, 4 F, 7 V, 1 IV	5·09
38	108·51	148·86	115·69	9 M, 6 F, 5 V, 1 IV	7·02
40	114·22	156·92	121·96	10 M, 7F, 3 V, 1 IV	4·24
42	119·93	165·80	128·86	10 M, 8 F, 2 V, 1 IV	5·95
44	125·64	180·72	140·35	10 M, 8 F, 1 V, 1 IV	9·96
46	131·35	205·63	159·81	10 M, 9 F, 1 IV	8·16
48	137·06	213·36	165·82	10 M, 9 F, 1 IV	1·66
50	142·78	212·28	164·98	10 M, 9 F, 1 IV	—0·46
52	148·49	211·54	164·41	10 M, 9 F	—0·61
54	154·20	209·86	163·10	9 M, 9 F	3·24
56	159·91	224·50	174·48	9 M, 9 F	..
58	165·62	220·73	171·55	9 M, 9 F	2·72
60	171·33	225·01	174·87	9 M, 9 F	0·13
62	177·04	220·38	171·28	9 M, 9 F	—0·09
64	182·75	201·71	156·77	8 M, 7 F	—5·83
66	188·46	188·79	146·72	8 M, 7 F	—7·9

(*a*) The first epoch in the life of the nymph covers the whole of the first stadium and part of the second for nine days, or nearly one-fourth of the pre-adult life. It comprises a very slow velocity of growth.



TEXT-FIG. 12.—Average rate of growth in live weights of *Camnula pellucida* fed on *Bromus inermis*. The average age at the time of moults is indicated above the X-axis by vertical strokes on the curve itself.

(*b*) The second epoch covers approximately the next 40 per cent of the pre-adult life and comprises a rapid acceleration in growth. The continuity of this acceleration is broken by two troughs following the second and third moults. Growth reaches its climax about the 24th day, when the nymph is in the fourth instar, adding weight at the rate of 7·21 mgm. per day. At this point of inflection, the velocity of growth stops increasing.

(*c*) The third epoch is a brief deceleration period of about four days. The acceleration in growth falls off at first gradually, when the nymph moults into the fifth instar, then rapidly declines to a rate of 2·99 mgm. live weight per day.

(*d*) The fourth epoch begins when the fifth instar nymph starts putting on weight rapidly. After the first burst of acceleration, the rate falls abruptly and remains, steadily low for a couple of days, when the nymph becomes adult. The rate then fluctuates a little and rises rapidly to 9·96 mgm. live weight per day on the 44th day after which it falls almost consistently to negative growth and senility.

The growth pattern on this grass shows a comparatively lower peak of somatic growth and a higher peak in the reproductive phase. In a smoothed curve, the second peak would look like a broad dome, suggesting greater reproductive vigour in the grasshopper starting towards the end of the fifth instar on the 32nd to the 44th day. This point, however requires experimental evidence.

(ii) *Rate of growth on intermediate wheat-grass* (Agropyron intermedium).—The live weights and the average rate of growth on intermediate wheat-grass are given in Table 18. The pattern of growth (Text-fig. 13) can be divided into the following four epochs :

TABLE 18

Live weights and rate of growth of Camnula pellucida (*Scudder*) *on an exclusive diet of Intermediate Wheat grass* Agropyron intermedium (*Host.*)

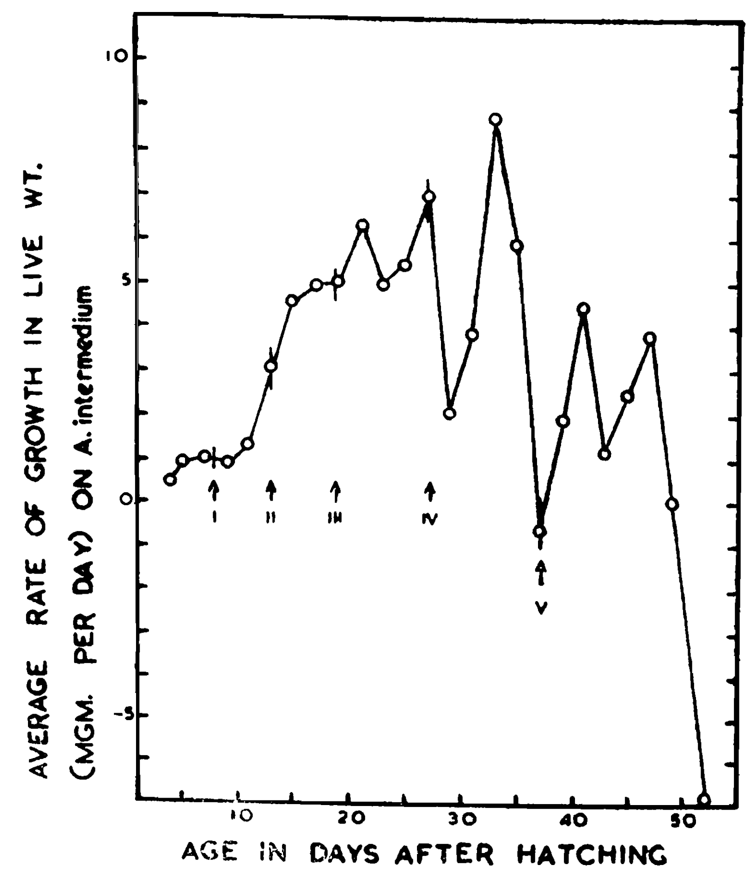
N.B.—The data in this table are an average of two replicates, each started with 25 nymphs. The number of individuals in a stage is given in Arabic numerals and the instars in Roman. M, males ; F, females.

	Days after hatching	Age: Per cent of pre-adult life (37·3 days)	Live wt. (mgm.)	Body weight: Per cent of transforming weight (137·25 mgm.)	Population composition	Rate of growth (running av. mgm. per day)
I instar	1	2·68	5·67	4·13	50 I	
	2	5·36	5·49	4·09	34 I	
	3	8·04	5·68	4·14	21 I	0·45
	4	10·72	6·39	4·66	20 I	
	5	13·40	7·48	5·45	17 I	0·92
	6	16·09	8·22	5·99	16 I	
	7	18·77	9·41	6·86	3 II, 12 I	1·06
	7·9		9·58			
II instar	8	21·45	9·79	7·13	13 II, 2 II	
	9	24·13	11·78	8·58	14 II	0·85
	10	26·81	14·20	10·35	13 II	
	11	29·45	12·81	10·70	1 III, 12 II	1·29
	12	32·17	17·06	12·43	1 III, 12 II	
	13	34·85	16·96	12·36	7 III, 2 II	3·07
III instar	14	37·53	20·92	15·24	9 III, 1 II	
	15	40·21	25·09	18·28	9 III, 1 II	4·54
	16	42·90	30·33	22·10	8 III, 1 II	
	17	45·58	35·10	25·57	1 IV, 7 III	4·90
	18	48·26	39·29	28·63	2 IV, 5 III	
	18·8		41·45			
IV instar	19	50·94	44·69	32·56	3 IV, 3 III	5·01
	20	53·62	43·42	31·64	5 IV, 1 III	
	21	56·30	55·14	37·58	4 IV, 1 III	6·29
	22	58·98	56·19	40·17	1 V M, 3 IV F	
	23	61·66	69·87	50·91	1 V M, 3 IV F	4·96
	24	64·34	74·89	54·56	1 V M, 3 IV F	
	25	67·02	74·78	54·48	1 V M, 3 IV F	5·43
	26	69·71	80·02	58·30	1 V M, 3 IV F	
	27	72·39	91·37	64·47	1 V M, 1 V F, 2 IV F	7·06
	27·3	73·19	91·78			
V instar	28	75·07	94·07	68·54	1 V M, 1 V F, 2 IV F	
	29	77·75	103·00	75·05	1 V M, 1 V F, 1 IV F	2·00
	30	80·43	105·08	76·56	1 M, 1 V F, 1 IV F	
	31	83·11	99·38	72·41	1 M, 1 V F, 1 IV F	3·77
	32	85·79	103·65	75·52	1 M, 1 V F, 1 IV F	

TABLE 18—*concld.*

Age	Days after hatching	Per-cent of pre-adult life (37·3 days)	Body weight: Live wt. (mgm.)	Body weight: Per cent of transforming weight (137·25 mgm.)	Population composition	Rate of growth (running av. mgm. per day)
V instar —*contd.*	33	88·47	114·08	83·12	1 M, 2 V F	8·71
	34	91·15	122·65	89·36	1 M, 2 V F	
	35	93·83	134·45	97·96	1 M, 2 V F	5·87
	36	96·51	133·08	96·96	1 M, 2 V F	
	37	99·20	137·78	100·39	1 M, 2 V F	—0·69
	37·3	100·00	137·25			
Adult	38	101·88	134·23	97·80	1 M, 1 F, 1 V F	
	39	104·56	131·70	95·96	1 M, 1 F, 1 V F	1·82
	40	107·24	152·18	110·88	1 M, 1 F, 1 V F	
	41	109·92	145·05	105·68	1 M, 1 F, 1 V F	44·9
	42	112·66	150·75	109·84	1 M, 1 F, 1 V F	
	43	115·28	149·65	109·03	1 M, 1 F, 1 V F	1·17
	44	117·96	149·00	108·56	1 M, 2 F	
	45	120·64	156·20	113·81	1 M, 2 F	2·40
	46	123·32	163·10	118·83	1 M, 2 F	
	47	126·01	165·72	120·74	1 M, 2 F	
	48	128·69	170·73	124·73	1 M, 2 F	3·78
	49	131·37	171·12	124·68	1 M, 2 F	0·01
	51	136·73	165·75	120·76	1 M, 2 F	
	52	139·41	142·20	103·61	1 M, 1 F	—6·78
	53	142·09	130·40	95·01	1 M	

(*a*) The first epoch covers the first stadium and part of the second for about nine days, or nearly one-fourth of the pre-adult life. During this period, the rate of growth is very slow and almost steady.



TEXT-FIG. 13.—Average rate of growth in live weights of *Camnula pellucida* fed on *Agropyron intermedium*. The average age at the time of moults is indicated above the x-axis by vertical strokes on the curve itself.

(*b*) The second epoch comes when the second instar nymph starts putting on weight with increasing rapidity, scarcely interrupted by the second moult. The growth rate of the third instar nymph slows down after a while and becomes steady at the time of the third moult. The fourth instar nymph now puts on weight at a fluctuating rate, which forms the first trough on the 23rd day, moulting about the 27th day. This is followed by a deep, second trough. The fifth instar nymph then puts on weight at a rapid rate, reaching the climax of somatic growth on the 33rd day, when it is growing at the rate of 8·71 mgm. per day.

(*c*) The third epoch begins in the middle of fifth instar, the nymph putting on weight at a declining rate. About the 37th day, it moults to become adult when its rate of gains stands at the lowest level (—0·69 mgm. per day.)

(*d*) The grasshopper once again puts on weight, but the climax of its reproductive growth is not well defined. In fact, two small peaks are formed in the adult life which need an explanation.

The cage population, after the fourth moult (27th day), contained only three individulals, one male nymph and two female nymphs. These moulted on widely different days to become adults. Thus, the male nymph became adult on the 30th day, one of the female nymphs became adult on the 38th day, while the other female became adult on the 44th day. There is a difference of eight days between the final moult of the male nymph and the first of the females, and a difference of six days between the final moults of the two females. The reproductive peak of the male grasshopper seems to have been incorporated into the large peak between the average, fourth and fifth moults, while the other two peaks in the average adult life, which are six days apart, seem to belong to the two individual females having their last moults exactly six days apart. If this explanation is true, it is interesting to see how regularly these two peaks (one in the fourth or fifth instar nymph representing somatic growth and the other in the adult life standing for reproductive growth) represent the two phasic growth waves in the life of the grasshopper.

(iii) *Comparison of growth rates on brome and intermediate wheat-grass.*—The growth rate of the grasshopper on brome differs from that on intermediate wheat-grass in the following way (Table 17, 18, and 22) :

First epoch.—On both the grasses the epoch occupies one-fourth of the pre-adult life, or nine days, comprising the whole of the first stadium and part of the second too. The acceleration in growth is also more or less the same on the two grasses ; perhaps it is a little greater on intermediate wheat-grass (average 0·82 *vs.* 0·70 on brome).

Second epoch.—The larger duration of this accelerating epoch is on intermediate wheat-grass (24 days *vs.* 15 days on brome). Apart from the duration, the acceleration of growth is also a little in favour of intermediate wheat-grass (average up to vegetative peak, 4·75 mgm. *vs.* 4·33 mgm. on brome). These two advantages in favour of intermediate wheat-grass produce heavier grasshopper on this diet than on brome.

In point of development, if the first trough is regarded as the 'landmark' for judgment, the nymph on intermediate wheat-grass is faster, for it is in the middle of the fourth instar, while the nymph on brome is in the beginning of the third. This difference is further increased in the second trough of the curve, showing that the nymph on intermediate wheat-grass is almost a whole stadium ahead of the nymph on brome diet.

Third and fourth epochs.—The nymph on brome is in the beginning of the fifth instar in the third epoch, while the nymph on the other grass is in the middle of its long fifth instar. The brome-fed nymph is, thus, fast catching up. The growth rate in this epoch becomes negative in the nymph feeding on intermediate wheat-grass, while it stays positive in the brome-fed nymph, indicating that the somatic and reproductive components of growth are a little overlaping in the brome-fed nymph, while they are separated better on the other grass.

