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A STUDY OF INSECT PESTS OF BRUSSELS SPROUTS
IN CANTERBURY; THEIR PHENOLOGY AND THE
RESULTANT CROP LOSSES

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ABSTRACT

The relationships between insect pests and damage in Brussels sprouts were studied for three seasons in Canterbury. Each season the major pest species, white butterfly (Artogeia rapae L.), diamondback moth (Plutella xylostella (Curt.)) and cabbage aphid (Brevicoryne brassicae L.), were monitored on unsprayed areas within the crop. White butterfly numbers followed the same pattern each season reaching a peak of between 2.9-3.4 larvae/plant in late March of each year. Diamondback moth was more variable between seasons but each year there was a shift in the population from the leaves into the developing sprouts as these became available from mid March onwards. Cabbage aphid was the least regular in both timing and intensity of attack. Peak numbers in 1979, 6.1 colonies/plant, were 15 times greater than in 1980, the year of the lowest attack.

Larvae of white butterfly and diamondback moth were confined in clip-cages for feeding tests on Brussels sprout leaves. For both species over 85% of the feeding occurred in the final instar.

Mean leaf area consumed at 20°C was 46.1 cm² for each white butterfly larva and 2.9 cm² for each diamondback moth larva. When tested over a range of temperatures it was found that pupae were lightest after development at the higher temperatures and that, for white butterfly, consumption dropped markedly at these temperatures.

The effects of artificial defoliation, simulating pest attack, on Brussels sprout plants were studied for two seasons in field plots. Greatest yield loss occurred following defoliation in the mid season. The plants were able to compensate for defoliation in the early stages of growth and to a limited extent in the mid season. In the late stages the plants were unable to compensate for defoliation but yield losses were low due to much of the yield already being formed. Removal of leaves from the mid zone of the plant caused the greatest yield loss.

Insecticides were used in two seasons to provide a range of pest numbers for damage assessment. In the first season the selective insecticides carbaryl and demeton-S-methyl were used to produce low numbers of lepidoptera and aphids respectively. The greatest marketable yield of sprouts was recorded from the carbaryl treatment and the weights of damaged sprouts/plot were positively correlated with diamondback moth larval numbers. In the second season the insecticide dichlorvos was used to control pests in early, mid or late periods of Brussels sprout growth. Resultant yields indicated that omission of sprays in the mid period resulted in the greatest loss of total sprout yield and that the greatest numbers of damaged sprouts followed mid and late spray-free periods.

A range of densities of larvae were confined in cages over individual plants at stages throughout the crop's growth. Yield was negatively linearly related to the estimated percentage defoliation caused by white

butterfly feeding. There was no relationship between diamondback moth and total yield but a positive linear relationship was found between larval numbers and numbers of damaged sprouts in the mid season.

When sprouts were examined on the stems, greatest numbers of damaged sprouts were found in the middle zone. Sprouts were not entered by the larvae until the sprouts were more than 7 mm diameter. Some reduction of damage occurred among the lower sprouts by shedding of the outer leaflets.

The relationship between white butterfly feeding and Brussels sprout growth was examined by using a simulation model. The model indicated that the cumulative effect of white butterfly feeding was greater than would be expected from a single defoliation and that 56% of yield loss could be prevented by use of a single insecticide spray 12 weeks after transplanting.

As a result of these investigations a rational spray programme is proposed utilizing pest thresholds and the size of the developing sprouts as indicators of the need for insecticides to be applied.

CHAPTER 1

INTRODUCTION

The last three decades have been aptly named "The Age of Pesticides" (Metcalf, 1980) because this period has seen a phenomenal increase in the manufacture and use of pesticides throughout the world. Thirty years ago the results of using insecticides were spectacular and gave credence to the strategy of total eradication of pest species (Knipling, 1979) but initial optimism gradually waned as it was realised that crop losses due to insects continued at the same time as the use of insecticides grew. Indeed, Pimentel et al. (1978) estimated that crop losses due to insects in the United States rose from 7% in the 1940's to 13% in 1978, despite a 100-fold increase in the use of pesticides over that period.

The failure of insecticides to provide long term solutions to pest problems has been attributed to the biological characteristics of the pest populations; insecticide resistance to chemicals has been known for 65 years but since the widespread use of synthetic pesticides the number of resistant pests has risen exponentially (Metcalf, 1980). Similarly, problems of pest resurgence and secondary pest outbreaks are modern phenomena and have become increasingly common with the use of broad spectrum insecticides (Coaker, 1976). Such biological

factors have caused many entomologists to call for a re-examination of insecticide dominated control strategies (e.g. van den Bosch, 1978) but unfortunately the most common response to apparent failure of insecticides has been to use more of the same, or to try another insecticide, thus embarking further on a "pesticide treadmill" while ignoring the underlying causes of the problem (Luckmann and Metcalfe, 1975); a strategy which in some areas has led to the collapse of whole farming systems (Adkisson, 1973). This throwaway mentality is being challenged today, not only by biological reality, but also by the escalation of costs in the pesticide industry. Current development costs for a new pesticide are estimated at \$20M with a doubling time of less than two years (Metcalfe, 1980). These high costs are reflected in the high prices of the new pesticides, but even traditional pesticide prices have risen dramatically over the past decade with the cumulative effects of inflation and oil price rises. The rise in pesticide prices has not been matched by a comparable increase in farm produce prices, catching the producer in a cost/price squeeze which acts as a further incentive to examine current pest control practices.

A critical evaluation of current pest control practices is particularly needed in horticultural crops where high values and stringent quality requirements have led growers to become "insurance" motivated (Norton, 1976a) with a consequent heavy use of insecticides. This

situation is exemplified by the production of Brussels sprouts in Canterbury. Insecticides are generally applied to the crop on a two weekly schedule with up to 14 applications within the season for some growers. Thus insecticides may account for 10-20% of the total costs of production (A. McErlich, pers. comm.) and are a major component of crop management in both financial and physical terms. Conversations with growers prior to this study indicated that they were 'risk averse' (Norton, 1976a) reacting to the threat of pest attack by insurance spraying. However, their perceptions of potential pest damage were ill-defined. This was not surprising as there have been few detailed studies of pest damage to brassicas and even fewer of damage to Brussels sprouts although, as Conway (1976) pointed out, these studies can reveal when pesticide use is unnecessary.

Much of the present overuse of pesticides occurs because of their application when the pests are not present (Stern, 1973). Thus a study of the occurrence and seasonality of pest attack as well as its variability between years is of vital importance. Fundamental to any such study is an understanding of the phenology of the crop which may allow the definition of critical periods of susceptibility to pest attack (Norton, 1976a). Once the occurrence of pests and the phenology of the crop are determined, key damage relationships can be studied which may be elucidated by the use of simple mathematical models (Norton, 1976b).

The aims of this study were, therefore:

- To monitor the seasonal distribution and abundance of the major brassica pest species on crops of Brussels sprouts.
- To quantify the amount of feeding by larval stages of white butterfly and diamondback moth on Brussels sprouts and determine how this is affected by changes in temperature.
- To examine the plant growth pattern, especially the development of sprouts and determine how this process is affected by defoliation simulating insect attack.
- To examine and analyse the relationship between pests and yield in field crops of Brussels sprouts.
- To investigate the relationships between insecticide, pests and yield using computer and graphical models.
- To develop a rational insecticide programme for the control of insect pests of Brussels sprouts based on an understanding of the characteristics of the pest population, the phenology of the plant and the characteristics of the pest/plant interaction.

CHAPTER 2

LITERATURE REVIEW

1. A History of Pest Control in Brassica Crops
in New Zealand

The brassicas now cultivated by man are thought to have originated in the Mediterranean region and from this area domesticated forms have spread throughout the world (Nieuwhof, 1969). All brassicas contain glucosinolates which are broken down by the enzyme myrosinase to produce bitter tasting goitrogenic substances (Thompson, 1976). The presence of glucosinolates acts as a "qualitative" barrier which deters general feeding insects (Feeny, 1975). Evolutionary adaptation, however, has allowed some insects to cross this barrier which is then believed to have no further effect on their growth and development (Blau et al., 1978). Such has been the success of these insects that today there are a large number of species contributing to a pest complex attacking cultivated brassicas. Of these pests, three cosmopolitan species dominate the pest complex on brassicas in New Zealand. These are the white butterfly, Artogeia rapae (L.), diamondback moth, Plutella xylostella (L.), and cabbage aphid, Brevicoryne brassicae (L.).

All three have become serious pests in New Zealand since the introduction of brassica food and fodder crops by European settlers in the latter half of the 19th century. White butterfly is a relatively more recent

introduction but both cabbage aphid and diamondback moth have been recorded since the early days of European settlement and could have existed earlier on native crucifers which are represented by seven genera, two of which are endemic (Allan, 1961). Today these plants are confined to mountain and coastal areas including off-shore islands (Moore and Irwin, 1978). Plutella xylostella has been found on wild crucifers on Rapa Island (Gates-Clarke, 1971) while the endemic species Plutella antiphona Meyrick has been found on Lepidium sp. on the Antipodes Islands (Dugdale, 1973). There is no record of cabbage aphid on native crucifers.

a. Cabbage aphid

Cabbage aphid is a pest found throughout temperate regions around the world (C.I.E., 1977). Its life history and population dynamics have been studied by Hughes (1963) in Australia, Hafaz (1961) in the Netherlands and McLaren (1975) in Central Otago, New Zealand. The first recorded attack on crops in New Zealand by cabbage aphid took place in 1884 causing 'near annihilation' of cabbages, cauliflowers, and turnips (Travers, 1884). In the early part of the century Hilgendorf (1924) estimated that aphids were causing losses of more than £1M per year and for control of the aphid in field crops he recommended the use of resistant varieties and management techniques such as early grazing. Insecticides were prohibitively

expensive for field application but in the home garden kerosine emulsion sprays could be used.