In the fourth epoch, there were too few nymphs left on intermediate wheat-grass diet to give a reliable estimate of the reproductive phase of growth. On brome, the nymph shows greater vigour in the fourth epoch (reproductive growth) than in the second (somatic growth) and it appears that this diet is better suited for later instar nymphs and adults.

(c) *Rate of Growth on Selkirk Wheat* (Triticum vulgare).

The original cage population of 40 freshly emerged nymphs consisted of both males and females. The mixed population was, however, separated into males and females at the first moult, on the basis of their external genitalia, by a quick examination under a binocular microscope. From then on the males and females were reared separately in two cages as single-sexed populations. The data of the first seven days, therefore, pertain to the males and females combined. This, together with the original data of males and females (Tables 20 and 21) recombined, forms Table 19.

TABLE 19

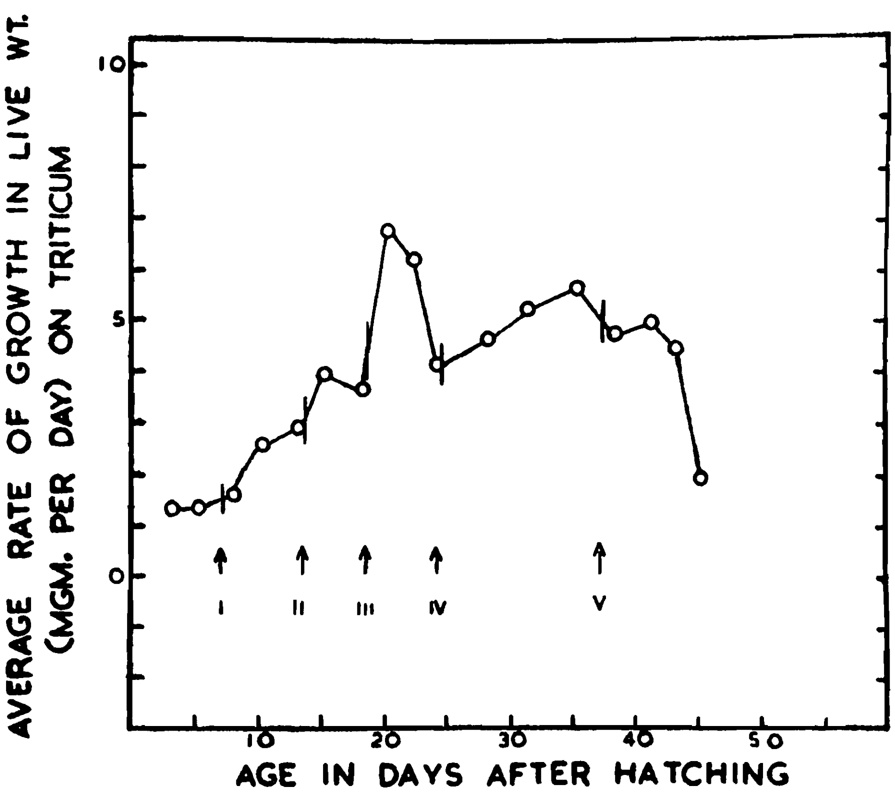
Live weights and rate of growth of Camnula pellucida *(Scudder) on an exclusive diet of Selkirk wheat* (Triticum vulgare)

N.B.—In this experiment the nymphs were separated into males and females soon after the first moult and thence reared separately in two cages. The data presented here were recombined to give the average values for the two sexes in a composite population. The number of individuals in a stage is given in Arabic numerals and the instars in Roman.

M, males ; F, females.

	Age		Body weight			
	Days after hatching	Per cent of pre-adult life (37·33 days)	Live wt. (mgm.)	Per cent of transforming weight (154·26 mgm.)	Population composition	Rate of growth (running av. mgm. per day)
I instar	1	2·68	6·10	3·95	40 I	
	2	5·36	6·82	4·42	37 I	
	3	8·04	7·48	4·85	36 I	1·29
	5	13·39	10·60	6·87	35 I	1·32
	7	18·75	12·77	8·28	17 II M, 12 II F	1·65 (on 8th day)
II instar	10	26·79	19·02	12·34	15 II M, 12 II F	2·59
	13	34·82	31·34	20·32	13IIIM,3IIM, 9 III F, 1 II F	2·89
	13·35		32·10			
III instar	15	40·18	35·88	23·26	13 III M, 10 III F	3·91
	18	48·21	50·30	32·61	8IV M,5III M, 7 IV F, 1 III F	3·61
	18·60		55·20			
IV instar	20	53·58	66·62	43·19	10 IV M, 3 III M, 8 IV F	6·75
	22	58·93	82·14	53·25	1 V M, 11 IV M, 2 V F, 6 IV F	6·23
	24	64·29	87·68	56·84	5VM,7 IV M, 6 V F, 2 IV F	4·19
	24·15		88·15			
V instar	28	75·01	100·16	64·93	6 V M, 7 V F	4·67
	31	83·04	124·13	80·47	4 V M, 5 V F	5·24
	35	93·76	145·37	94·24	3 M, 5 V F, 1 V M	5·67
	37·33	100·00	154·26			
Adult	38	101·79	156·82	101·66	4 M, 4 F, 1 V F	4·73
	41	109·83	171·39	111·10	4 M, 4 F	4·97
	43	115·19	185·13	120·01	4 M, 4 F	4·48
	45	120·55	188·09	121·93	4 M, 4 F	1·98
	48	128·58	185·22	120·07	4 M, 4 F	0·02

(i) *Rate of growth of males and females together considered as a single mixed population.*—The pattern of growth rates (Text-fig. 14) can be divided into four epochs as follows :



TEXT-FIG. 14.—Average rate of growth in live weights of *Camnula pellucida* fed on *Triticum vulgare* (var. *selkirk*). The average age at the time of moults is indicated above the x-axis by vertical strokes on the curve itself.

(*a*) The first epoch is of a short duration of a few days and seems to end before or at the first moult. It consists of a slow and steady acceleration in growth from 1·29 to 1·32 mgm. live weight per day.

(*b*) The second epoch runs from about the first moult to about the 20th day, or nearly half of the pre-adult life. For most of this duration (18 days), the rate of growth rises only gradually (1·65 to 3·61 mgm. per day), the second and third moults occurring on the rising slope. The first trough on the curve is very shallow and is formed about the 13th day, close to the second moult, when the growth acceleration is 2·89 mgm. live weight per day. The second trough is comparatively much deeper (3·61 mgm.) and is formed about the 18th day before the third moult. Soon after the third moult, the rate of growth is accelerated to the somatic peak at 6·75 mgm. live weight per day, which, indeed, is the lowest peak for all the six grasses tested.

(*c*) The third epoch is of a short duration of about four days, when the growth acceleration falls off to the rate of 4·19 mgm. per day on the 24th day at the time of the fourth moult.

(*d*) The fourth epoch starts with the fourth moult, after which the growth acceleration in the fifth instar nymph is gradual, rising from 4·19 to a peak of 5·67 mgm. live weight per day on the 35th day, shortly before the final moult. After this peak, the rate falls for a while until the nymph becomes adult and then rises again to a small ridge on the 41st day, when the rate of gain is 4·97 mgm. per day. After this small irdge, the growth rate consistently decelerates. indicating senility in the grasshopper.

It is of interest to note that the grasshopper on wheat diet has its reproductive growth peak towards the end of fifth instar instead of in the early adult life and that only a small ridge is formed in the adult life. Perhaps, when smoothed, the reproductive peak and the small ridge in the adult life together would form a broad, dome shaped curve, extending from the end of the fifth instar to about a week in the adult life. This diffuse peak (dome) suggests an early start in the development of gonads on wheat diet, but low potentiality of egg production. Further work is needed to establish this contention.

(ii) *Rate of growth of males and females considered as separate populations.*—The analysis of the data pertaining to the rearings of early instar male and female nymphs separately shows how the pattern of growth differs in the two sexes. The live weights and rates of growth of the male and the female grasshopper on Selkirk wheat are given in Tables 20 and 21, respectively, and their rate of growth patterns are shown in (Text-fig. 15). Because the growth rates at the time of the first moult were calculated in relation to the mixed populations, it would be more appropriate to consider the rate of growth curves (Text-fig. 15) of the two sexes only after the first moult, when the two populations are in the second epoch.

TABLE 20

Live weights and rate of growth of male Camnula pellucida (*Scudder*) *on an exclusive diet of Selkirk Wheat* (Triticum vulgare)

N.B.—The data presented here consist of average values for the males as actually observed. The number of individuals in a stage is given in Arabic numerals and the instars in Roman.

M, males.

	Age		Body weight			
	Days after hatching	Per cent of pre-adult life (35·75 days)	Live wt. (mgm.)	Per cent of transforming weight (132.71 mgm.)	Population composition	Rate of growth (running av. mgm. per day)
I instar	7	19·58	15·41	11·61	17 I	1·68 (on 6th day)
II instar	10	27·97	16·61	12·52	15 II	1·20 (on 8th day)
	13	36·36	21·82	16·44	10 III, 3 II	1·07 (on 11th day)
	13·46	37·65				
III instar	15	41·96	28·51	21·48	13 III	2·38 (on 13th day)
	18	50·35	39·30	29·61	8 IV, 5 III	3·50 (on 16th day)
	18·83	52·67				
IV instar	20	55·94	52·66	39·68	11 IV, 3 III	4·83 (on 18th day)
	22	61·54	60·68	45·72	11 IV, 1 V	5·35 (on 21st day)
	24	67·13	67·41	50·79	7 IV, 5 V	3·69 (on 23rd day)
	24·33	68·06				
V instar	28	78·32	83·85	63·18	6 V	3·86 (on 26th day)
	31	86·71	116·30	87·63	4 V	6·98 (on 28th day)
	35	97·90	129·83	97·83	3 M, 1 V	6·57 (on 32nd day)
	35·75	100·00	132·71	100·00		
Adult	38	106·29	140·23	105·67	4 M	3·42 (on 35th day)
	41	114·69	148·18	111·66	4 M	3·08 (on 39th day)
	43	120·28	153·68	115·80	4 M	2·69 (on 41st day)
	45	125·87	154·08	116·10	4 M	1·48 (on 44th day)
	48	134·27	141·50	106·66	4 M	—2·44 (on 46th day)

TABLE 21

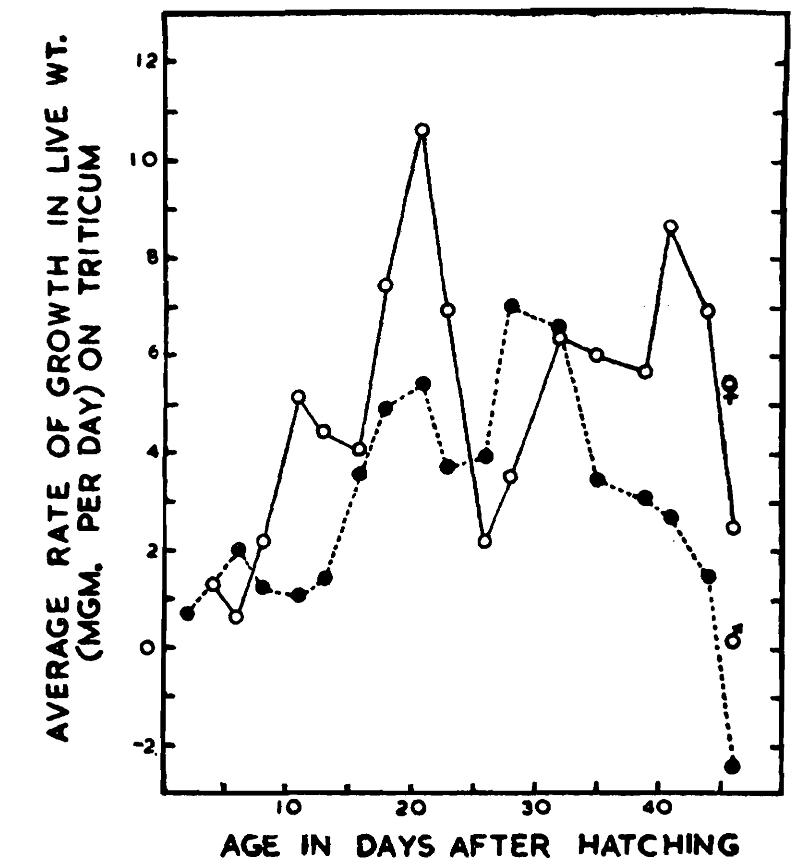
Live weights and rate of growth of female Camnula pellucida (*Scudder*) *on an exclusive diet of Selkirk Wheat* (Triticum vulgare)

N.B.—The data presented here consist of average values for the females as actually observed. The number of individuel in a stage is given in Arabic numerals and the instars in Roman.

F, females.

	Age: Days after hatching	Age: Per cent of pre-adult life (38·60 days)	Body weight: Live wt. (mgm.)	Body weight: Per cent of trans-forming weight (177·64 mgm.)	Population composition	Rate of growth (running av. mgm. per day)
I instar	7	18·13	10·13	5·70	12 II	0·66 (on 6th day)
II instar	10	25·91	21·45	12·07	12 II	2·17 (on 8th day)
	13	33·68	40·86	23·00	9 III, 1 I	5·12 (on 11th day)
	13·20	34·13				
III instar	15	38·86	43·25	24·35	10 III	4·36 (on 13th day)
	18	46·63	61·29	34·50	7 IV, 1 III	4·09 (on 16th day)
	18·25	47·28				
IV instar	20	51·81	80·58	45·36	8 IV	7·47 (on 18th day)
	22	56·99	103·59	58·31	2 V, 6 IV	10·58 (on 21st day)
	24	62·18	107·95	60·77	6 V, 2 IV	6·84 (on 23rd day)
V instar	28	72·54	116·47	65·57	7 V	2·15 (on 26th day)
	31	80·31	131·96	74·29	5 V	3·43 (on 28th day)
	35	90·67	160·90	90·58	5 V	6·35 (on 32nd day)
	38	98·45	173·40	97·41	4 F, 1 V	5·92 (on 35th day)
	38·60	100·00	177·64	100·00		
Adult	41	106·22	194·60	109·55	4 F	5·62 (on 39th day)
	43	111·40	216·58	121·92	4 F	8·64 (on 41st day)
	45	116·58	222·10	125·03	4 F	6·88 (on 44th day)
	48	124·35	228·93	128·93	4 F	2·47 (on 46th day)

From Text-fig. 15 it is clear that the growth rates follow a different pattern in the male and female grasshopper. In the beginning of the second instar, on the seventh day, the male nymph weighs (15·41 mgm.) more than the female (10·13 mgm.),



TEXT-FIG. 15.—Average rate of growth in live weights of male and female *Camnula pellucida* fed on *Triticum vulgare* (var. Selkirk).

but the growth acceleration of the female is much faster than that of the male up to the age of 11 days (rates : male, 1·07 mgm. ; female, 5·12 mgm.). As a result of this, the female, by the 10th day, puts on enormous weight quickly and is 29 per cent heavier than the male $\left[\left(\frac{\text{Mean female}}{\text{Mean male}}-1\right)\times 100\right]$. After this, although the female, continues to weigh more than the male, its growth rate (Table 21 and Text-fig. 15) starts falling and continues to fall through the second moult on the 13th day and beyond, till the 16th day, forming the only trough in the second epoch. On the other hand, the growth rate of the male nymph (Table 20 and Text-fig. 15), which was falling after the first moult only up to the 11th day, now gains momentum in acceleration and increases steadily after the second moult, which is about the same time as that of the female. It seems that the rate of gains in one sex are virtually in anti-phase of the rates in the other sex. The reason for this would be clear if the troughs in the two curves are examined.

Both the male and the female nymphs show only one trough each and it occurs at different times on their curves. The trough on the curve of the male occurs earlier, about the 11th day, when it is putting on weight at the rate of 1·07 mgm. per day ; the trough on the curve of the female, on the other hand, occurs on the 16th day, when its rate of gain is 4·09 mgm. per day. The two troughs on the curve of the mixed population (Text-fig. 14.) thus belong to the male and the female nymphs separately, occurring at different times.

TABLE 22

Comparison of the rates of growth of mixed populations of Camnula pellucida (*Scudder*) *on a sedge and five grasses*

Epoch in growth rates during development	Involute-leaved sedge	Red fescue	Kentucky blue grass	Smooth brome	Intermediate wheat-grass	Selkirk wheat
(*a*) Steady rate—						
(i) Duration . .	7 days	7 days	5 days	9 days	9 days	7 days
(ii) Nature of curve and rate	Declining, 0·51-0·23 mgm.	Slow rise, 1·46-2·15 mgm.	Fast sweep, 1·50-3·42 mgm.	Level, 0·85-0·998 mgm.	Slow rise, 0·45-0·85 mgm.	Slight rise, 1·29-1·32 mgm.
(*b*) Accelerating rate—						
(i) Duration . .	7-25 (18 d.)	7-27 (20 d.)	5-29 (24 d.)	9-24 (15 d.)	9-33 (24 d.)	7-20 (20 d.)
(ii) Trough 1 : rate, av. age and instar.	2·72, 17th d. 3rd instar	5·67, 17th d. 4th instar	7·67, 13th d. 3rd instar	2·94, 15th d. 3rd instar	4·96, 23rd d. 4th instar	2·89 13th d. 2nd instar
(iii) Trough 2 : rate, av. age and instar.	6·80, 23rd d. 4th instar	6·50, 23rd d. 5th instar	6·93, 24th d. 5th instar	4·62, 23rd d. 4th instar	2·00, 29th d. 5th instar	3·61, 18th d. 3rd instar
(iv) Somatic peak : rate, av. age and instar.	8·64, 25th d. 4th instar	11·19, 27th d. 5th instar	16·58, 29th d. adult	7·21, 24th d. 4th instar	8·71, 33rd d. 5th instar	6·75, 20th d. 4th instar
(*c*) Declerating rate—						
(i) Duration . .	25-35 (10 d.)	27-33 (6 d.)	29-39 (10 d.)	24-28 (4 d.)	33-37 (4 d.)	20-24 (4 d.)
(ii) Rate at end . .	0·09, 35th d.	—3·54, 33rd d.	2·09, 39th d.	2·99, 28th d.	—0·69, 37th d.	4·19, 24th d.
(*d*) Accelerating rate and senile decay—						
(i) Duration up to reprodn. peak	35-39 (4 d.)	3-3	39-41 (2 d.)	30-44 (14 d.)	37-47 (10 d.)	24-35 or 41
(ii) Rate at reprodn. peak.	5·14	26·22	9·07	9·96	Two peaks : 4·49 & 3·78	5·67 or 4·97 5th instar too prolonged

After 16 days, the rate of growth of the female accelerates again, uninterrupted by the third moult, about the 18th day (7·47 mgm. per day on the 18th day and 10·50 mgm. on the 21st day) ; this acceleration is much faster than that of the male, who undergoes the third moult about the 19th day and is by this time close to the somatic or vegetative climax, putting on live weights at the rate of 4·83 mgm. on the 18th day and 5·35 mgm. on the 21st day. Although both the male and the female reach the climax of their vegetative growth on the same day (21st day), the female at this time, by her faster rate of gains, is about 70 per cent heavier than the male and has completed half of her pre-adult life while achieving about 50 per cent of her pre-adult weight. The male, on the other hand, has completed about 60 per cent of his pre-adult life and acquired nearly 60 per cent of his pre-adult live weight.

In the third epoch, after the common point of inflection of their curves (on 21st day), the deceleration of the female nymph is much greater than that of the male. The average days of the fourth moult in the two sexes are very close together, but greater deceleration in the rate of the female makes the duration of her third epoch a little longer than that of the male.

In the fourth epoch, the peak of reproductive growth is formed in the male quite a bit earlier than in the female. In the male, the peak is formed about the 28th day when the grasshopper is still in the fifth instar, perhaps suggesting that the male gonads start developing in the fifth instar and may be fully developed in the teneral adults. In the female, on the other hand, the fourth epoch is longer and the rate of growth fluctuates a little before the final moult and the peak of reproductive growth occurs a few days after she has become adult. The two reproductive peaks in the curve of the mixed population (Text-fig. 14) perhaps represent a disparity in time when the gonads start developing in the two sexes.

4. *Utilization of, and Survival on, Exclusive Diets*

Freshly hatched nymphs were given weighed amounts of food and the oven-dry weights of food ingested and faeces voided were determined (*vide supra*, pp. 114-115). The following sedge and grasses were used in this experiment :

(i) Involute-leaved sedge (*Carex eleocharis*)
(ii) Smooth brome grass (*Bromus inermis*)
(iii) Red fescue (*Festuca rubra*)
(iv) Kentucky bluegrass (*Poa pratensis*)

(a) *Utilization of Exclusive Diets*

(i) *Utilization of involute-leaved sedge* (Carex eleocharis).—To analyse the utilization of food ingested by the grasshopper, it is necessary to take into account the amounts of food eaten by it in a given time and the amounts of faeces voided during the same interval.

Table 23 gives the amount of food (sedge) ingested in terms of oven-dry weight per 100 mgm. body weight of the insect (Text-fig. 16), the amount of oven-dry faeces voided (Text-fig. 17) and the amount of oven-dry food utilized (Text-fig. 18), the latter two on the same basis as the former. The fifth column has been provided in the table to give an idea of the live weight produced out of the dry matter utilized. Thus, 100 mgm. of freshly hatched nymphs (reared collectively) ingested 43 mgm. of oven-dry food by the second day. Out of this amount, nine mgm. were voided as faeces and 34 mgm., or 79 per cent of ingested food, were utilized for producing 13 mgm. of live weight, the rest having been used up in various metabolic activities.

TABLE 23

Involute-leaved Sedge (Carex eleocharis) : *Food ingested, faeces voided and food utilized by* Camnula pellucida (*Scudder*)

N.B.—The increase in live weight $= \left(\frac{\text{Wt. increase}}{\text{Live wt. on previous day}}\right) \times 100.$

Age in days after hatching		Oven-dry matter (Sedge) ingested per 100 mgm. body weight	Oven-dry faeces voided per 100 mgm. body weight	Oven-dry matter utilized per 100 mgm. of food ingestion	Live weight increase per 100 mgm. body weight
I instar	2	43	9	79	13
	4	85	17	80	25
	6	70	20	77	1
	8	12	25	—66	5
I instar	10	100	36	66	14
	12	254*	39	74*	25
	14	158*	39	74*	38

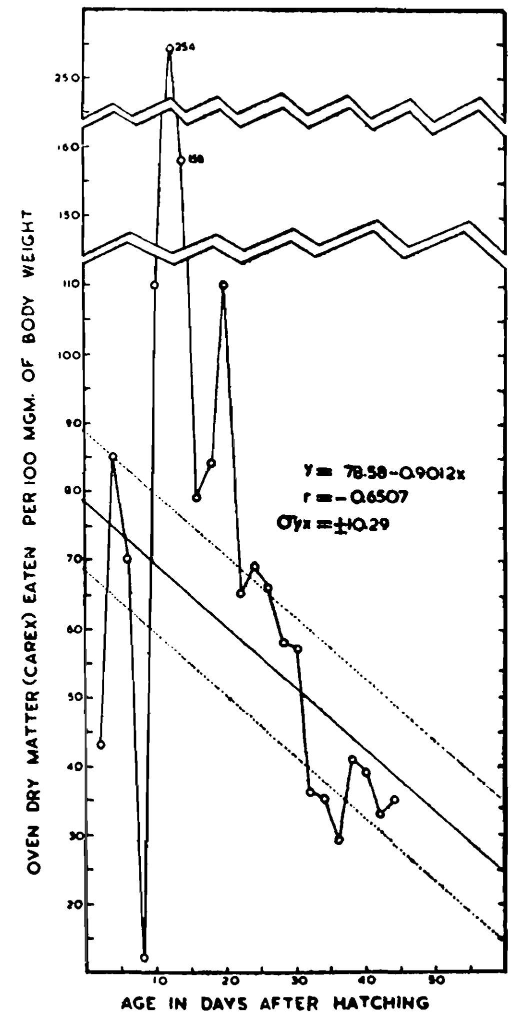
* Extraordinarily large quantities ingested and utilized.

TABLE 23—*concld.*

Age in days after hatching		Oven-dry matter (Sedge) ingested per 100 mgm. body weight	Oven-dry faeces voided per 100 mgm. body weight	Oven-dry matter utilized per 100 mgm. of food ingestion	Live weight increase per 100 mgm. body weight
III Instar	16	79	54	70	40
	18	84	53	67	22
	20	103	82	62	37
	22	65	54	—59	35
IV Instar	24	69	50	57	25
V Instar	26	66	53	55	25
	28	58	41	54	19
Adult	30	57	34	54	15
	32	36	27	53	7
	34	35	28	52	4
	36	29	23	51	..
	38	41	35	50	2
	40	39	34	49	8
	42	33	24	49	1
	44	35	24	48	..

$$\text{Food utilized} = \frac{(\text{Dry weight of food ingested—Dry weight of faeces voided}) \times 100}{\text{Dry weight of food ingested}}$$

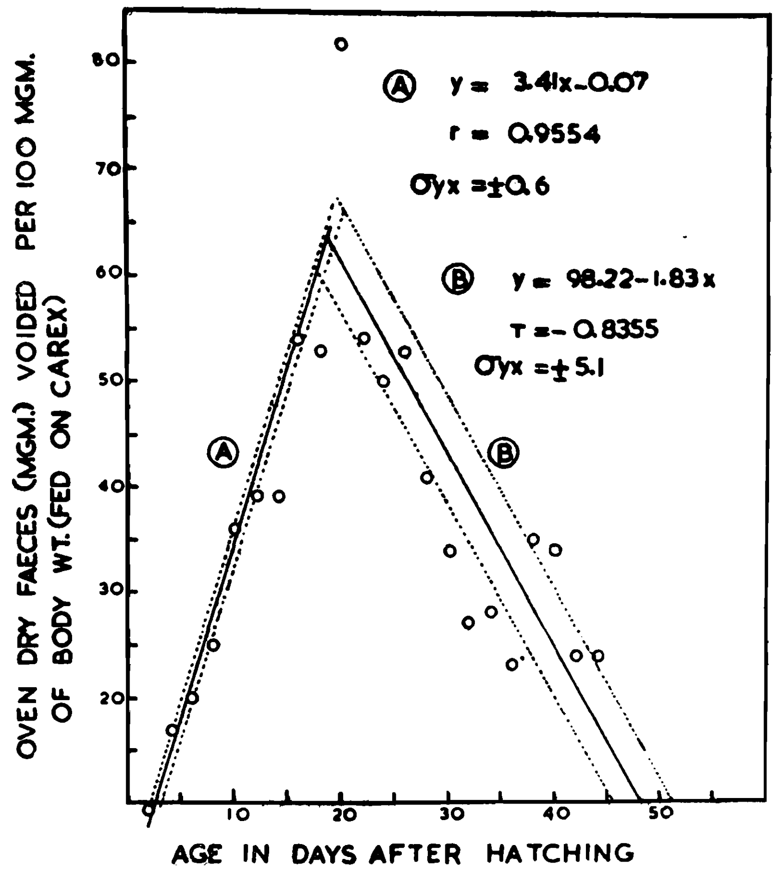
In the graphs (Text-figs. 16, 17 and 18), the amounts ingested, voided and utilized have been plotted along the y-axis, while the age of the grasshopper has been plotted along the x-axis. In case of the food ingested (Text-fig. 16) and utilized (Text-fig.18), the points have been joined by continuous and broken lines, respectively, while in case of faeces voided, the points have been left unjoined. A trend line (solid line) with its *standard deviation* has been fitted for the points by the straight line equation $y=a+bx$.