The first recommendations for widespread insecticide use against cabbage aphid in New Zealand were given by Lowe (1956) who recommended the use of lindane to control this pest. This was followed by recommendations for parathion (Anon., 1957) and demeton-S-methyl (Whatman, 1958; Lowe, 1960) and more recently by a wide range of contact and systemic organophosphates (Ferro, 1976) as well as carbamates and synthetic pyrethroids (Anon., 1979). Little attention appears to have been given in recent years to non-insecticidal forms of control except for the selection of aphid resistant rape (Palmer, 1960).

b. Diamondback moth

The diamondback moth is a cosmopolitan pest species capable of severe damage to brassica crops in a variety of climates from sub-arctic (Shaw, 1959) to tropical conditions (Yaseen, 1974). Its population dynamics have been extensively studied by Harcourt (1957, 1960, 1961b, 1963a, 1963b) and aspects of its biology have been studied in England (Hardy, 1938) and New Zealand (Robertson, 1939).

The diamondback moth has been recognised in New Zealand since the mid-19th century (Anon., 1887) and was reported as widespread by Meyrick (1886). Particularly

bad attacks occurred in 1885 and 1887 when the pest could be seen in "countless thousands". Control measures were elaborate and time-consuming - "In bad cases of attack ... it might answer to send a man and boy through the field, the one with a bough to sweep with, the other with soot or (in careful hands) with gas lime to throw under the plants on the fallen caterpillars" (Anon., 1887).

The life history of diamondback moth was described by Hilgendorf (1901) who estimated that in some conditions it could diminish brassica crops by 75%. Hilgendorf (1924) considered that there were no satisfactory methods of control and estimated national losses from the pest as £500 000 per annum. In small areas such as market gardens, arsenical sprays combined with kerosine emulsion were said to give some success. Muggeridge (1930) considered the cost of insecticides to be prohibitive for farm crops but recommended spraying with Paris Green for market gardens. He also proposed the introduction of parasites for biological control of the pest.

Robertson (1939) examined the biology of diamondback moth and its parasites and called for further consideration to be given to the introduction of parasites. In 1938 and 1939 two ichneumonid parasites, Angitia cerophaga Grav. and Diadromus collaris Grav. were introduced to Nelson and Hawkes Bay (Muggeridge and Given, 1941).

However, where insecticides were still necessary, Muggeridge and Given (1941) recommended the use of Paris

Green, arsenical and derris dust, particularly in market gardens. Cottier and Jacks (1945a, b) evaluated rotenone, arsenates and nicotine sulphate for control and later DDT was recommended (Taylor, 1948; Kennelly, 1961). More recent recommendations include those for organo-phosphorus, carbamate (Ferro, 1976) and synthetic pyrethroid insecticides (Anon., 1979).

c. White butterfly

White butterfly is also found as a pest of brassicas throughout the temperate regions of the world (C.I.E., 1952). Its biology and population dynamics have been studied by, among others, Richards (1940), Muggeridge (1942), Harcourt (1966), Dempster (1967) and Ashby (1972). It was first recorded in New Zealand by West (1930) in Hawkes Bay from where it rapidly spread throughout the North Island (Muggeridge, 1932) and later to the South Island (Muggeridge, 1942). Following the accidental introduction of the butterfly, massive populations were described and in some cases were reported to have caused complete destruction of crops (Muggeridge, 1935a). However, as Muggeridge (1932) wrote much of the alleged white butterfly damage was in fact caused by diamondback moth.

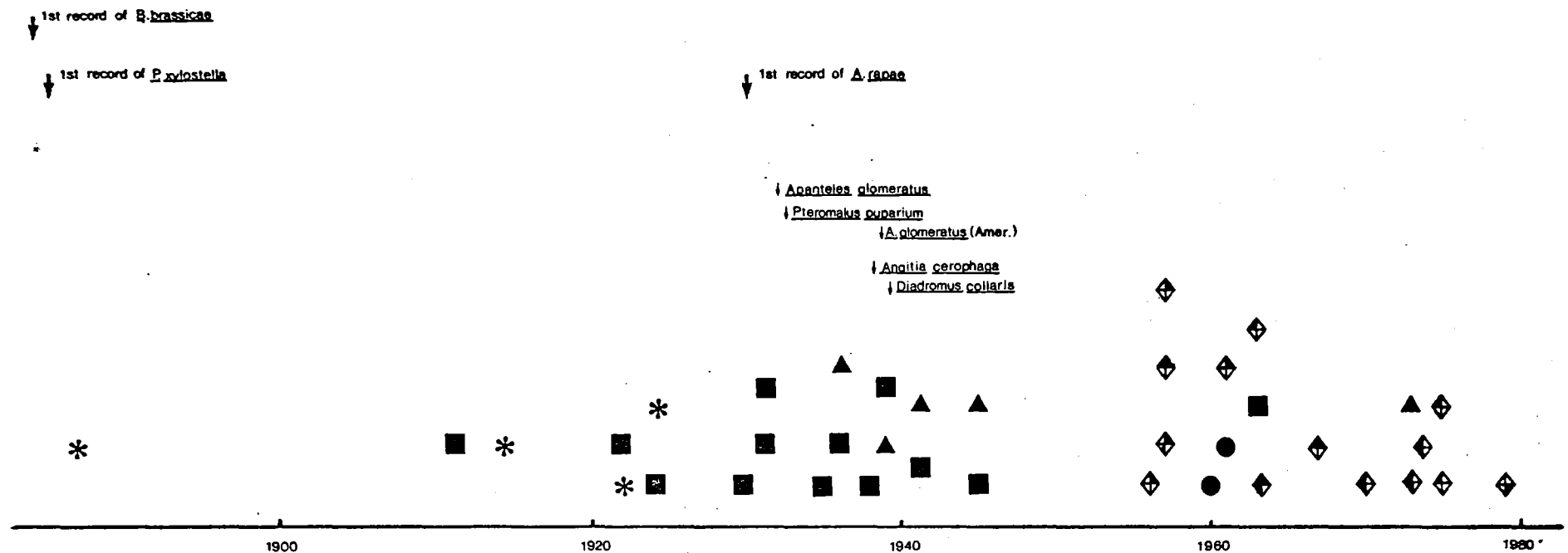
Shortly after white butterfly introduction, Muggeridge (1931) listed insecticide control recommendations from overseas and also reported on the introduction of the parasites Apanteles glomeratus L. and Pteromalus puparum L.

to control it. The latter rapidly became established in the North Island but it was not until the introduction of an American strain of A. glomeratus to Nelson in 1938 that this parasite became widely established. The successful establishment of the two parasites led to a decline in the white butterfly population but sprays or dusts of Paris Green or derris were still recommended for heavy attacks on horticultural crops (Muggeridge and Given, 1942). Chamberlain (1957) recommended lindane for control while Todd (1960) urged caution before using insecticides, recognising the potential of virus epizootics to reduce the population in the autumn. More recently, as with diamondback moth, organophosphorus carbamate and synthetic pyrethroid insecticides have been recommended (Anon., 1979).

The history of pest control for each of these pests has followed the same trends. In the late 19th and early 20th century chemicals for pest control were not particularly effective and were prohibitively expensive in relation to crop value. Pest control measures were therefore, generally managerial. In the 1930's both biological control and chemical control measures were developed while the last 30 years have seen the introduction and widespread use of synthetic pesticides (Fig. 2.1).

With the introduction of efficient pesticides came the expectation of high product quality standards which

Fig. 1.1. A history of brassica pest control in New Zealand. First recordings of pest species (↓), introduction of parasites (↓) and control recommendations: *, cultural; ■, inorganic pesticides; ▲, biological pesticides; ◆, synthetic pesticides (◆, organochlorines; ◆, organophosphate; ◆, carbamate; ◆, synthetic pyrethroid); ●, resistant plants.



Ivey, 1888; McConnell, 1911; Berridge, 1914; Taylor, 1922; Hilgendorf, 1924; Muggeridge, 1930; Muggeridge, 1931; Sinclair, 1931; Cottier, 1935; Cottier, 1936; Anon., 1938; Cottier, 1939; Muggeridge and Given, 1941; Cottier and Jacks, 1945; Lowe, 1956; Barrer, 1957; Anon., 1957; Chamberlain, 1957; Whatman, 1958; Palmer, 1960; Anon., 1961; Kennelly, 1961; Anon., 1963; Gunning, 1963; French and Douglas, 1967; Helson, 1970; Helson, 1973; Helson, 1974; Ridler, 1975; Trought, 1975; Ferguson, 1978; Ag. Chem. Board, 1979.

resulted in schedule spraying without serious consideration of the necessity for each spray (Newsom, 1973). The dangers of this excessive use of chemical pesticides have often been stated (e.g. van den Bosch, 1978). Resistance of diamondback moth to organophosphate insecticides has been recorded in Taiwan (Sun et al., 1978) and in Malaysia (Sudderuddin, 1978). Pesticide pollution has become such a problem that horticultural brassicas which have been sprayed with DDT may not be fed to stock (Agricultural Chemicals Board, 1979). With the rapidly increasing costs of pesticides, blanket spray schedules which keep a virtually constant cover of insecticide are becoming even more questionable on economic grounds (Haskell, 1977). These trends, therefore, make it imperative to examine the nature of insect damage to brassicas to ascertain the potential for reducing the insecticide load of these crops. While many researchers have studied brassica pests, there are relatively few studies of the relationship between insect attack, crop growth, and yield despite a considerable research effort in this area in other crops.

The remainder of this review, therefore, examines the importance of insects in crop management and the relationship between pest attack and yield in both theory and practice. Methods of assessing crop losses are also reviewed. Reference, wherever possible, is made to brassicas, their pests and production but when this is not possible relevant examples are taken from other crops.

2. Components of Pest Management

The idea that pest control should not be viewed in isolation but as a part of a wider system of crop management is not new. Stern et al. (1959) proposed the concept of integrated control and more recently Geier and Clark (1961) proposed the term "pest management" implying the integration of pest control into the management of the crop. Pest management involves the interaction of pest, crop and grower, and the "pest problem" can best be seen as an interaction between grower management decision, pest attack and plant response (Fig. 2.2).

a. Grower management decisions

A grower's management decisions will depend on the control options available to him and the constraints on his actions set by economic and social factors. A grower may seek to minimise losses either by taking measures to limit the dimensions of pest attack (e.g. pesticides, cultural controls) or by enhancing plant response (e.g. irrigation, fertilizer).