TEXT-FIG. 16.—Ingestion of sedge (*Carex eleocharis*) by *Camnula pellucida* during the course of development. Food ingested is plotted in terms of oven-dry matter eaten for each 100 mgm. body weight of grasshopper. A regression line has been fitted for the points. The standard deviation is shown by the dotted lines. Two extra ordinarily large meals, on the 12th and 14th days, have been disregarded for the purpose of plotting the trend line, but have been set in the graph by breaking the y-axis.

In case of the graph showing food ingestion (Text-fig. 16), two points, *viz.*, those on the 12th and 14th days, were disregarded for the purpose of determining the trend line and the correlation coefficient, because they varied from the rest of the points to a very high degree. However, these points have been indicated on the graph and joined to the rest of the points by breaking the scale on the y-axis. In the case of the graph showing the faeces voided (Text-fig. 17), the trend of points showed a bilateral symmetry about the 20th day. Two trend lines, therefore, were fitted by considering separately the data before and after this day, the value for the 20th day being included in each plot. Therefore, there are two trend lines and two correlation coefficients in the graph. The slope constant *b* is positive up to the 20th day and is negative for the remainder.

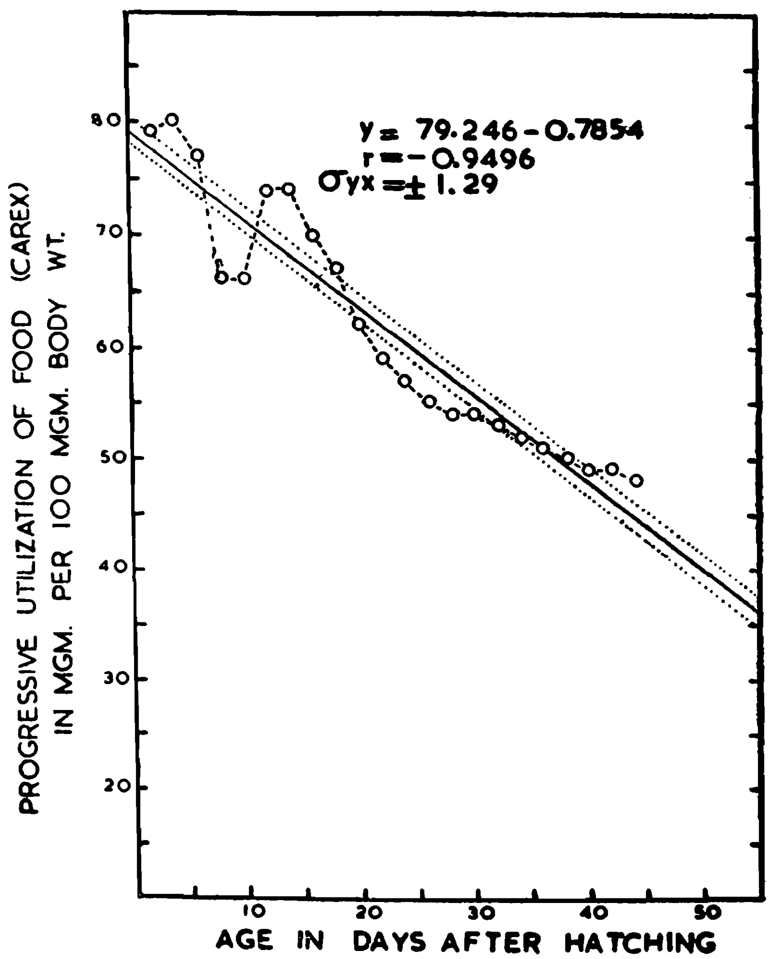
The trend lines, intended to represent the highly tortuous curves (Text-figs. 16 and 17), cannot represent the exceptional points of the graphs, but, as indicating the general tendency, they are, no doubt, very helpful.



TEXT-FIG. 17.—Faeces voided by *Camnula pellucida* fed on *Carex eleocharis* during the course of its development. Faeces voided is plotted in terms of dry quantities per 100 mgm. body weight of grasshopper. Two trend lines with their standard deviations have been fitted by considering separately the data before and after the 20th day about which day the trend showed bilateral symmetry.

On the sedge diet, there is a trend of progressive decrease, with age, in the amount of food ingested by 100 mgm. body weight of nymphs (Table 23 and Text-fig. 16), although they, for some reason, took an exceptionally big meal on the 12th and 14th days ; they were, at this time, on the verge of changing into the average second instar. The faeces voided on the following days do not show a corresponding increase beyond what the positive slope of the trend line indicates. In fact, the amount of faeces voided is in line with the amounts voided on the preceding and the following days. This indicates an enormous amount of food utilization by the second instar nymph, only a small fraction of which appears as live weight increase on those two days. A considerable portion of this utilized food must have been spent for some metabolic activities which are not visualized at present. However, for a long time afterwards the live weight increase in the nymph shows a rise which is greater than the oven-dry weight of food utilized would justify. This apparent discrepancy would be cleared if it is realized that the amount of food utilized is in terms of dry weight and its correspondence with the live weight produced does not take into account the amount of water present in the tissues and the expenditure of utilized food in energy and other metabolic activities.

Taking a general view of the utilization of sedge food by the grasshopper, the graph (Text-fig. 16) indicates that the young nymph, on the average, was ingesting the sedge food in the proportion of about 80 per cent of its body weight per day ; at transformation time, about the 30th day, the corresponding value was about 50 per cent. Over the same time, the utilization (Text-fig. 18) of food ranged from an average about 80 per cent of the dry weight of food ingested to about 55 per cent at transformation time. On this diet, the grasshopper attained the live weight of 124 mgm. at transformation time (Table 14 and Text-fig. 2).



TEXT-FIG. 18.—Utilization of sedge (*Carex eleocharis*) by *Camnula pellucida* during the course of development. Progressive utilization of food is plotted in terms of percentage of cumulative food ingested. A trend line along with its standard deviation has been fitted for all the points in the graph.

(ii) *Utilization of smooth brome grass* (Bromus inermis).—The oven-dry weight of brome grass ingested, the dry weight of faeces voided and the oven-dry weight of food utilized per 100 mgm. body weight of the grasshopper are given in Table 24. The first two of these data are graphically presented in Text-figs. 19 and 20 and the third given as a percentage in Text-fig. 21.

TABLE 24

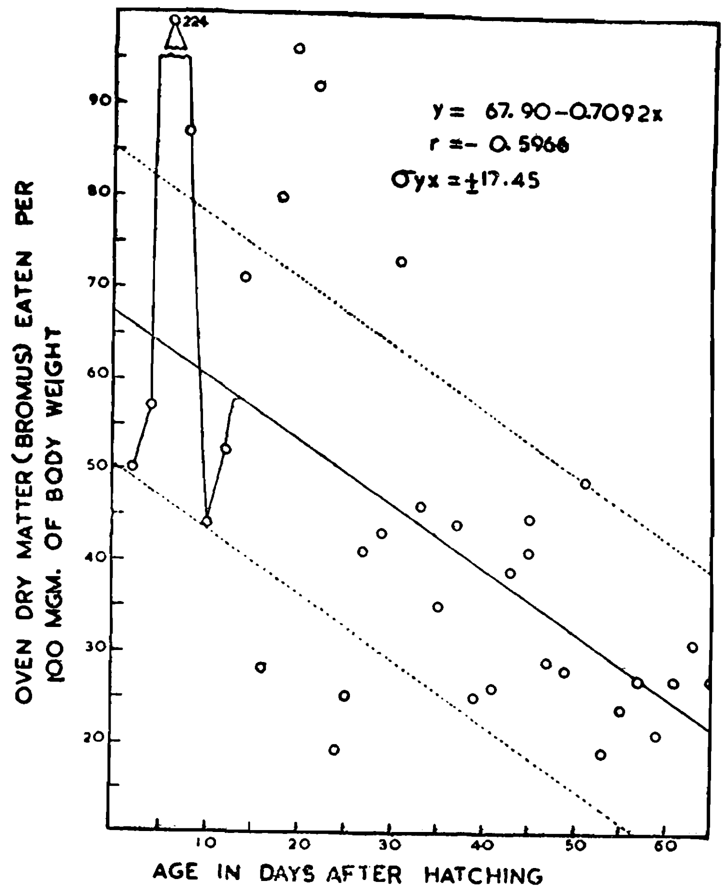
Brome Grass (Bromus inermis): *Food ingested, faeces voided and food utilized by* Camnula pellucida (*Scudder*)

N.B.—The increase in live weight = $(\frac{\text{Wt. increase}}{\text{Live wt. on previous day}}) \times 100.$

	Age in days after hatching	Oven-dry matter (Brome ingested per 100 mgm. body weight	Oven-dry faeces voided per 100 mgm. body weight	Oven-dry matter utilized per 100 mgm. of food ingestion	Live weight increase per 100 mgm. body weight
I instar	2	50	32	36	16
	4	57	40	33	24
	6	224*	29	70	21
II instar	8	87	45	65	19
	10	44	27	63	13
	12	52	42	58	25
III instar	14	71	57	54	36
	16	28	36	50	24
	18	80	40	50	23
	20	96	41	51	29
IV instar	22	92	36	52	27
	24	19	18	51	15
V instar	25	25	25	49	16
	27	41	22	49	..
	29	43	34	48	10
	31	73	32	49	6
	33	46	30	48	14
	35	35	31	47	9
Adult	37	44	29	46	8
	39	25	26	45	10
	41	26	22	45	6
	43	39	32	44	7
	45	41	28	44	11
	47	29	23	43	8
	49	28	23	43	2
	51	49	28	43	—1
	53	19	16	42	—1
	55	24	18	42	3
	57	27	19	42	3
	59	21	17	41	0·1
	61	27	17	41	—0·07
	63	31	19	41	—5

*Extraordinarily large quantities ingested.

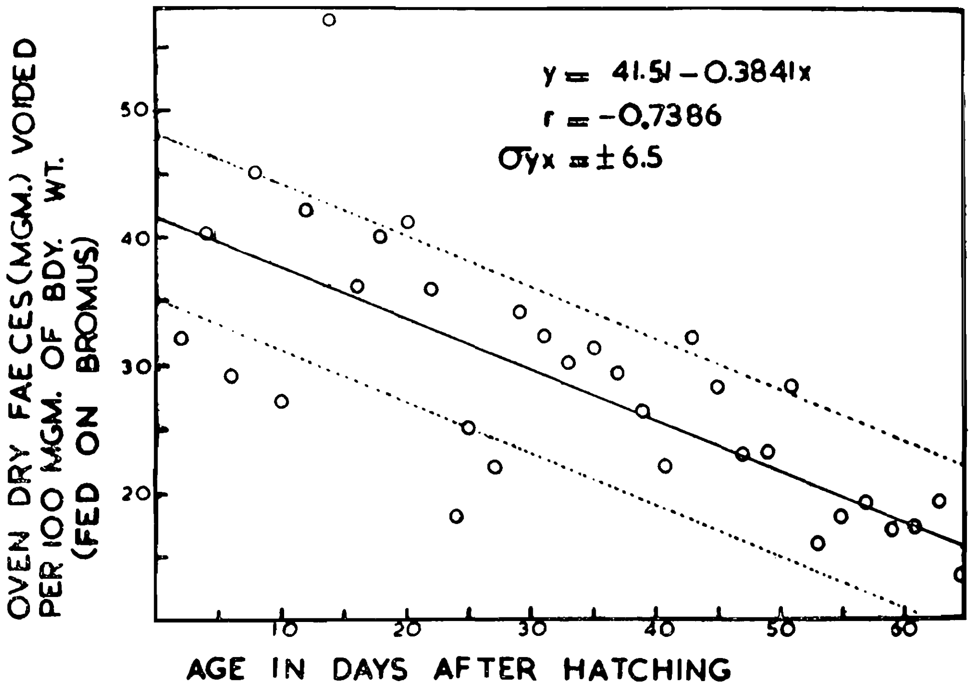
The young nymph took the biggest meal of brome on the sxth day (much like the nymph feeding on sedge). The size of this meal is out of line with the size of the other observed meals of brome grass. This meal has, therefore, been disregarded for the purpose of determining the trend line and the correlation coefficient, but has been indicated on the graph (Text-fig.) 19 by breaking the scale on the y-axis. The



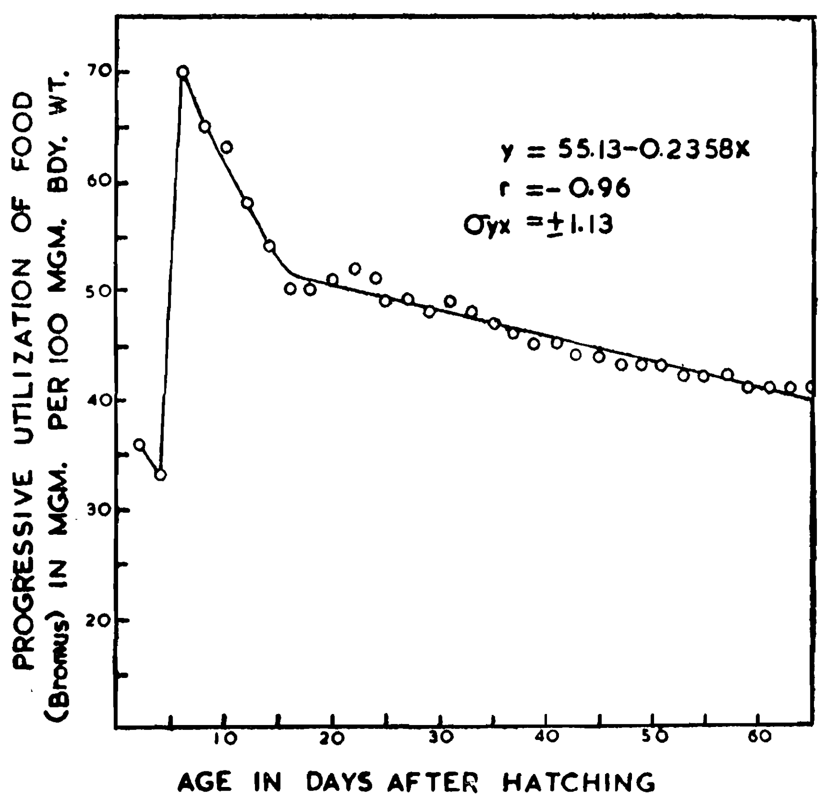
TEXT-FIG. 19.—Ingestion of smooth brome (*Bromus inermis*) by *Camnula pellucida* during the course of development. Food ingested is plotted in terms of oven-drv matter eaten for each 100 mgm. body weight of grasshopper. A regression line has been fitted for the points. The standard deviation is shown by the dotted lines. One extraordinarily large meal on the sixth day has been disregarded for the purpose of plotting the trend line, but has been set in the graph.

amount of faeces voided does not show a corresponding rise on the sixth day nor the following day. In fact, the amount voided was even less than what was voided on the previous day. The amount of food utilized on this day was enormous, and only a small fraction of it appears in the live weight increase of the nymph. A great deal of it must have been expended in some other metabolic requirement, which is not visualized at present.

The trend in food ingestion of brome grass is similar to that of sedge, the main difference being that the insect throughout its life ingested, comparatively, a smaller meal of brome than the nymph reared on sedge and that its drop in ingestion of brome meal, with age, was less steep than that of the sedge meal, as can be made out from the slope constants in the two graphs (b for brome = —0·7092 ; b for sedge = —0·9012 ; Text-figs. 19 and 16). The young nymph on brome diet was ingesting, on the average, about 70 per cent of its body weight per day as compared to 80 per cent of sedge, and at transformation time (about 35 days) it was ingesting a little over 40 per cent of its weight in dry grass per day, while the nymph on sedge was ingesting 50 per cent. Over



TEXT-FIG. 20.—Faeces voided by *Camnula pellucida* fed on *Bromus inermis* during the course of development. Faeces voided is plotted in terms of dry quantiites per 100 mgm. body weight of grasshopper. A line of regression along with its standard deviations in dotted lines has been fitted for the points.



TEXT-FIG. 21.—Utilization of smooth brome (*Bromus inermis*) by *Camnula pellucida* during the course of development. Progressive utilization of food is plotted in terms of percentage of cumulative food ingested. A trend line along with its standard deviation has been fitted for all the points in the graph after the 14th day. The points before this day were disregarded for the purpose of plotting the trend line, but are shown on the graph.

this time, the utilization of food by the grasshopper on brome does not follow the pattern of the grasshopper on sedge. In the young nymph, the average utilization was relatively low (35 per cent), compared to over 70 per cent on sedge, sharply rising at the time of the first moult to a high of 70 per cent, falling steadily to about 55 per cent during the second stadium, and then declining gradually to about 50 per cent at transformation time. The average weight attained by the grasshopper at transformation was 128·67 (about the 35th day ; Table 9, p. 118).

TABLE 25

Red Fescue Grass (Festuca rubra) : *Food ingested, faeces voided and food utilized by* Camnula pellucida (*Scudder*)

N.B.—The increase in live weight $\left(\frac{\text{Wt. increase}}{\text{Live wt. on previous day}}\right) \times 100$.

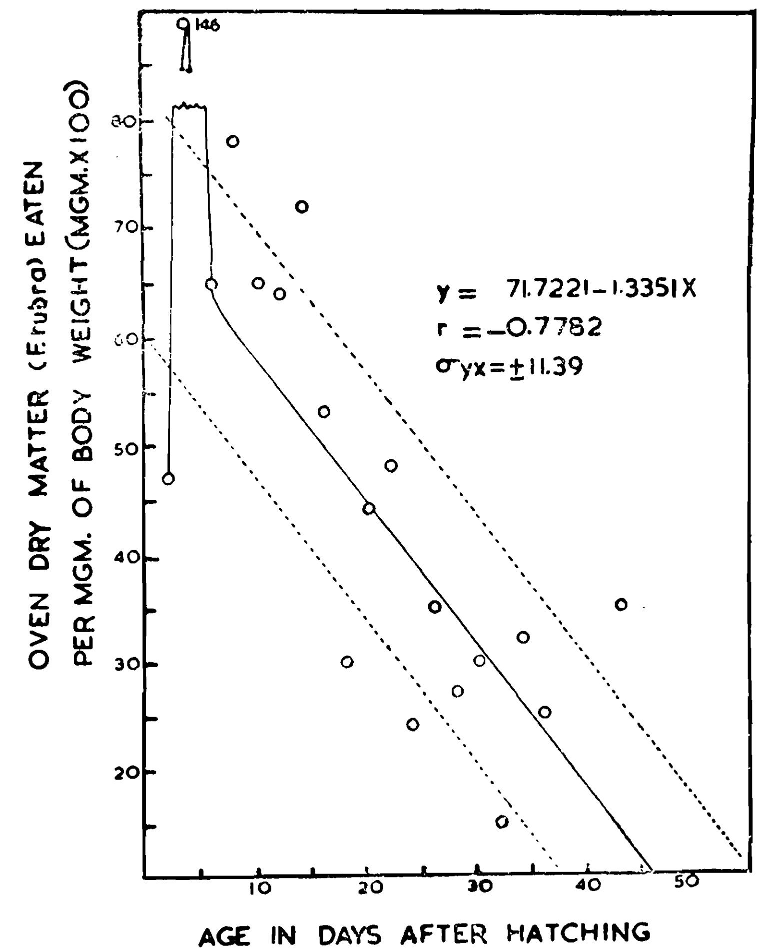
Age in days after hatching		Oven-dry matter (fescue) ingested per 100 mgm. body weight	Oven-dry faeces voided per 100 mgm. body weight	Oven-dry matter utilized per 100 mgm. of food ingestion	Live weight increase per 100 mgm. body weight
I instar	2	47	16	66	11
	4	146*	82*	49	41
	6	65	37	48	42
II instar	8	78	45	46	31
	10	65	36	46	35
III instar	12	64	47	43	46
	14	72	33	45	23
IV instar	16	53	32	44	28
	18	30	26	43	19
	20	44	27	43	18
V instar	22	48	26	43	18
	24	24	18	42	13
	26	35	21	42	13
	28	27	21	41	18
Adult	30	30	20	1	8
	32	15	11	41	—2
	34	32	21	41	5
	36	25	18	40	9
	38	35	17	41	26

*Extraordinarily large quantity ingested and faeces voided.

It will be noticed that throughout life the nymph on brome ingested less food and retained for utilization less of that eaten than did the nymph reared on sedge, and yet the weight attained was probably somewhat greater. On the other hand, however, the transformation time of the nymph on brome is just enough later to account for the small difference between their transforming weights.

If the graphs of live weights for sedge and brome grass (Text-figs. 2, 3 and 4) are examined for the post-transformation life, it is seen that the sedge-fed grasshopper gained very little weight as an adult, while the brome-fed grasshopper very nearly doubled its transformation weight. On the basis of this observation, it can be concluded that brome may be more nutritious than sedge, at least insofar as increase in adult live weight is concerned.

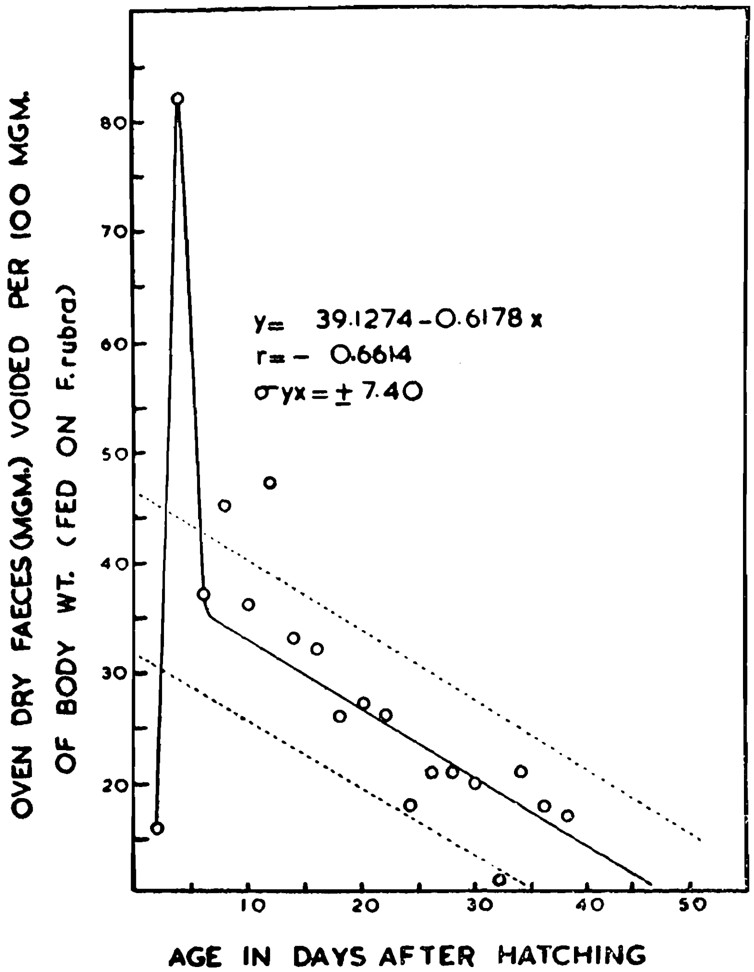
(iii) *Utilization of red fescue grass* (Festuca rubra).—The oven-dry weights of fescue ingested, faeces voided, food utilized and live weights produced are given in Table 25. The first two of these data are graphically presented in Text-figs. 22 and 23, while the third are given as percentages in Text-fig. 24.



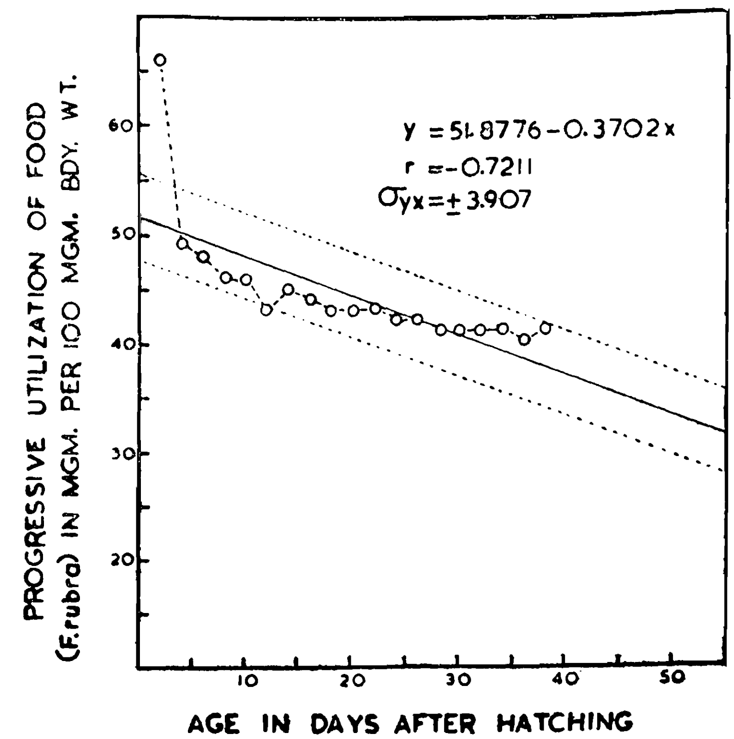
TEXT-FIG. 22.—Ingestion of red fescue (*Festuca rubra*) by *Camnula pellucida* during the course of development. Food ingested is plotted in terms of oven-dry matter eaten for each 100 mgm. body weight of grasshopper. A regression line along with the standard deviation in dotted line has been fitted for the points. One extraordinarily large meal on the fourth day was disregarded for the purpose of plotting the trend line, but has been set in the graph on the y-axis.