Pest control options will fall broadly into two categories, prophylactic and threshold measures (Norton, 1975). Prophylactic measures, such as selection of resistant varieties or a fixed spray schedule, are determined before the pest attack takes place while threshold measures will be initiated only when predetermined pest population levels are exceeded in the crop.

PEST CONTROL DECISION MAKING

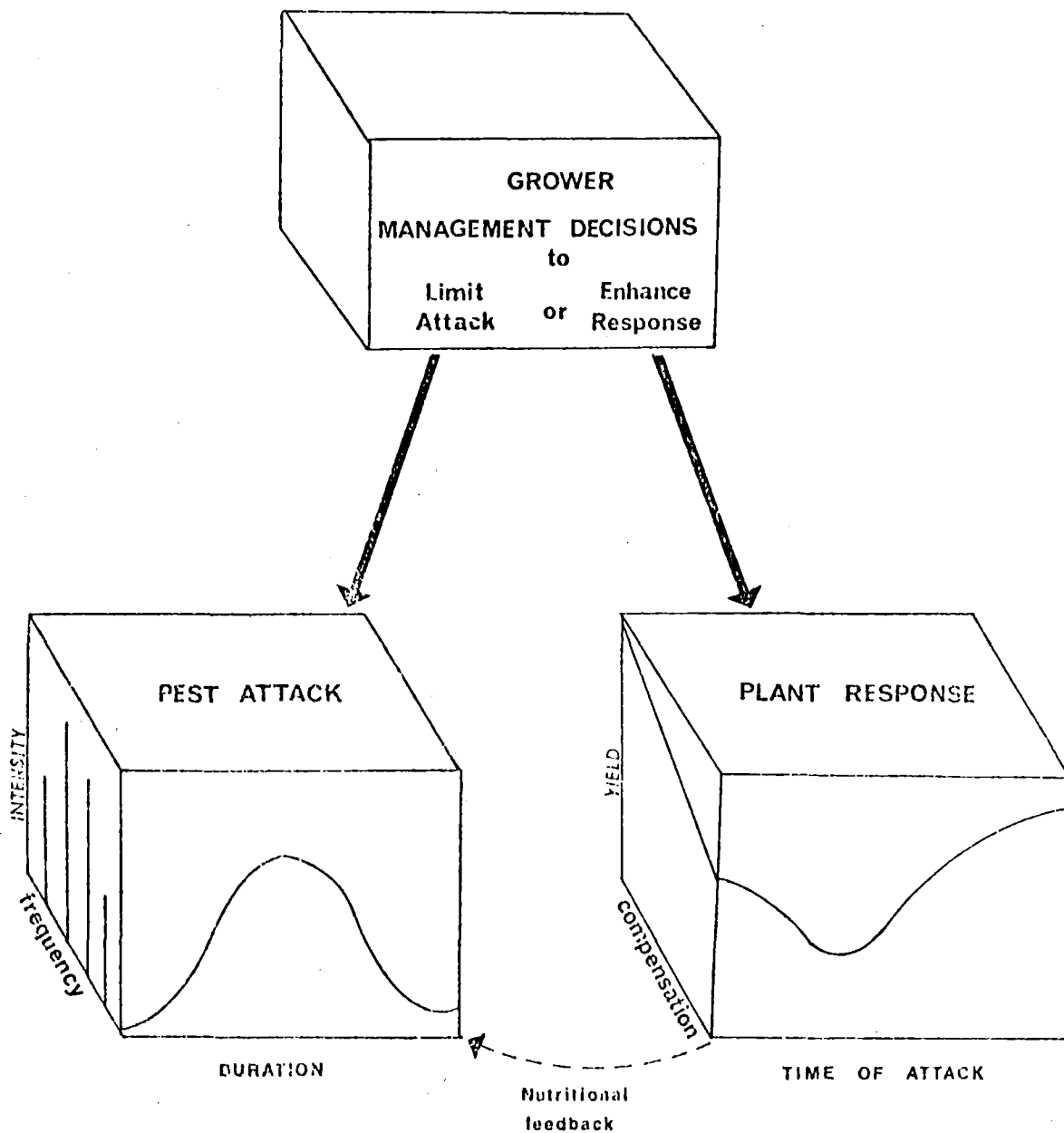


Fig. 2.2. The "pest problem" - an interaction between grower management decisions, pest attack and plant response.

Using the economist's tool of marginal analysis, Headley (1972) defined the optimal level of pest control as that set by the economic threshold where the marginal revenue gained from an increment of control is equal to the costs of producing it. However, as Headley (1975) later pointed out, to carry out this analysis requires perfect knowledge of the damage and control functions and is a static analysis where the real problems are dynamic. It may also avoid consideration of the social costs of pest control.

In fact most growers operate under conditions of uncertainty with only a vague awareness of the relationship between the true costs and benefits of pest control. In this situation, pest control actions will be guided more by the farmer's perception of the pest problem than its actual dimensions (Mumford, 1977). His actions will also be influenced by his attitude to risk. Often young farmers with high outstanding debts will be "risk averse", seeking to guarantee a fixed level of income rather than being "profit maximisers" seeking the maximum profit regardless of risk (Norton, 1976a). The farmer's pest management decisions will be determined, therefore, by his perception of the pest problem and by his attitude to risk. Norton (1976b) has suggested that farmers adopt new measures on the basis of trial and error accepting those which have proved satisfactory while rejecting those which are unsatisfactory.

However, a grower's perceptions of a problem are influenced not only by his own past experiences, but also by the advice he receives from advisory officers, chemical company representatives, university extension services and others. To improve decision making for crop protection Norton (1976b) considered that research and advisory programmes should be aimed at widening the range of crop protection measures available, increasing the farmer's perception of relevant information and improving the rules by which farmers operate.

b. The pest attack

The importance of a pest in crop management is determined by its potential to damage the crop which in turn depends on three factors - the intensity, the duration and the frequency of pest attack.

Intensity

The intensity of attack is determined not only by the numbers of insects present but also by the amount and rate of food consumption. The amount of feeding varies considerably between pests. Given (1944) calculated that a white butterfly larva consumed 12.8 times more leaf area than a diamondback moth larva; the rate of feeding however, was only 9.3 times greater due to the shorter development time of the latter. Food quality also affects consumption (Slansky and Feeny, 1977) as does parasitism of the insect (Rahman, 1970). The total injury to a crop

is usually linearly related to the numbers of pests present (Conway, 1976) and often single measurements of their numbers form the basis for control thresholds (Sylvén, 1968) or economic thresholds (Stern et al., 1959). Grading according to intensity of infestation may also be used as a basis for initiation of control actions (Chalfant, 1979).

Duration

Peak intensity may be of less importance than the duration of attack in causing yield loss. Pests such as diamondback moth are generally present throughout the year in the tropics (Yaseen, 1974) while cabbage aphid is more likely to be restricted in its attack by late spring and autumn flights (Lowe, 1966).

For pests of short duration and only one generation in the crop little regard need be given to factors such as density dependence between generations of the population. However, for pests that pass through several generations within the crop the density dependent relationship between generations and possible pest resurgence should be taken into account when determining control strategies (Conway et al., 1975). The possibilities of resurgence are greatest for those pests with short generation times such as cabbage aphid, 9.3 days at 20°C (Hughes, 1963), and less for pests like white butterfly with only three generations a year in Canterbury. Climate will affect the rate of development and hence the opportunity for

resurgence. In Britain white butterfly passes through only one full generation with a partial second each year (Dempster, 1967) while in the southern USA it exceeds six generations (Parker, 1970). Diamondback moth, with six generations per year in New Zealand (Valentine, 1975) completes 24 in Trinidad (Yaseen, 1974). Both duration and intensity are combined in the concept of pest-days. Hughes (1963) measured aphid attack in terms of aphid-days while Norton and Evans (1974) related froghopper-days to yield loss in sugar cane.

Frequency

In determining the value of prophylactic treatments, the frequency of pest attack should be established. In the south of England Mumford's (1978) survey indicated that black bean aphid was present in sugar beet three years in ten, while green peach aphid was present every year and hence posed a greater pest problem.

Brassica pests also show differences in their frequency of attack. White butterfly has shown a certain regularity of attack between years (Dempster, 1967) while attacks by diamondback moth are more variable especially in those areas such as Canada and Northern Europe which are occasionally subjected to large immigration flights (Shaw, 1959; Harcourt, 1963).

The frequency of pest attack was incorporated into a "crop vulnerability index" by Bullen (1966) to identify areas at most risk from locust attack thus enabling

improvement in the allocation of resources for its control.

c. The plant response to pest attack.

The effects of pest attack on yield will be determined not only by the number and feeding of the pests but also by the plant response to their attack (Conway, 1976). Whilst yield loss generally follows insect attack, there have been many reports of no yield loss and some of increased yields following pest feeding (Bardner and Fletcher, 1974). This ability of the plant to compensate or over-compensate may be better understood by examining the morphology and physiology of the plant in question.

First, desired yield may be increased by the pruning effects of pests, i.e. while overall biological yield may decline, the size of the harvested part of the plant may increase (Kincade et al., 1970). Insect feeding at the growing point of graminaceous plants may induce tillering which at some plant densities, may lead to an increase in yield (Taylor, 1972).

Secondly the plant may directly respond to insect feeding by producing more leaves (Taylor and Bardner, 1968b), a greater surface area of the remaining or undamaged leaves (Aung and Kelly, 1966) or longer retention of old leaves (Taylor and Bardner, 1968b). Evans (1972) described the pattern of leaf growth and indicated that removal of 50% of a young leaf will not necessarily produce a mature

leaf of the same reduced proportions relative to undamaged leaves.

Thirdly, it has been shown that plants can increase the rate of photosynthesis in the remaining leaf tissue when leaf area is removed either by insects or artificially (French and Humphries, 1977). This appears to be related to assimilate sink-source relationships reviewed by Stoy (1969) who indicated that there is often an overcapacity in potential supply of assimilates.

The frequent occurrence of compensation in pest-yield studies led Tammes (1961) to propose a sigmoid curve as the generalised pest-yield relationship (see Fig. 2.3). The upper portion represents a compensation plateau where no yield loss occurs despite pest damage, and increasing pest numbers past this plateau will cause yield loss to the point where competition between pests is such that further loss does not occur.

Southwood and Norton (1973) reviewed this proposal and concluded that usually only a portion of the curve is visible in experimental results. They suggested that where attack occurs on foliage or roots compensation is likely to occur, while for direct attack on the product, the loss relationship is likely to be linear.

The plant response to pest attack varies between species and even varieties. Similar plants such as turnip and radish have shown widely different compensatory abilities (Taylor and Bardner, 1968b). Tolerant varieties may be able to compensate for pest attack while

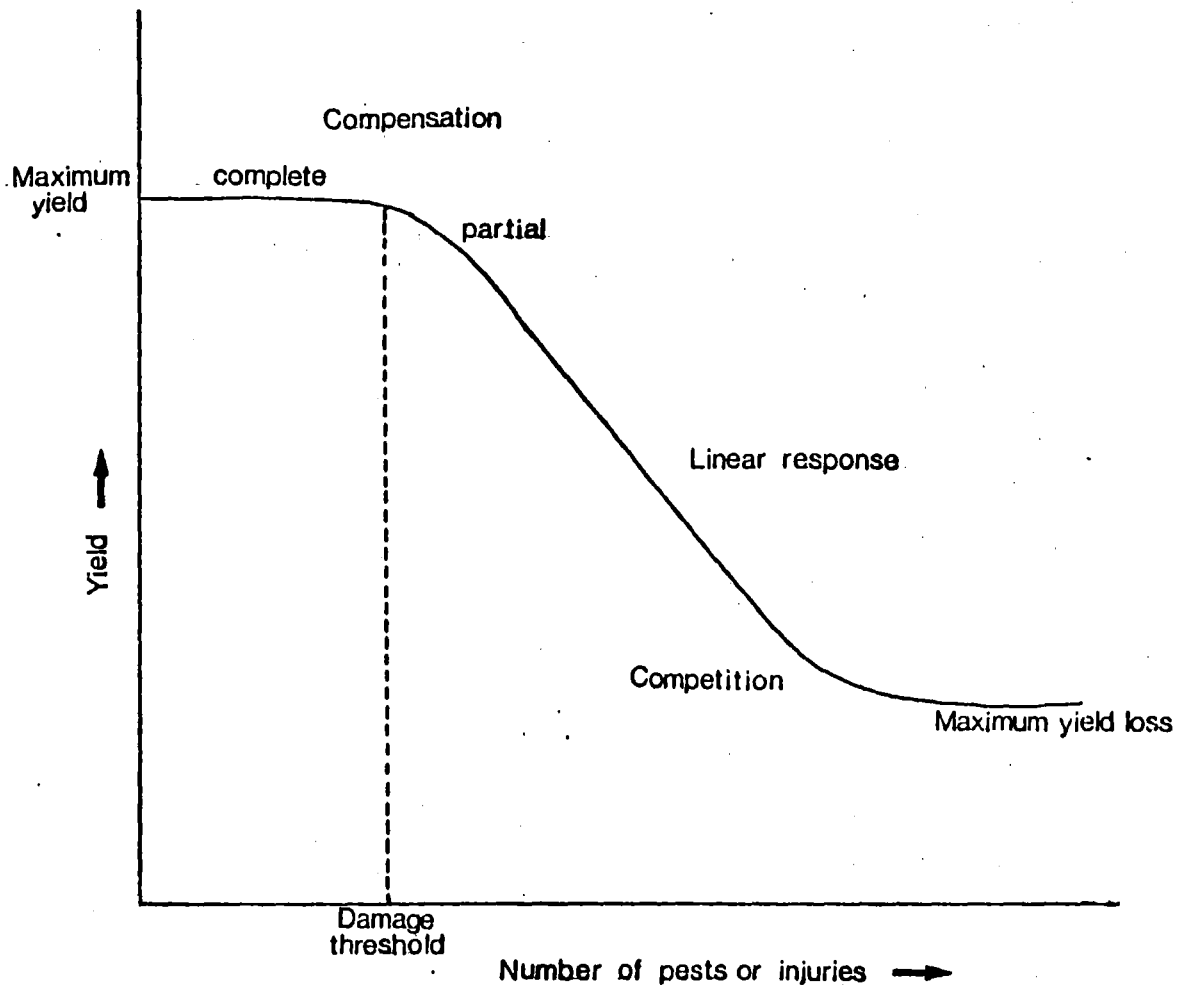


Fig. 2.3. The generalised pest/yield relationship. Adapted from Tammes (1961).

nutritional and other feedback processes may make the plants resistant to attack by affecting the growth of the pest population.

The effect of insect attack on the plant may vary widely according to the time of that attack. Coaker (1970), for instance, reported that root fly attack within a few weeks of transplanting cabbages had the greatest effect on subsequent growth whilst Stone and Pedigo (1972) showed that soya bean yields were most affected by defoliation at podfill rather than at other times. Thus a knowledge of those periods of greatest susceptibility to pest attack is critical in the evolution of pest control strategies.

3. Causes of Yield Loss in Brassica Production

Smith (1967) defined two types of pest damage. Direct damage where the product itself is attacked by the pest and indirect damage where the non-yielding plant parts, such as leaves and roots, may be attacked and the effect on yield is due to a reduced flow of assimilates to the product. As forms of plant damage have been reviewed by a number of authors (Strickland and Bardner, 1967; Smith, 1967; Bardner and Fletcher, 1974) only those with direct relevance to brassicas at stages throughout their growth will be discussed here.

a. Loss of establishment

Seedling establishment is particularly important in direct sown crops. A wide range of pests including springtails (Lowe, 1956), wheat bug (Trought, 1975), and stem weevil (Upritchard and Park, 1976) may all kill seedlings at, or before, emergence. The effects of seedling pests may be markedly affected by weather. In Europe, during hot periods in spring, flea beetles may cause severe losses of brassica seedlings (Jones and Jones, 1974). The number of plants killed may be less important than their distribution: Jones et al. (1955) showed that greater yield loss occurred when the attacked plants were clumped rather than spread evenly throughout the crop. Loss of seedlings has become particularly important in horticultural crops since the widespread introduction of precision drilling.

A patchy stand will lead not only to a loss in yield but variations in development and harvesting problems caused by lack of uniformity (Wheatley, 1971).

b. Reduction in growth rate

Once the plant is successfully established further feeding by insects may reduce the growth rate of the plant thus lowering yields. Feeding by white butterfly larvae or diamondback moth larvae will reduce the leaf area of brassicas (Harcourt et al., 1955) and thus the potential of the plant to photosynthesize will be diminished (Watson,

1956). Assimilates may be removed directly by plant bugs or aphids (Nieuwhof, 1969) where feeding by large colonies may result in a major relocation of assimilates within the plant (Way and Cammell, 1970). In brassicas, aphids may also transmit viruses such as cauliflower mosaic virus and cabbage rain spot virus while flea beetles may transmit the less important turnip yellow mosaic virus (Nieuwhof, 1969).

A number of pests including grass grub (Cottier, 1956), cabbage root fly (Coaker, 1965) and nematodes (Rhoades, 1971) will feed on the roots of brassicas. This feeding will generally lower the plant growth rate although in cases such as turnips where the root is the product, this constitutes direct damage.

c. Direct damage to the product

Direct damage to the product may be caused by a number of pests. In Britain cabbage root fly larvae are frequently found within the sprouts of Brussels sprouts (Coaker, 1967) and similar damage is caused by diamondback moth in New Zealand. In severe attacks white butterfly and cabbage moth larvae will eat into the hearts of cabbages while in seed crops the cabbage seed-pod weevil and the seed-pod midge may cause serious losses of seed (Jones and Jones, 1974).

d. Contamination

Contamination by insects or their products may

make the crop unsaleable or at least reduce quality. Insect attacks close to harvest can cause major problems. Cabbage looper larvae in broccoli heads are undesirable as is frass in the heart of a cabbage. Aphid attacks on Brussels sprouts may make the sprouts unpalatable due to the production of honeydew and the subsequent growth of fungi on the sprouts (Nieuwhof, 1969).

4. Methods of Crop Loss Assessment

Methods of crop loss assessment have been reviewed by a number of authors (Smith, 1967; Strickland and Bardner, 1967; Ruesink, 1975; Kogan, 1976). Loss assessment studies may take three forms. First those that seek to show the potential for a pest to cause yield loss (Goldson and Penman, 1979). Secondly those that seek to establish a quantitative relationship between pest numbers and yield (Wilson et al., 1969) and thirdly those that seek to investigate the effects of pests on the underlying determinants of yield (Cock, 1978). In all cases yield comparisons between attacked and un-attacked plants are necessary and these may be obtained in a number of ways.

a. Surveys

Farm surveys have been used to estimate crop losses caused by vertebrate pests (Williams, 1974), diseases (King, 1977) and insects (Gage and Mukerji, 1978). Pest populations assessed close to harvest may accurately

reflect yield loss but more often pest incidence is viewed as a rough indicator of the damage or pest numbers may be used together with an experimentally established yield-loss relationship (Church, 1971). Pinstруп-Andersen et al. (1976) used a combination of subjective and experimental methods to establish levels of crop losses in beans. However, subjective estimates of damage may be highly variable as Mumford (1977) showed for farmer estimates of yield losses in sugar beet. Gage and Mukerji (1978) related grasshopper survey data to yield of cereals and estimated regional yield losses through a multiple regression model and Strickland (1957) used survey data to estimate national yield losses from aphids on Brussels sprouts but found large errors in converting from ranked results to quantitative terms. It appears, therefore, that surveys are often appropriate for estimation of crop losses on a regional basis, but models and estimates based on survey data may be imprecise due to the many factors causing yield variation at the farm level.

- b. Direct comparisons of attacked and unattacked plants within a naturally infested crop

This procedure involves yield comparisons from marked plants (Judenko, 1973) or areas of a crop that have received different levels of attack within a naturally infested crop. Plants may be marked at the

time of pest attack according to the presence of pests (Judenko, 1969), or severity of attack (Lawson, 1979). Alternatively, plants or plant parts may be marked at the beginning of the season and regularly checked for selective oviposition by the pest. White butterfly females, for example, will tend to oviposit on the largest brassicas in the crop (Latheef and Irwin, 1979) making it difficult to distinguish between yield loss caused by the pest and yield variations caused by plant size.