The young nymph took the biggest meal on the fourth day (much like the nymphs fed on sedge and brome grass), the size of which is out of line with the quantities ingested by it at any other time. This observation, therefore, has not been regarded for the purpose of determining the trend line and the correlation coefficient, although it has been included in the graph.

The young nymph, although, took the biggest meal on the fourth day (Table 25 and Text-fig. 22), voided about 56 per cent of it as faeces and retained 44 per cent in the body, which is about the average utilization ratio for the fescue-fed nymph on any size of meal. The fescue-fed nymph resembles the nymph fed on sedge and



TEXT-FIG. 23.—Faeces voided by *Camnula pellucida* fed on *Festuca rubra* during the course of development. Faeces voided is plotted in terms of dry quantities per 100 mgm. body weight of grasshopper. A trend line along with the standard deviation in dotted lines has been fitted for all points excepting the one on the fourth day.



TEXT-FIG. 24.—Utilization of red fescue (*Festuca rubra*) by *Camnula pellucida* during the course of development. Progressive utilization of food is plotted in terms of percentage of cumulative food ingested. A trend line along with the standard deviation has been fitted for all the points in the graph.

brome in taking the biggest meal early in life but differs from them in the matter of utilization of that meal. Thus, while the sedge- and brome-fed nymphs retained enormous portions of their meal, the fescue-fed nymph voided in proportion to the size of the meal ingested. The curves on fescue diet show food ingested, faeces voided and food utilized, all three attaining a high level in early life and then dropping off with age at varying slopes. The drop in food ingestion, with age, is steepest in grasshoppers feeding on fescue (b=—1·3351 ; Text-fig. 22), being nearly twice as steep as on brome (b =—0·71 ; Text-fig. 19). The amount of faeces voided by the fescue-fed grasshopper falls off, with age, much less abruptly than the amount of food ingested, as the slope constants on the graphs will show.

In a general way, after an initial wide variation, the ingestion of fescue ranged from about 65 per cent of the live weight in the young nymph to about 30 per cent in the transforming nymph. During the same period, utilization ranged from about 50 per cent to 41 per cent. The weight attained at the transformation time of 30 days was 159 mgm. on the average, and growth continued during the adult life at a somewhat slower pace during the time the experiment was continued.

Utilization ratio of fescue differs little from that of brome, but the animal regularly ate a relatively smaller meal of fescue, yet the live weight increased at a faster rate (Text-figs. 10 and 12) throughout life on fescue diet. On the basis of live weights attained, fescue is, therefore, a more nutritious grass than brome or *Carex*.

(iv) *Utilization of Kentucky bluegrass* (Poa pratensis).—The oven-dry weights of Kentucky bluegrass ingested, faeces voided, food utilized and live weights produced are given in Table 26. The first two of these data are graphically presented in Text-figs. 25 and 26, while the third are given as percentages in Text-fig. 27.

TABLE 26

Kentucky Bluegrass (Poa pratensis) : *Food ingested, faeces voided and food utilized by* Camnula pellucida (Scudder)

N.B.—The increase in live weight = $\left(\frac{\text{Wt. increase}}{\text{Live wt. on previous day}}\right) \times 100$.

Age in days after hatching		Oven-dry matter (Kentucky bluegrass) ingested per 100 mgm. body weight	Oven-dry faeces voided per 100 mgm. body weight	Oven-dry matter utilized per 100 mgm. of food ingestion	Live weight increase per 100 mgm. body weight
I instar	2	73	33	55	16
	4	67	40	48	42
	5·41				
II instar	6	85	54	43	67
	8	44	26	43	57
	9·10				
III instar	10	58	41	41	49
	12	56	29	42	43

TABLE 26—*concld.*

Kentucky Bluegrass (Poa pratensis) : *Food ingested, faeces voided and food utilized by* Camnula pellucida (Scudder)

	Age in days after hatching	Oven-dry matter (Kentucky bluegrass) ingested per 100 mgm. body weight	Oven-dry faeces voided per 100 mgm. body weight	Oven-dry matter utilized per 100 mgm. of food ingestion	Live weight increase per 100 mgm. body weight
IV instar	15	50	34	41	34
	17	45	29	40	37
	17·94				
V instar	19	36	26	39	27
	21	29	28	37	19
	23	20	16	37	14
	26	25	18	36	10
	27·30				
Adult	28	31	22	36	15
	30	40	24	36	15
	32	22	21	35	8
	34	54	25	37	5
	36	32	21	37	4
	38	25	14	37	2
	40	21	18	36	1
	43	22	10	37	7
	45	12	10	36	6

An examination of the data on food ingestion (Table 26 and Text-fig. 25) shows that the nymph, like those feeding on sedge, brome and fescue, also did take a big meal early in its life, on the sixth day. But unlike the others, the meal is not enormous in proportion to what had been taken on the previous days. The amount of faeces voided from that meal are also larger in proportion to the quantities voided on other days, but not strictly great. The same statement holds good for food utilization also. The trend line and the correlation coefficients determined for all these three, therefore, also take into account the data on the sixth day.

The slope of the trend lines shows that the food ingestion of the insect feeding on Kentucky bluegrass drops (b =—1·20), with age, somewhat less abruptly than that of the nymph feeding on fescue (b =—1·34), that the amount of faeces voided drops (b =—0·69), with age, more or less to the same extent as on fescue (b =—0·62) and that the amount of food utilized drops (b =—0·27) even less abruptly than that of the nymph feeding on fescue (b =—0·37). There being a close correspondence between the early, big meal, the faeces voided and the food utilized, as in the case of the nymph feeding on fescue, the curve of Kentucky bluegrass utilization (Text-fig. 27) presents the same general appearance as the one for fescue (Text-fig. 24).

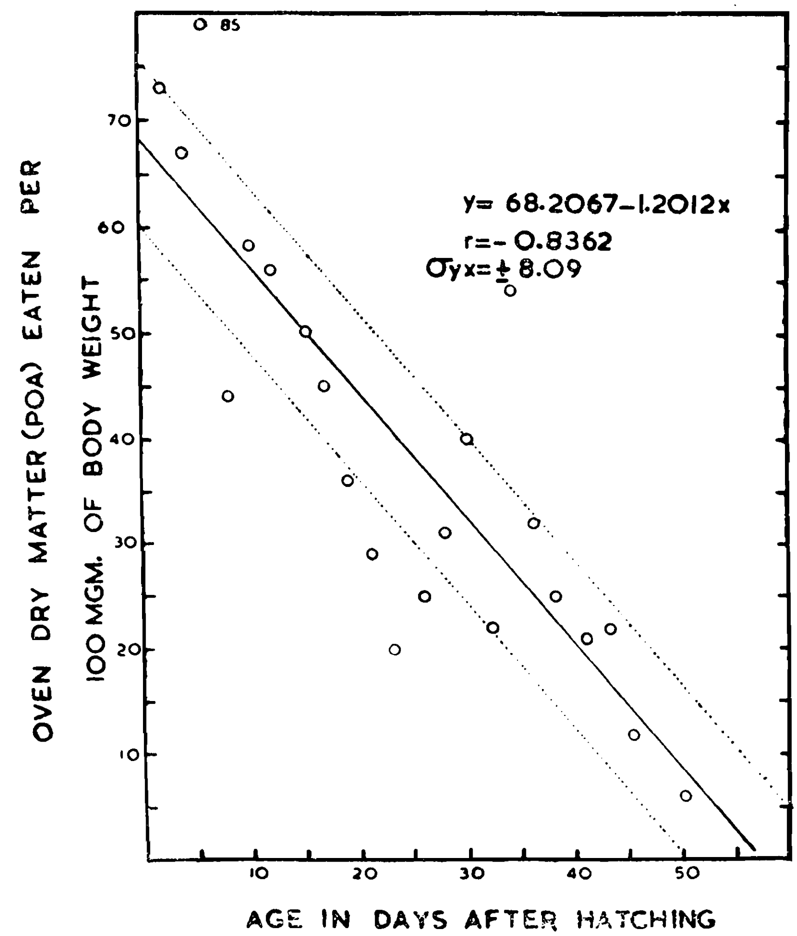
Kentucky bluegrass ingestion by the insect ranges from about 70 per cent of the body weight at the beginning of nymphal life to about 35 per cent at transformation time. After a short initial flurry, the utilization of food settles down to a steady rate of 45 to 40 per cent. In fact, if the trend line for food utilization of the grasshopper is fitted after the 10th day, it would be a horizontal line close to 40 per cent.

In order to compare the live weights attained by the grasshopper on various diets it is of importance to keep in mind the fact that the grasshopper population feeding on Kentucky bluegrass at the average transformation time consisted entirely of females (Table 26). The transforming weight of the grasshopper on this diet being 208 mgm. has, therefore, to be judged with qualifications. However, a rough estimate of live weight of transforming males and the average live weight of the mixed population at transformation time can be made by assuming that the sexual dimorphism in live weights of teneral adults is about the same on Kentucky bluegrass and fescue (fescue : live weights of teneral female, 195·88 mgm., male, 120·06 mgm.; *vide supra*, p. 120). From this assumption, the average live weight of the mixed population on Kentucky bluegrass can be estimated, which comes to 168 mgm. (*cf.* fescue, 159·38 mgm.; Table 10, p. 120). From this and on the basis of equal sexual dimorphism on both these grasses, the live weight of the teneral male on Kentucky bluegrass comes to 169 mgm. The estimated live weights of the mixed population and that of the males and females on Kentucky bluegrass are somewhat greater than observed on fescue.

However, some peculiar features of the food were noticed while rearing the grasshopper on Kentucky bluegrass under controlled conditions of temperature and humidity, which were also observed in the greenhouse experiments (p. 121). This grass, when fed exclusively, seemed to have some kind of toxic effect on the grasshopper. Nearly all the nymphs and adults seen dying showed tremors of the hind and fore legs and many of them were seen to pass out a red-coloured fluid from the anus and mouth. A small portion of faeces, particularly of fifth stage nymphs and adults, was always observed to be in more slender pellets than the normal ones and always coloured red. Another special feature of this food noted is the fact that there was not a single male adult at the average transformation time. Whether it is purely a fortuitous coincidence that 100 freshly emerged nymphs reared on this grass in four replicate cages should give this result is difficult to say.

(b) *Survival on Exclusive Diets*

One hundred freshly emerged nymphs were used for each experiment on red fescue, brome, sedge, and Kentucky bluegrass in four replicate cages (*vide supra*, p. 114). For the experiment on intermediate wheat-grass, however, two replicate cages were used,

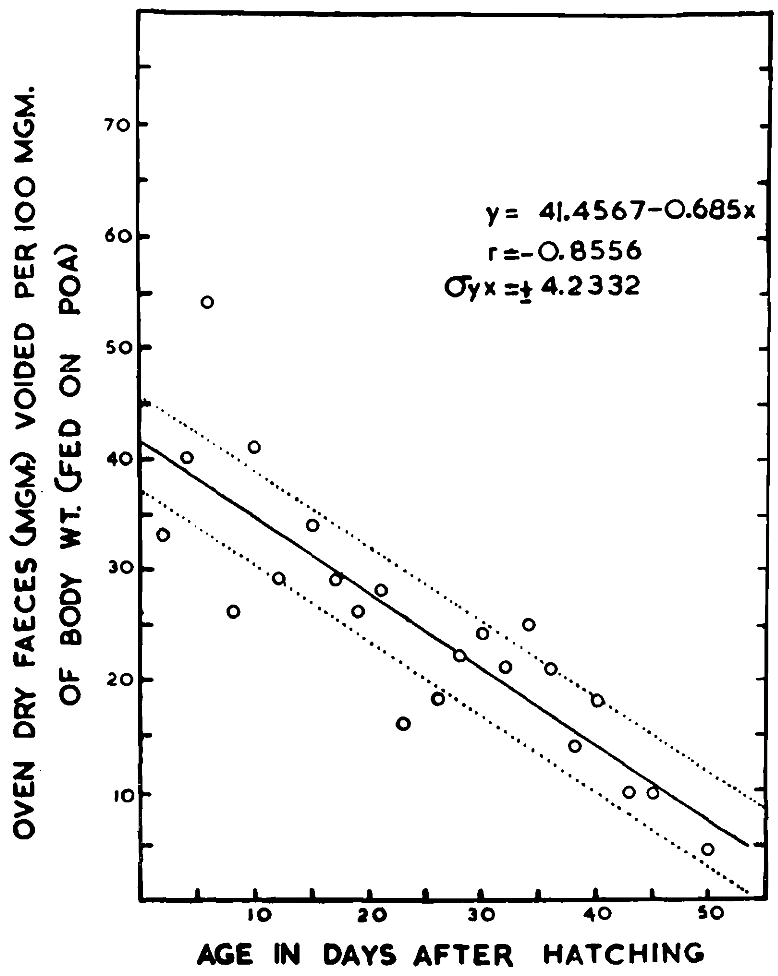


TEXT-FIG. 25.—Ingestion of Kentucky bluegrass (*Poa pratensis*) by *Camnula pellucida* during the course of development. Food ingested is plotted in terms of oven-dry matter eaten for each 100 mgm. body weight of grasshopper. The nymphs took a big meal on the sixth day, but the quantity being not extraordinarily large, has been included for the purpose of regression line and the standard deviation.

each containing 25 freshly emerged nymphs, and the experiment on wheat was started with 36 freshly emerged nymphs in one cage ; after the first moult the nymphs were reared in two cages (*vide supra*, p. 124). In all the experiments, the nymphs were subjected to the same temperature and, more or less, to the same relative humidity. The only factor that differed was, therefore, the food, which was supplied fresh on alternate days, inserted through a cork into a vial filled with water ; this arrangement kept the food succulent for the time the nymphs were eating it. It can, therefore, be said that the nymphs had free access to the food in its best condition. The survival, or mortality, occurring in the cages is, therefore, supposed to be due to some factor inherent in the food itself.