Harcourt (1970) monitored plants within an unsprayed crop to build a life table for cabbage survival. He suggested that the budgetary nature of the life table format allowed determination of the monetary value of each factor causing loss to be obtained. However, the method as applied, does not seem to allow for plant compensation and includes the highly subjective decision as to what constitutes death for the plant. It may be for these reasons that life tables have not been widely adopted in damage assessment studies.

c. Artificial manipulation of pest numbers

Naturally infested crops may not give the range of levels of attack necessary to determine the relationships between pests and yield. For this reason many researchers have artificially manipulated the numbers of pests on plants.

Sedentary stages of a pest may be merely placed on a plant. However, the distribution of the pests both over plants and in time needs careful consideration (Lynch et al., 1980). More mobile stages may be confined by barriers such as electric fences (Taylor and Bardner, 1968a) or physical barriers (Muller and Engoff, 1980). Barriers can also be used for pest exclusion (Williams, 1974) or for the exclusion of predators thus allowing the development of higher than normal levels of pest population (Coaker, 1965). For highly mobile insects it is often necessary to use cages. These may cover part of a crop (Ignoffo et al., 1978), the plant (Tamaki and Hagel, 1978), or a plant part (Gutierrez et al., 1977). Bracken and Butcher (1977) used cages only for the period of pest attack and maintained the plants insect-free with insecticides throughout the remainder of the crop's growth.

Insecticides may be used to exclude pests in a number of ways. Goldson and Penman (1979) maintained check plots insect-free by frequent applications of insecticides. Wilson et al. (1969) used a range of concentrations of insecticides and Getzin (1978) used a different number of times of spraying to achieve pest gradients. Dina (1976) used sprayed and sprayfree periods to examine the susceptibility of cowpeas to insect pests at stages throughout their growth.

The interpretation of the results from trials with artificially manipulated numbers of pests requires care.

High pest numbers may result in competition between pests that does not occur in the field (Pedigo et al., 1977), the distribution or timing of pest attack may be abnormal (Lynch et al., 1980) or cages may limit light intensity or change leaf microclimate (Strickland and Bardner, 1967). The use of insecticides may enhance yield (Toms, 1967) or cause loss due to phytotoxicity (Hussey, 1970).

d. Artificial simulation of damage

Many insects damage plants by feeding on their leaves, roots or other plant parts. It therefore seems logical to attempt to mimic the action of pests by artificial removal of portions of the plant. Artificial defoliation studies simulating pest attack have been made on plants as diverse as cotton (Goodman, 1956), corn (Hanaway, 1969), rice (Taylor, 1970); sugar beet (Dunning and Winder, 1972), soybean (Thomas et al., 1974; Poston and Pedigo, 1976), radish (Jackson, 1980) and potatoes (Cranshaw and Radcliffe, 1980). Cotton bolls have also been removed to simulate pest attack (Goodman, 1956) as have roots from grasses (Davidson and Roberts, 1968) and the buds of apple trees (Howell, 1978).

While artificial methods can produce accurately defined levels of injury, Smith (1967) pointed out that simulated damage is not always equivalent to insect damage. He questioned whether artificial damage is intrinsically the same as insect feeding and how the

position and rate of insect feeding will affect the results. The former question has been investigated by Poston et al. (1976) who examined the net carbon exchange rates of artificially and insect defoliated soybean leaves and found that both methods generally caused a reduction in the rate of photosynthesis in the remaining leaf area. They concluded that insect defoliation could be adequately simulated by a number of methods with the exception of cutting across the leaf which increased the rate of photosynthesis in the remaining tissue.

Hall and Ferree (1976) compared types of artificial defoliation of apple leaves and found that photosynthesis was suppressed further when lateral veins were cut or when many small holes were made rather than a few larger ones. Similarly, in western wheat grass Detling et al., (1979) found that the rate of photosynthesis was reduced by artificial defoliation. However, the effects of defoliation on a single leaf may not accurately reflect the plant response because, while injury of individual leaves may reduce the rate of photosynthesis in the remaining leaf tissue, yield compensation by plants to pest attack is a common phenomenon (Bardner and Fletcher, 1974). The rate of photosynthesis will be markedly affected by the demands of metabolic sinks, hence, removal of part of the leaves, the metabolite source, will result in an increase in the rate of photosynthesis of the remaining leaves (Stoy, 1969). Thus the rate of photosynthesis may be increased in adjacent leaves

or those produced following defoliation.

Taylor and Bardner (1968a) found that the position of defoliation of turnips had a considerable effect on the plant response while Gupta (1968) recorded an increase in sugar beet yield following removal of the crown leaves. The effect of rate of leaf removal on yield was examined by Jackson (1980) who found that yield of radish was directly proportional to leaf area duration and that this relationship was unaltered by either single or periodic defoliation. Comparisons of artificially and insect defoliated plants are rare. Mukerji and Pickford (1976) found that defoliation of spring wheat by grasshoppers caused seven times more yield loss than that expected from artificial defoliation studies and grasshopper feeding trials. They suggested that the difference was due to wastage of foliage by the grasshopper feeding action. However, Dyer and Bokhari (1976) suggest that regrowth may be affected by some inhibitory salivary factor and Capinera and Roltsch (1980) found that severe grasshopper feeding resulted in a significantly lower rate of wheat seedling growth when compared with manual clipping. However, for turnips, Jackson (in prep.) has shown similar effects on bulb yield from both artificial and insect defoliations. It seems, therefore, that artificial methods can reasonably approximate pest attacks and as such have been widely used, but it is clear that they should be used with caution and where possible compared with other methods.

5. Economic Thresholds as a Basis for Pest Control

The development of cheap, effective insecticides and consumer demands for high quality produce have led to the adoption of schedule applications of pesticide without regard to pest numbers or potential damage (Wheatley, 1970). As a result the amount of pesticide used far exceeds that actually necessary for pest control (Metcalf, 1980). This overuse of pesticides is not only wasteful but may also have deleterious effects on the environment. Thus the attraction of applying insecticides only when needed is obvious and led to the development of the economic threshold concept (Stern et al., 1959) which defines levels of pest attack for the initiation of pest control measures.

Central to the concept is the recognition of an 'economic injury level' defined as the level of pest attack that will cause economic damage thus justifying the cost of artificial control measures (Stern et al., 1959). This justification was later interpreted as being the loss of revenue equal to the cost of the control measure (N.A.S., 1969).

Chiang (1973) later pointed out that where the cost of control equals the value of yield lost there will be no gain to the grower. Chiang, therefore, proposed that the economic threshold is 'the population level which is capable of causing sufficient damage so that the value of increased crop yield resulting from

the control action will be twice the cost of control'. However the alleged greater benefits are illusory as pesticides in themselves almost never increase yields (Headley, 1975) and their use is aimed at preventing loss from the potential yield (Smith, 1967), thus Chiang's proposed alteration of the concept seems unwarranted.

The economic threshold concept has been examined by Headley (1972) and Carlson (1971) who proposed that the economic threshold is the point at which incremental control costs equal the incremental losses in the value of production. Headley's economic threshold population is different in concept from that of Stern et al. (1959). It is seen as the population level below which it is unprofitable to control the pest assuming that control costs increase at an accelerating rate as the population gets smaller. The pest population then is controlled down to the economic threshold. This is conceptually different from the definition given by Stern et al. (1959) where the economic threshold population is not the optimal but the maximum allowable before control measures are initiated.

There are therefore, two distinct approaches to the development of economic thresholds. The first, essentially empirical, is followed by adherents such as Stern et al. (1959), Stone and Pedigo (1972) and Kogan (1976) who view each pesticide application as a marginal control input to be balanced against the benefits of

control. The second, more holistic approach, followed by Carlson (1971), Headley (1972) and Gutierrez et al. (1979) is where the overall pesticide level is balanced against potential savings. While even Stern (1973) is critical of the simplicity of the former approach the successful application of the latter requires a sophistication of information that we seldom have (Geier and Springett, 1974).

It may be more than just difficulty of calculation that has hindered the adoption of economic threshold strategies for, even in areas where economic thresholds have been established such as on cotton crops in Arizona, farmer acceptance has been low (Adkisson, 1973). Norton (1976a) considered that lack of acceptance is often due to the failure to recognize the objectives of the farmer. The objective of the economic threshold is one of finding the optimal solution while the farmer will often normally be content with a satisfactory solution to his pest problems. This was illustrated in a survey of sugar beet growers by Mumford (1981) who found that most farmers in the survey were insurers, more interested in guarding against occasional severe losses than in maximizing profits.

Economic threshold studies, though, have pinpointed times in crop growth where there is little yield loss from pests and also those times most sensitive to pest attack and thus, where thresholds have been adopted, there has often

been a reduction in pesticide use (Newsom, 1974). The majority of thresholds that have been incorporated into pest management programmes have been obtained empirically and often refined with further experimentation (Stern, 1973). These have been widely implemented in field crops such as cotton (Stern, 1973), soybeans (Kogan, 1976) and sugar beet (Hull, 1968) but greater difficulties exist with their application to perennial crops (Kain, 1975; Wearing, 1975).

Difficulties in establishing accurate thresholds arise as levels will be altered by changes in prices of both the insecticide and the product (Headley, 1975), management practices (Kain, 1975) and the attitudes and capabilities of the farmer (Farrington, 1977). While these factors may cause adjustments in threshold levels general principles are probably more broadly applicable than implied by Reynolds et al. (1975) who hold the view that 'each field has to be viewed as a separate unit with its own unique limits, tolerances and requirements'. It appears, to quote Stern (1973), that "obviously the economic threshold concept is not so simple as originally proposed" and that up to the present the concept has gained more theoretical acceptance than practical interpretation.

6. Modelling as an Aid to Pest Control Decision Making

The decision of whether or not to use an insect control measure or which control measure to use is a complex problem. Increasing dependence on chemicals with higher costs and higher quality standards for produce make the penalty for making a wrong decision much greater, yet correct decisions may be hard to identify. This was shown dramatically by Gutierrez et al. (1979) who suggested that Lygus control in cotton for the last 20 years in California, where it has been regarded as the key pest and where control measures have caused serious secondary pest outbreaks, was probably unnecessary.

In dealing with complex problems we create algorithms, which for simple decisions may be purely mental, but with increasing complexity of problems the algorithms are likely to take the form of more sophisticated, often mathematical, models as imitations or representations of the real world (Ruesink, 1975). There is a vast array of model types to choose from, varying from simple qualitative models (Norton, 1976a), which can help to provide a conceptual framework within which to examine problems, to complex mathematical models seeking to represent whole ecosystems (MacNaughton, 1979). Models, therefore, can be simple or extremely complex and tend to be found at both extremes of this range with few in intermediate positions (Gutierrez et al., 1979).

Some of the most simple models are those utilising linear or curvilinear regressions (Waters and Ewing, 1976). Many of the early economic threshold models fall into this category (Ogunlana and Pedigo, 1974). However, these simple inductive models can be dangerous as they tend to mould biological reality (Conway, 1973) and as Shoemaker (1976) pointed out there are numerous variables that will affect the crop yield with insect number being only one of them. She, therefore, proposed the use of more complex mathematical models to describe the interaction between plants, pests, weather and other variables. Multivariate models were first developed by Watt (1962) to explain pest dynamics and later put to practice in the analysis of spruce budworm dynamics in Canada (Morris, 1967).

Many more recent pest control models have used differential equations as the basis for modelling as these are considered more appropriate for dealing with dynamic processes (Waters and Ewing, 1976). Gutierrez et al. (1979) used differential equations to construct simulation models for cotton, alfalfa and grape pest systems. Simulations can provide good descriptive models of the pest/crop ecosystem which can be used for further experimentation including dynamic programming techniques to find the optimal control solutions (Shoemaker, 1976).

Despite the research effort into modelling in recent years, Way (1973) questioned the benefits for

practical pest control programmes concluding that complex mathematical models have provided "no examples of improvement on straight forward mental models or on simple predictive techniques in research and practice of pest control". Indeed Menke (1974) provided an illustration by building a simulation model of soybean and velvetbean caterpillar and used the model to examine pest control strategies with the aim of minimising the percentage defoliation due to the caterpillar. He concluded by suggesting that the kill factor should be applied early in the first generation and that early instars should be killed as it is impossible to kill later instars with normal rates of conventional insecticides. Both factors were reasonably well known before the simulation experiments and not elucidated by them. The simulation experiment also avoided the central question in pest management in soybean, that of the relationship between defoliation and yield which will vary throughout the crop growth (Kogan, 1978).

While there have been apparently few models that have directly improved pest management, Norton (1977) considered that this must be the prime objective of pest management modelling and called for a more pragmatic approach to the subject. He considered that modelling can achieve this objective by performing two roles. First, by improving perception of pest problems and second, by the more tangible means of improving research and extension programmes by evaluating new forms of

control and providing more information on pest attack and the decision rules for coping with it. Within these rules decision theory techniques may enable the outcome of alternative control strategies to be evaluated (Norton, 1977). Forecasting for outbreaks or susceptible stages of pest population may be carried out by phenological models such as PETE (Welch et al., 1978) and models that give "on-line" instructions to decision makers may be applicable in some circumstances (Tummula, 1976). Norton (1977) concluded by propounding the value of simple descriptive models to determine explicit questions which are followed by empirical experimentation to determine the answers, e.g. the effects of simple control strategies, or the shapes of key relationships in the pest management system. In this way the chances of improvements in real life systems will be greatly increased.

CHAPTER 3

EXPERIMENTAL SITES AND CROP

MANAGEMENT

Crops of Brussels sprouts, var. Jade Cross, were grown for three seasons at the Horticultural Research Area, Lincoln College. In the first season, 1977/78, approximately 5000 Brussels sprout plants were grown in five beds, 65 x 6 m, at a spacing of 0.6 x 0.6 m between plants in a trial area of 0.25 ha (Fig. 3.1, Plate 3.1). Beds were separated by gaps of 1.5 m to allow tractor access. Seedlings were grown in a seedbed where the first sowing was made on 2 November 1977 but poor germination and establishment necessitated a second sowing on 27 November 1977. Plants from the first sowing were transplanted on the 22 and 23 December 1977 into approximately half the area in eight three-row blocks randomly selected from within the five beds. The remaining seven blocks were filled with plants from the second sowing on the 12 and 13 January 1978.

Beds A and B were used for the artificial defoliation experiment (6.1) and were sprayed with a mixture of insecticides (carbaryl, 200 kg a.i./ha and demeton-S-methyl 0.15 kg a.i./ha) with a boom spray at three weekly intervals, to minimize the effects of insect pests.

Beds D and E and half of bed C were divided into five, 6 x 6 m plots and subjected to a selective spray

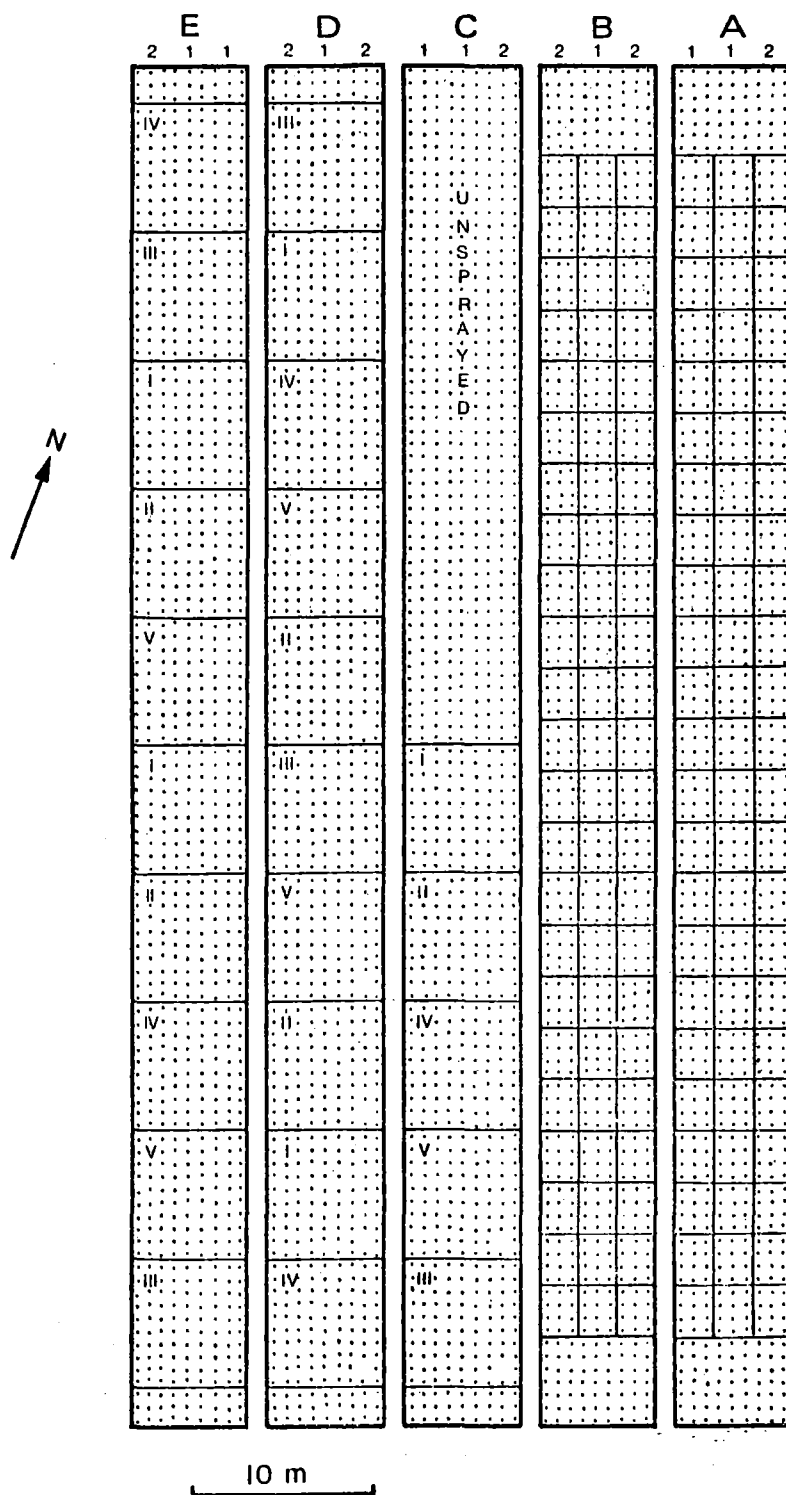


Fig. 3. 1. Experimental site, 1977/78 season, at the Horticultural Research Area, Lincoln College. A - E, bed labels; I - V, treatments (see text). (•), Brussels sprout plants, var. Jade Cross. 1, three-row beds from sowing 1. 2, sowing 2.

programme for Experiment 7.1. The crop was hoed twice to maintain control of weeds and irrigated as necessary. The whole crop was sprayed with copper oxychloride fungicide in April and May to prevent the spread of disease. Plants were 'stopped' by removal of the terminal bud on 30 April 1978 and harvest of the sprouts took place in late May and early June.

In the 1978/79 season approximately 6000 Brussels sprout plants were grown in a similar 0.25 ha site at the Horticultural Research Area (Plate 3.2). A single sowing took place on 11 November 1978 and the plants were transplanted into five and a half beds of the same size and spacing as the previous season (Fig. 3.2). The majority of the sprouts were variety Jade Cross but two beds of seven different varieties were transplanted each into five blocks with the varieties in randomly alternating rows.

Beds A and B contained the artificial defoliation experiments, 6.2 and 6.3, and were maintained under a regular three weekly spray programme with permethrin and demeton-S-methyl applied at rates of 50 g a.i. and 200 g a.i./ha respectively with a boom spray. Beds C and D were divided into four blocks of eight plots to examine the effects of spray-free periods on pest populations and damage. Beds E and F were unsprayed. A 9" Johnson and Taylor suction trap was placed in Bed E to monitor insect flight.



Plate 3.1 Experimental site 1977/78 at the Horticultural
Research Area, Lincoln College.



Plate 3.2 Experimental site 1978.79 at the Horticultural
Research Area, Lincoln College.