The survival of the original population of nymphs fed on single diets is given in Table 27. In the case of fescue, smooth brome, Kentucky bluegrass, and involute-leaved sedge, the original population consisted of 100 freshly emerged nymphs, while the original population on intermediate wheat-grass consisted of 50 nymphs and on wheat only 36. In the two latter cases, the percentage figures have been calculated from the actual number of survivals (given within parentheses). The survival of the grasshopper is shown graphically in Text-fig. 28.

It will be seen in the table and the figure that, out of all the six grasses and the sedge tested, fescue seems to be the most promising grass from the point of view of giving the grasshopper the highest and most steady survival. Thus, out of 100 nymphs, 61 transformed successfully and the loss at each stage was the least of all grasses



TEXT-FIG. 26.—Faeces voided by *Camnula pellucida* fed on *Poa pratensis* during the course of development. Faeces voided is plotted in terms of dry quantities per 100 mgm. body weight of grasshopper. A trend line along with the standard deviation in dotted lines has been fitted for all the points.

and sedge. In Text-fig. 28, the graph of survival of the grasshopper on this grass shows almost a straight line relationship within the stadia. The second-best grass is wheat, on which 25 out of 36 young nymphs reached the adult stage and the mortality at each stage was steadily low after the third stadium. These conclusions are corroborated from earlier experiments reported in Chapter IV (pp. 104-113 ; Text-Fig. 1). The third position should be given to Kentucky bluegrass and brome, in which 20 and 22 out of the original 100 reached the adult stage. Sedge and intermediate wheat-grass come fifth and sixth, respective

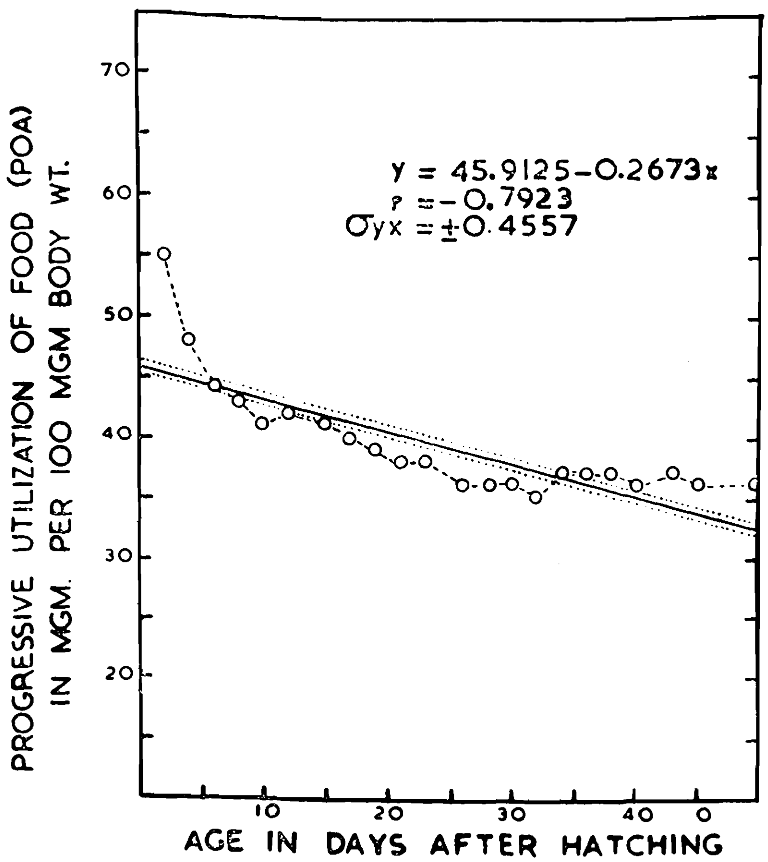
TABLE 27

Survival of Camnula Pellucida (*Scudder*) *on five grasses and a sedge.*

N.B.—In the cases of intermediate wheat-grass and wheat, the actual survival figures are given within parentheses beside the calculated percentage figures.

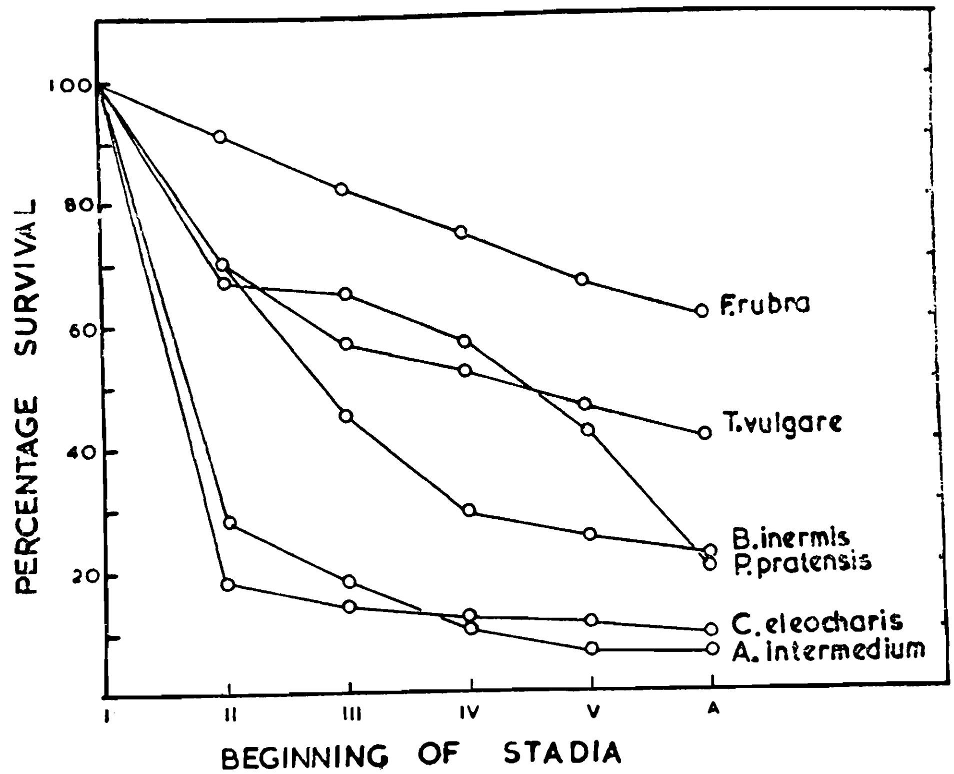
Stadium (instar)	Red fescue	Selkirk wheat	Smooth brome	Kentucky bluegrass	Involute-leaved sedge	Inter-mediate wheat grass
O-I	100	100 (36)	100	100	100	100 (50)
I-II	91	81 (29)	70	67	18	28 (14)
II-III	82	64 (23)	45	65	14	18 (9)
III-IV	75	56 (20)	29	57	12	10 (5)
IV-V	67	36 (13)	25	42	11	6 (3)
V-Adult	61	25 (9)	22	20	9	6 (3)

The first stadium is the period of greatest danger for the grasshopper and in all the experiments reported in this work the largest mortality was seen in this stage. During this stage, next to fescue, wheat (*Triticum vulgare*) and brome (*Bromus inermis*) seem to be equally good, the survival on these grasses being 81 and 70 per cent, respectively. Kentucky bluegrass (*Poa pratensis* ; survival, 67 per cent) comes third, while intermediate wheat-grass (*A. intermedium* ; survival, 28 per cent) and sedge (*Carex eleocharis* ; survival, 18 per cent) are fourth and fifth, respectively.



TEXT-FIG. 27.—Utilization of Kentucky bluegrass (*Poa pratensis*) by *Camnula pellucida* during the course of development. Progressive utilization of food is plotted in terms of percentage of cumulative food ingested. A trend line along with the standard deviation in dotted lines has been fitted for all the points.

After the first stadium sedge appears to be a very promising food for the grasshopper insofar as survival is concerned ; in Fig. 28, the graph of survival on this food runs almost in a horizontal line, showing that, if the critical stage of first instar is passed over on a more favourable grass available under actual field conditions, sedge would



TEXT-FIG. 28.—Survival of *Camnula pellucida* on five grasses and a sedge. Percentage survival of the grasshopper at the beginning of each stadium is shown.

perhaps be the best food for the subsequent survival. From the graph of survival, intermediate wheat-grass and brome appear to be meritorious for survival after the third or fourth instars, when their graph turns horizontal.

VI—DISCUSSION

"How does environment influence the animal's chance to survive and multiply?" This was the question posed by Andrewartha and Birch (1954). They wrote a book answering the question, saying that, "the search for an answer leads, on the one hand, to an examination of the animal's physiology and behavior and, on the other, to the four basic components of environment : weather, food, other animals, and a place in which to live." Of these basic components, food is the only one considered in this thesis.

Food preference.—Camnula is found almost all over the United States and southern Canada, but it assumes great economic importance by its abundance only in comparatively limited areas where, to a large extent, the food factor is reponsible for its becoming a plague. The food factor operates, in a general way, by making available the preferred plants in green and succulent condition, by enabling the grasshopper to complete its development quickly, by producing vigorous, heavy and long-lived insects and by stimulating their fecundity to enable them to dominate the environment by their numbers.

Of the 62 host plants examined for preference it was found that this grasshopper has preference for the grasses as follows (preference values given) the reed canary-grass (131), western couch-grass (105), cultivated Vantage barley (100), Selkirk wheat (80), sloughgrass (79), awned northern wheat-grass (71), big bluegrass (64), Kentucky bluegrass (64), wild barley (59), intermediate wheat-grass (57), redtop (55), green speargrass (53), eastern couch-grass (50), slender wheat-grass (50), perennial ryegrass (50), sedge (50) and Canada bluegrass (43). Besides these, fescue (35) and brome (24) are known to have figured importantly in the ecology of the *Camnula* and oats (20) and tall wheat-grass (9) may be considered also of interest from the same point of view. Significance of food preference is discussed earlier (pp. 102-103).

Some of the grasses, it seems, are preferred for their great succulence, *e.g.*, reed canary-grass (P.V. 131). But, although succulence may be an important physical factor in selection, other grasses, also very succulent, have failed to attract the grasshopper strongly ; *e.g.*, redtop, eastern couch-grass, oats, sloughgrass, brome, fescue, Kentucky bluegrass, as well as many forbs, have preference values much lower than reed canary-grass. It appears that the physical factors are unimportant if the composition of the plant is nutritionally unfavourable to the grasshopper. Although it is generally thought that grasshoppers are able to discriminate nutritionally favourable plants from unfavourable ones, the present study did not give sufficient evidence to show that this discrimination is a fine one. Six grasses (in descending order of preference values), *viz.*, wheat, intermediate wheat-grass, Kentucky bluegrass, sedge, fescue and brome, examined in detail for the growth of *Camnula* on each one of them as an exclusive diet (part V) did not turn out in the same order insofar as course of growth, rate of growth and survival are concerned. Perhaps the discrimination is a gross one and it would be necessary to do detailed work on more grasses differing more widely in their nutritional values before the question of discriminatory ability of the grasshopper can be satisfactorily answered.

Effect of food on survival and development.—The effect of food on the survival and development was quantitativey measured as the "survival and development index" of the grasshopper for the various host grasses. The analyses of 23 grasses (including one sedge and four cereals and 18 other grasses) showed that the grasses change their positions on the scale of survival and development indices from one week to another. Thus the grasses best for the grasshopper in the first week of life may turn out to be unfavourable in the fourth or fifth week, and *vice versa*. The grasses can be divided into three general categories, *viz.*, development-promoting, 'borderline' grasses, and development-retarding grasses. Red fescue turned out to be the best of all grasses in giving the grasshopper a steadily high survival and rapid development. The three *Poa* spp. seem to form a group of second-best grasses. Brome, crested wheat-grass, the two northern wheat-grasses, intermediate wheat-grass and sedge belong to the borderline group of grasses, which are very important in the ecology of breeding places of *Camnula* because they are able to keep up populations of the grasshopper at a steady level till better food plants become available. No one grass, excepting, to some extent, fescue, is equally good for all developmental stages of the grasshopper. This is understandable because the nutritional requirements of the grasshopper cannot be the same for all its developmental stages, during which growth pattern varies. The position of the cereals (wheat and barley) is unpredictable on account of the inconsistent results obtained.