Weeds were controlled by hoeing and irrigation was given as necessary. The plants were 'stopped' on 25 April 1979 and harvesting took place in late May and early June.

In the 1979/80 season one bed, 60 x 6 m, of Brussels sprouts was grown in another similar site on the Horticultural Research Area. The plants were sown on 5 November and transplanted on 21 December 1979. The crop was managed as in previous years except that no insecticides were used.

CHAPTER 4

THE CHARACTERISTICS OF PEST ATTACK ON
BRUSSELS SPROUTS IN CANTERBURY1. Introduction

In Canterbury the major insect pests affecting Brussels sprout production are the white butterfly, diamondback moth and cabbage aphid (Harvey et al., 1979; Brandenburg, 1980). The biology and population dynamics of these pests have been extensively studied (e.g. Dempster, 1968; Ashby, 1972; Harcourt, 1966; Hughes, 1963; McLaren, 1975). However, there is little information available on the characteristics of their attack as defined in Chapter 2 by its timing, intensity and frequency. The only information on these characteristics in Canterbury is contained in studies by Lowe (1968), which indicated great variability in flights of cabbage aphid, and work by Ashby (1972), who suggested a second peak of white butterfly occurred in January.

To determine the characteristics of pest attack in Canterbury, Brussels sprout crops were examined and pest populations monitored for three consecutive growing seasons between 1977 and 1980. Population estimates of white butterfly, diamondback moth and cabbage aphid were obtained by direct counts, destructive harvest of plants and also, for diamondback moth in the developing sprouts,

by an extraction technique.

Close examination of the plants following destructive sampling allowed determination of the pest distribution pattern on the plant together with changes throughout the season to be monitored. The immigration potential at three sites was also monitored for white butterfly and cabbage aphid. Historical data were also used, where available, to reach some conclusions on the frequency of pest attack.

2. Materials and Methods

a. Population estimation by direct counting

In each season population estimates of the three major pest species were obtained at approximately three-weekly intervals by direct counts on marked plants in the field. In 1978 ten plants were randomly selected from each of the five unsprayed blocks in the selective insecticide trial (Fig. 3.1, Beds C, D and E). Counts from these plants were used to provide seasonal population data based on an initial population size of 50 plants. In 1979 and 1980 50 and 30 plants respectively were randomly selected from the unsprayed beds and sampled throughout the season.

In each year the following listed stages of the pests were categorized and noted:

White butterfly - eggs, larvae, pupae.

Diamondback moth - larvae, pupae.

Cabbage aphid - alatae, colonies greater
than 50 apterae.

In 1979 and 1980 white butterfly and diamondback moth larvae were visually separated into instars based on the head capsule width and larval characteristics given by Ashby (1972) and Robertson (1938).

To ensure that the regularly sampled plants were representative of the crop as a whole, a further 25 plants were randomly selected from the crop on 16 February for comparison with the marked plants. The marked plants were also sampled the following day for a check on variation in time of sampling and searching efficiency of the observer.

b. Population estimation by destructive sampling

In 1978 and 1979 plants were cut at ground level and brought back to the laboratory where leaves and sprouts were stripped and the pests upon them counted so that not only population estimates could be made but also the position of the pests on the plant could be determined. Comparisons could also be made between the population estimates so obtained and those determined from plants examined in situ.

In 1978 one marked plant was randomly selected and taken from each plot in beds C, D and E at

approximately monthly intervals through the growing season and in 1979 three samples of 20 randomly selected plants were taken from the unsprayed area (Fig. 3.2, Bed E) at approximately six-weekly intervals. In the laboratory the crown or terminal bud was first removed from the stem followed by the leaves in groups of ten. Within each group records were made of pest numbers. Sprouts were then cut from the stem and, after a superficial examination, diamondback moth larvae were extracted from them.

c. Extraction of larvae from the sprouts

To monitor the movement of the population of diamondback moth larvae into the sprouts it was necessary to develop a method to extract the larvae from them. In 1978 several methods were attempted and initially the most successful seemed to be by shaking with a wrist action shaker set at low speed. Sprouts were placed in a funnel and shaken for two minutes. Larvae thus extracted were shaken into a tray below the funnel. However, it seemed that as the sprouts grew larger fewer larvae were extracted and it was not clear whether this was the result of a population decline or decreasing efficiency of the extraction method. Subsequent tests revealed that efficiency was reduced with increasing sprout size and number (Table 4.1). At the end of the first season a passive extraction method was developed to overcome this problem. Sprout samples were placed in

TABLE 4.1 The effect of increasing sprout number and size the efficiency of shaker extraction tested by seeding sprout samples with diamondback moth larvae. Means \pm standard error.

Trial 1		Sprout number (Mean size 19.2 mm)			
		10	20	30	40
% of seeded larvae extracted		67 \pm 6.7	47 \pm 13.4	20 \pm 6.7	27 \pm 13.4
Trial 2		Mean sprout size (mm)			
		11.4	17.8	22.4	26.5
% of seeded larvae extracted	Instar IV	67 \pm 17.6	53 \pm 17.6	60 \pm 11.5	20 \pm 11.5
	Instar III	35 \pm 9.6	20 \pm 8.2	10 \pm 5.8	5 \pm 5.0

five litre liver pails with gauze covered holes top and bottom (Fig. 4.1). The adhesive 'Tack Trap'^R was placed in a 2 cm strip on the remaining area of lid to catch the moths after emergence. The containers were then placed in a 25°C controlled temperature (C.T.) room with a 50% relative humidity (R.H.) and examined at intervals until all the moths had emerged from the sample. This method was tested by 'seeding' samples of sprouts with known numbers of larvae from a particular stage. This test resulted in 84% recovery of the moths with no bias towards the older stages (Table 4.2). This method, therefore, was adopted in preference to shaker extraction for diamondback moth larvae.

The development of diamondback moth populations in the sprouts was estimated throughout the latter part of the season by harvesting 15 plants at approximately two-weekly intervals from the unsprayed bed (Fig. 3.2, E). The leaves were removed, the stems subsequently cut into three parts corresponding to upper, mid and lower zones and each placed in the pails in groups of five.

d. Flight activity and immigration

The potential pest infestation level is indicated by the flight activity and immigration of the pest. This was monitored by trap plants or flight traps depending on the pest characteristics. In 1978 weekly sowings of Brussels sprouts, var. Jade Cross, were made into

^R Animal Repellents Inc.

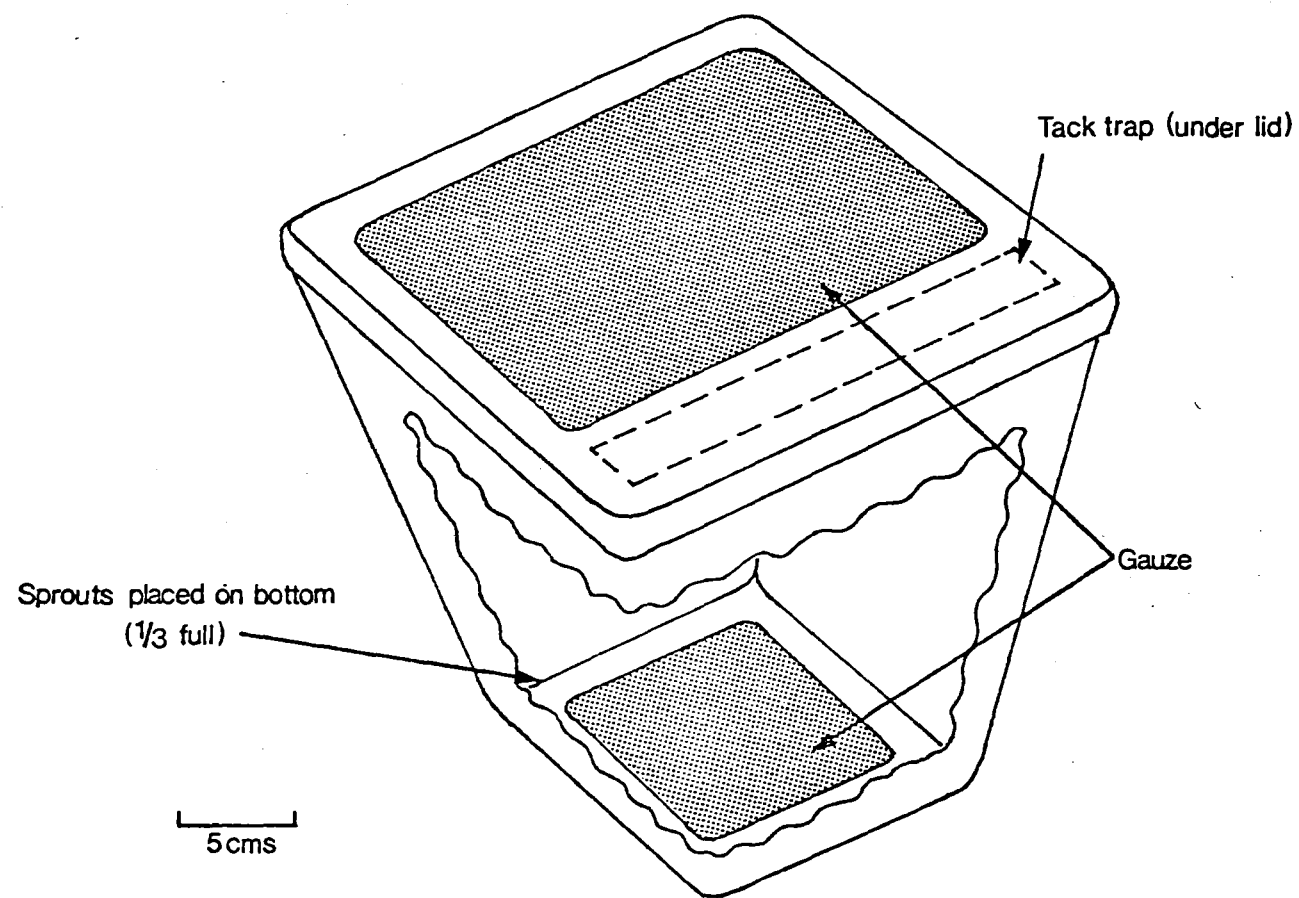


Fig. 4. 1. Five litre container for extraction of diamondback moth from samples of sprouts.