Course of growth on exclusive diets.—Six host plants were used as exclusive diets for the study of the course of growth of *Camnula* ; these include the sedge (*Carex eleocharis*) and five grasses, *viz.*, brome, red fescue, Kentucky bluegrass, intermediate wheat-grass and wheat. It was found that the development was quickest on Kentucky bluegrass (transformation time, 27 days) ; on the other host plants, the development was completed in the following order : fescue (about 30 days), sedge (about 31 days), brome (about 35 days) and intermediate wheat-grass and wheat in about 37 days each. Thus Kentucky bluegrass and fescue are not only good for survival but are also good for rapid development.

Rate of growth.—The grasshopper feeding on Kentucky bluegrass may complete its pre-adult life in about 27 days, 10 days sooner than the one completing its pre-adult life on wheat, but even if the wheat-fed grasshopper grows at a somewhat slower rate than the other, as an adult it will become the heavier of the two. The best diet for the insect, therefore, should not only enable it to complete the pre-adult life quickly, but should also make it grow in live weight at a much faster rate if the adults are to be heavy. It is necessary to examine the host plants from the point of view of rate of growth they give. The highest rate of growth for the grasshopper feeding on wheat is less than seven mgm. per day. A comparative idea of growth rates on the different host plants relative to the rate on wheat can be had if a line is drawn at this mark across the rate of growth curves (Text-figs. 9 to 14) on the six host plants. It would be found on the curve of Kentucky bluegrass (Text-fig. 11) that there are eight points above the line up to the pre-adult life out of the total number of 12 points. This means that the insect was growing 66 per cent of the time above the rate of seven mgm. per day ($8/12 \times 100$). All the host-plants examined compare as follows :—

	Per cent
Kentucky bluegrass	66
Red fescue	21
Sedge	17
Brome	12
Intermediate wheat-grass	11
Selkirk wheat	0

The above comparison shows that Kentucky bluegrass and fescue remain the best grasses for the high rate of growth they give and ensure a heavy teneral insect.

Utilization of food.—In the utilization of food also, Kentucky bluegrass and fescue turned out to be the best grasses. The ingestion on both these grasses bears similar ratio to the body weight. The utilization of Kentucky bluegrass ranged from 45 per cent at the first moult to about 36 per cent at the transformation time (Mean $\pm$ S. D., 36·5 $\pm$ 6.31), while on fescue the range was 47 to 41 per cent (Mean $\pm$ S. D., 41.9 $\pm$ 7·3). These figures are broadly of the same order as given by Chauvin (1946) and Davey (1954) for the desert locust, *Schistocerca gregaria*. The utilization on Kentucky bluegrass showed an almost horizontal disposition in the graph (Text-figs. 27 and 24) and this grass promoted the fastest growth of all the grasses tested during the nymphal life of the grasshopper (the adult life of the grasshopper on this grass cannot be discussed because of the all-female population).

Survival.—From the point of view of survival, fescue supersedes Kentucky bluegrass in Text-fig. 28. However, in the three experiments on survival and development (part IV), the three *Poa* spp. showed a good survival and are second to fescue, but Kentucky bluegrass showed a toxic effect on the later instars and adults and a heavy mortality was observed.

VII—SUMMARY

1. Sixty-two host plant species, including 27 grasses, one sedge and the rest forbs, the last belonging to 15 families of Dicotyledones, were tested for the preferential feeding of adult *Camnula pellucida* collected in the fall of 1955 from a road allowance near Cypress Lake in Southwestern Saskatchewan, Canada.

2. When these plant species are arranged in order of their preference values for the grasshopper, in the class interval of 10, it is found that 10 out of 11 classes are occupied by the grasses and the last class, having the range of preference values below 10, is occupied by one grass and 18 forbs. The one grass in the class of least preference is tall wheat-grass (*Agropyron elongatum*). An analysis of the results of all the plants tested suggests that the grasshopper is primarily a grass feeder.

3. From the preference values, it is found that the grasshopper has the greatest predilection for the following grasses (preference values given) : reed canary-grass (131), western couch-grass (105), cultivated Vantage barley (100), Selkirk wheat (80), sloughgrass (79), awned northern wheat-grass (71), big bluegrass (64), Kentucky bluegrass (64), wild barley (59), intermediate wheat-grass (57), redtop (55), green speargrass (53), eastern couch-grass (50), slender wheat-grass (50), perennial ryegrass (50) and Canada bluegrass (43). Among the forbs, the grasshopper shows the greatest preference for the Russian pigweed (84) and alfalfa (60.)

4. To judge the host plants for their values in the survival and development of the grasshopper, three experiments were performed over a period of two years, using 22 grasses and a sedge. Most of the grasses were tested twice so that the results of one experiment could be checked from those of another. Wheat and cultivated Vantage barley were used as checks in all the three experiments. The survival and development together were expressed quantitatively as the "survival and development indices" of the grasshopper fed exclusively on the different grasses. These indices were compared and analyzed at weekly intervals for five weeks for analyses of variance. The grasses were compared on the basis of "least significant difference" between the mean values from the maximum as well as minimum values. Except in the case of inconsistent results on wheat, barley and slender wheat-grass, there is a general agreement in the results of the experiments. The survival and development on the two cereals (wheat and barley) deteriorated in the second and third experiments, while the slender wheat-grass showed an improvement up to the first four weeks on its results of the first experiment but proved to be development-retarding for the fifth week. The weekly tests indicate that the position of the grasses keeps on changing weekly, so that the grasses best in the first week may prove to be development-retarding in the fourth or fifth week, and *vice versa*. This change in positions of the grasses might be due to changing nutritional needs of the grasshopper and the changing growth of the grasses. Since the grasses offered to the grasshopper were all in the leaf stage, it is thought that the changes in position of the grasses reflect the changing nutritional needs of the grasshopper during the course of its development, rather than changes in the grasses used as food.

5. The three experiments showed that the grasses most beneficial to the grasshopper are fescue, the three species of *Poa*, wheat, intermediate wheat-grass, and crested wheat-grass. In fact, no one grass, excepting, to some extent, fescue, is equally good for the grasshopper throughout its entire life. It is, therefore, thought that a mixed diet would be most beneficial to the grasshopper.

6. In order to see which grasses produce the heaviest grasshopper, which give the quickest development and rate of growth to the grasshopper, the growth of *Camnula* was studied on exclusive diets. Six grasses, *viz.*, sedge, brome, fescue, Kentucky bluegrass, intermediate wheat-grass and wheat, were selected as exclusive diets for studying the course of growth, rate of growth, and the survival of the grasshopper.

7. The course of growth of the grasshopper on all the six grasses shows a pattern of initial slow growth followed at first by a gradual and then by a quick increase in live weights till about the end of the average fourth instar, when the growth in live weight slackens. The live weights attained by the grasshopper at the transformation are : on sedge about the 31st day, 125 mgm.; on brome about the 25th day, 129 mgm.; on fescue about the 30th day, 159 mgm.; on Kentucky bluegrass about the 27th day, 208 mgm.; on intermediate wheat-grass and wheat about the 37th day (in each case), 137 and 154 mgm., respectively.

8. The progression growth factor varies on the different grasses a little, but, on the average, is close to two. On sedge, there is more than a doubling of live weights between second and third and fourth instars and the average of all the five stages is 1·89. On brome, the doubling occurs between first and second instars and between third and fourth instars and the change from second to third is close to the doubling ratio, the average progression factor for all the five stages being 1·86. On fescue, the live weights more than double themselves from first instar to the second and more or less so between each successive instar from second to the adult instar, the average progression factor being 1·9. On Kentucky bluegrass, there is more than a doubling of live weights between first and fourth instars and in the rest of the stages the ratio is close to the doubling ratio. On intermediate wheat-grass, the doubling occurs between the third and fourth to fifth instars and the average of all the five stages is 1·9. The progression growth factor of males and females on wheat is different ; in the females, the average live weight almost triples from second instar to the third. On the average, there is an actual doubling of weights in the females, while in the case of males the ratio is slightly less than double.

9. In the rate of growth, four epochs were noted in the growth patterns of the grasshopper on the six host plants examined. The first epoch consists of an initially slow and steady rate of growth, the second is characterized by a rapid acceleration in growth leading to a peak which is believed to be the peak of vegetative or somatic growth; the third epoch consists of a rapid deceleration and the fourth consists of a rise again leading to another peak in the adult life which is believed to be the peak of reproductive growth. The second peak is generally lower than the first. After the reproductive peak there is a fluctuating fall in the rate of growth leading to senile decay. The six grasses, judged from the rate of growth they give, were found to fall in three categories, *viz.*, grasses giving the fast rate of growth (sedge, fescue, and Kentucky bluegrass); grasses giving slow rate of growth (smooth brome and intermediate wheat-grass) ; and a grass giving very slow rate of growth (Selkirk wheat). The rates of growth were studied separately for male and female populations on wheat and it was found that the two differ from each other. It was found that the female weighs less than the male at the beginning of the second instar, but she gains weight at a much faster rate than the male and surpasses him in a couple of days, and thereafter keeps on weighing more than him. The average days of moult for the males and females, excepting the final moult, are close to each other, the male becoming adult about eight days earlier than the female.

10. In food ingestion, a tendency of taking a big meal early in life was noted in grasshoppers reared on the exclusive diets. The size of this meal was found to be inversely proportional to the nutritive quality of the food, being the largest on sedge and less on brome, lesser on fescue and least on Kentucky bluegrass. The amount

of faeces voided from this meal indicated an enormous utilization of sedge and brome but about the average utilization of fescue and Kentucky bluegrass. The young nymph on sedge utilized, on the average, about 80 per cent of dry weight of food ingested to about 55 per cent at transformaton time and attained the live weight of 124 mgm. at transformation time. The brome-fed young nymph utilized as low as 35 per cent in the beginning, improved the utilization sharply at the first moult to a high of 70 per cent and fell to a steady rate of about 55 per cent during the second stadium, gradually falling to about 45 per cent at transformation time. The average live weight attained at transformation time is 129 mgm. The brome-fed nymph, however, nearly doubled its transformation weight during the post-transformation period.

In the case of the fescue-fed nymph, the utilization declined from 66 in the first instar to 41 per cent towards the end and the live weight attained at transformation time was 159 mgm., while on Kentucky bluegrass the utilization was even more steady, declining from 55 to 36 per cent and the live weight attained at transformation time is estimated to be 169 mgm. Because of the population on this grass being all female, the live weight at transformation time was estimated from a comparison with weights on fescue. Kentucky bluegrass is suspected of being toxic to late instar nymphs and adults.

11. Survival for all the stages on fescue was noted to be the highest; the second-best survival was noted on wheat, the third and fourth positions are occupied by brome and Kentucky bluegrass, while sedge and intermediate wheat-grass occupy fifth and sixth positions, respectively. In the earlier experiments, the three species of *Poa* were second to fescue. However, after the first catastrophe, the survival on sedge is the most steady of all the plants tested in this experiment.

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EXPLANATION OF PLATE VII

FIG. 1.—*Camnula pellucida* adults in differential feeding experiments. In the cage two light bulbs, of 25 watts each, are seen (one in the ceiling and the other fixed in the back panel of the cage) giving uniform light and a temperature of 90°F (32·92°C). On the floor of the cage are seen 12 vials containing four grasses in triplicate scattered at random.

FIG. 2.—Four grasses on which survival and development of *Camnula pellucida* were recorded at weekly intervals.

From left to right : Russian wild rye (*Elymus junceus*), Canada wild rye (*E. canadensis*), Vantage barely (*Hordeum vulgare*) and Selkirk wheat (*Triticum vulgare*).

FIG. 3.—Four grasses on which survival and development of *Camnula pellucida* were recorded at weekly intervals.

From left to right : Downy chess (*Bromus tectorum*), smooth brome (*B. inermis*), slender wheat-grass (*Agropyron trachycaulum*), and tall wheat-grass (*A. elongatum*).

FIG. 4.—Four grasses on which survival and development of *Camnula pellucida* were recorded at weekly intervals.

From left to right : Big bluegrass (*Poa ampla*), Canada bluegrass (*P. compressa*), Kentucky bluegrass (*P. pratensis*) and green speargrass (*Stipa viridula*).

FIG. 5.—The cage (Sealright container) used for rearing *Camnula pellucida* in exclusive diet experiments.

A few nymphs can be seen resting on the plastic screen which gives them a foothold at the time of moulting and provides excellent ventilation, keeping down the humidity from the vegetation.

FIG. 6.—The grasshopper rearing cabinet.

On the top are seen, from left to right : (1) the relay for controlling the current to the humidifier (baby bottle warmer) which is also connected to the limited-range humidity-sensing element (to the left, a small obliquely suspended metal piece inside the cabinet); (2) The direct-reading A. C. current Aminco-Dunmore humidity and temperature indicator ; and beside it, (3) the small pilot light bulb. To the right of the cabinet is seen a gallon bottle containing distilled water feeding the humidifier by a siphon arrangement. Inside the cabinet are seen the rearing cages and an addtional dial-type relative humidity and temperature reading instrument. The panelled compartment of the cabinet houses an electric fan whose motor is outside.

FIG. 7.—The Thelco-Precision vacuum oven.

On top are seen : (1) The pressure gauge ; (2) the inlet (under dial) on the right which is connected to the water tap aspirator (for creating vacuum, not shown in the photograph) through a trap flask and a three way stop cock (on top of oven) ; and (3) the outlet on the left which is connected to a tube containing anhydrous calcium chloride (for letting in dry air whenever it is desired to break the vacuum). Inside, through the glass door, can be seen on the left samples of grasses wrapped in paper and on the right one of the vials containing faeces to be dried.

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