TABLE 4.2 Efficiency of pail extraction for different stages of diamondback moth tested by seeding samples of Brussels sprouts, 300 g fresh weight, with known numbers of larvae and eggs.

	Larval stage				
	IV	III	II	I	EGG
Trial I	95.0 \pm 5.8	87.0 \pm 5.1	81.5 \pm 3.5	-	51.0 \pm 5.0
No. replicates	4	4	2	-	2
Trial II	67.5 \pm 7.5	100.0 \pm 14.7	72.5 \pm 17.5	71.5 \pm 11.1	42.8 \pm 6.9
No. replicates	4	4	4	4	4

Mean figures expressed as a percentage of initial larval number (\pm S.E.) after correction for moth emergence from controls.

individual pots. After six weeks four plants were placed in water-filled 0.5 m^2 metal trays at each of three sites for a period of 7-10 days. They were then removed and replaced with fresh plants from the subsequent sowing. In the laboratory the plants were examined for eggs of white butterfly and alatae of cabbage aphid.

The three sites were:

1. Lincoln College Horticultural Research Area - placed within the 0.23 ha experimental block of Brussels sprouts.
2. Junction Road, Halswell - placed in a vegetable garden on the edge of a residential area.
3. Research Farm, Lincoln College - placed in a lucerne paddock over 1 km from the nearest brassica crop.

In 1979 flights of cabbage aphid and diamondback moth were monitored by a suction trap placed in the Brussels sprout crop. The trap was sunk into the ground so that the opening was 25 cm above ground level and below the crop canopy at the later stages of its growth.

3. Results and Discussion

a. Evaluation of sampling methods

The results of further sampling by direct counting to check the validity of the method are shown in Table 4.3. Neither recounting a selection of marked plants nor counting unmarked plants gave rise to any doubts about

TABLE 4.3 Comparison of pest population estimates from marked plants in situ with recounts of a sample of marked plants and counts from a further sample of unmarked plants (16 February 1979).

	White butterfly		Diamondback moth Larvae	Cabbage aphid	
	Eggs	Larvae		Alatae	Colonies
50 plant sample	1.68 ± 0.21	0.84 ± 0.16	1.26 ± 0.23	11.5 ± 0.77	4.9 ± 0.77
25 plant recount	1.20 ± 0.21	0.82 ± 0.19	1.48 ± 0.31	10.8 ± 1.25	3.9 ± 0.72
Comparative count of 25 plants	1.32 ± 0.23	0.64 ± 0.17	1.24 ± 0.36	11.33 ± 1.10	5.7 ± 1.07

the consistency of the method in providing an accurate estimate of the population.

However, as Southwood (1966) suggested, it is better to estimate the population by more than one method, in particular to ensure that a proportion of the population is not being missed by the sampling method. Comparisons of population estimates from direct counts and destructive sampling for both seasons are shown in Figure 4.2. While both methods reflect the population trends throughout the season it appears, as expected, that destructive harvesting and close examination in the laboratory gave the more accurate estimate of total numbers. The only exceptions were two occasions when considerably more white butterfly eggs were recorded in the field than in the laboratory examination, perhaps because these eggs are easily dislodged from the foliage during transport of the plants.

Large differences occurred between numbers of diamondback moth recorded by each sampling method, due to the presence of larvae concealed within the sprouts. Extraction of larvae from the sprouts of harvested plants in both years showed clearly that, in the later harvests, the major portion of the population was found within the sprouts, thus making it impossible to make accurate estimates of the total population from direct counts alone.

It seems clear that direct counting is most reliable for the large, relatively sessile larvae of white butterfly

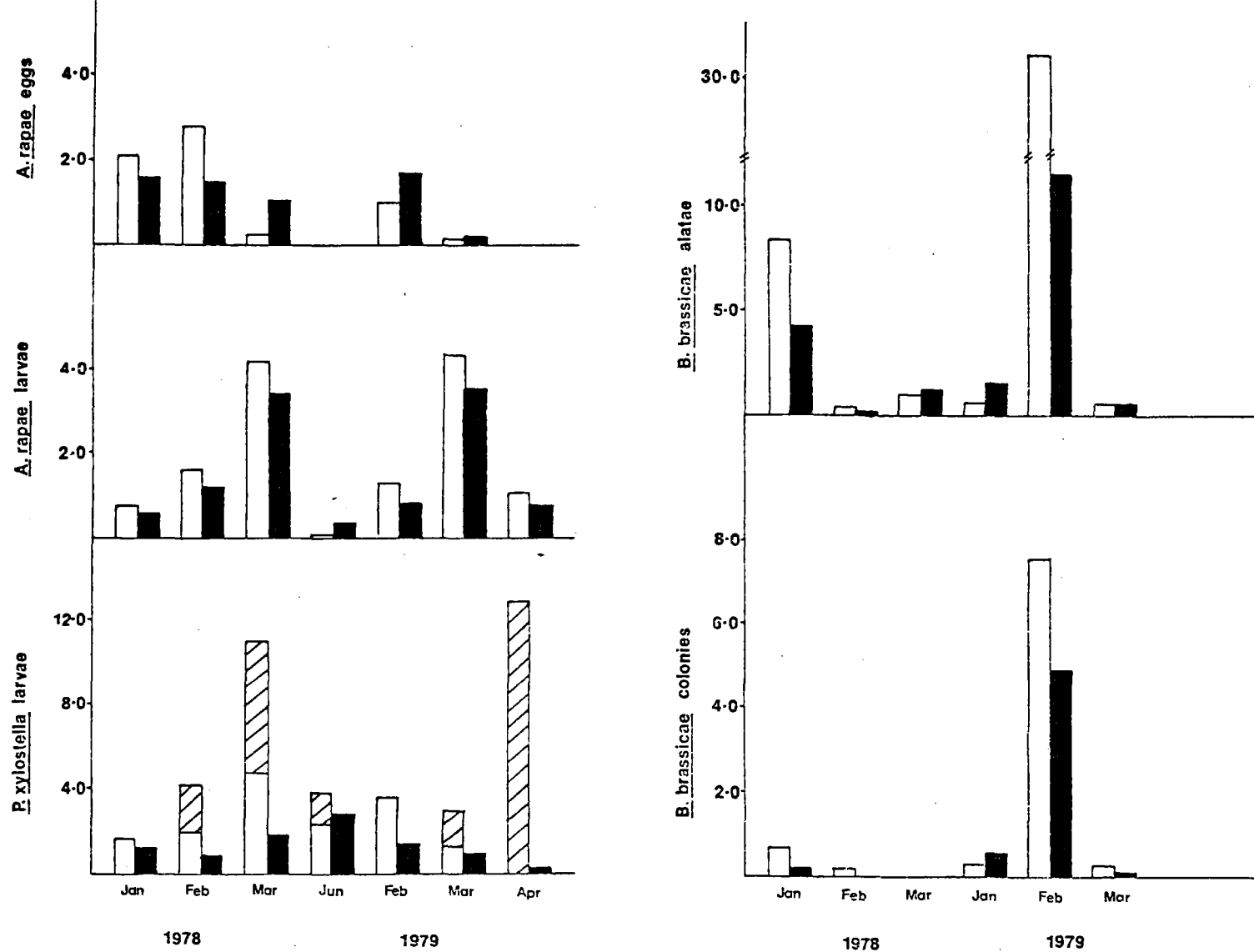


Fig. 4.2. Comparison of pest population estimates obtained by direct counts in the field (■) and from harvested plants examined in the laboratory (□) at stages throughout crop growth, 1978/79. (▨), diamondback moth extracted from the sprouts.

and less efficient for the smaller diamondback moth larvae particularly when these are concealed in the crown or sprouts of the plant. This lower efficiency is clearly shown when larvae of the two lepidoptera are separated into instars (Table 4.4). It appears that with direct counts the smaller early instars of both species are more likely to be overlooked. In selection of sampling methods, however, the efficiency of the sampling method must be balanced against other factors:- time needed for sampling and disruption of the habitat. Direct counts have the advantage of speed; five minutes/plant compared with 25 minutes for a sampled plant subsequently examined in the laboratory, and at peak populations direct counts of 50 plants produced population estimates with standard errors of the means of 10% and 18% for white butterfly and diamondback moth respectively in 250 minutes. To have attained the same level of accuracy for white butterfly by destructive sampling would have taken over 1500 minutes and required the destruction of 43 plants at each sampling. Direct counts of pest populations were, therefore, used as the major method of population estimation throughout the growth of the crop on the grounds of reliability and speed with minimum disruption of the habitat. Nevertheless destructive harvest is useful when used at stages throughout the growth of the crop as a check on the population, to determine the position of insects in the plant and, by extraction of larvae from the

TABLE 4.4 Comparison of estimates of population structure of white butterfly and diamondback moth on Brussels sprouts at peak populations estimated by direct counting (DC) and destructive sampling (DS).

Instar:-		V	IV	III	II	I
White butterfly						
26/3/79	DC	0.92	0.84	1.16	0.42	0.22
	DS	0.90	1.05	1.40	0.55	0.50
Instar:-		IV	III	II	I	
Diamondback moth						
16/2/79	DC	0.94	0.32	0	0	
	DS	2.10	0.95	0.55	0	

sprouts, to estimate populations of diamondback moth throughout the later part of the growing season.

b. Immigration and flight activity

White butterfly

The pattern of egg laying at each of the three sites is presented in Figure 4.3. Differences existed between sites in both the timing of egg laying and the number of eggs laid. Most eggs were laid at the field site with the highest peak recorded in late March. At the Halswell site numbers fluctuated over the season with peaks recorded in February and March while at the Research Area site numbers declined from an initial peak in January to low numbers later in the season. The decline in egg numbers laid at the Research Area site may be due to growth of the surrounding crop which was soon larger than the trap plants and thus more likely to receive eggs (Latheef and Irwin, 1979). The greatest number of eggs were laid on the isolated plants at the Field site and least at the Research Area site suggesting a dilution effect through the availability of large numbers of possible oviposition sites at the latter. This would suggest that small areas of brassicas are at greater risk from this pest than large ones, which is borne out by the observations of growers (P. Bull, pers. comm.).

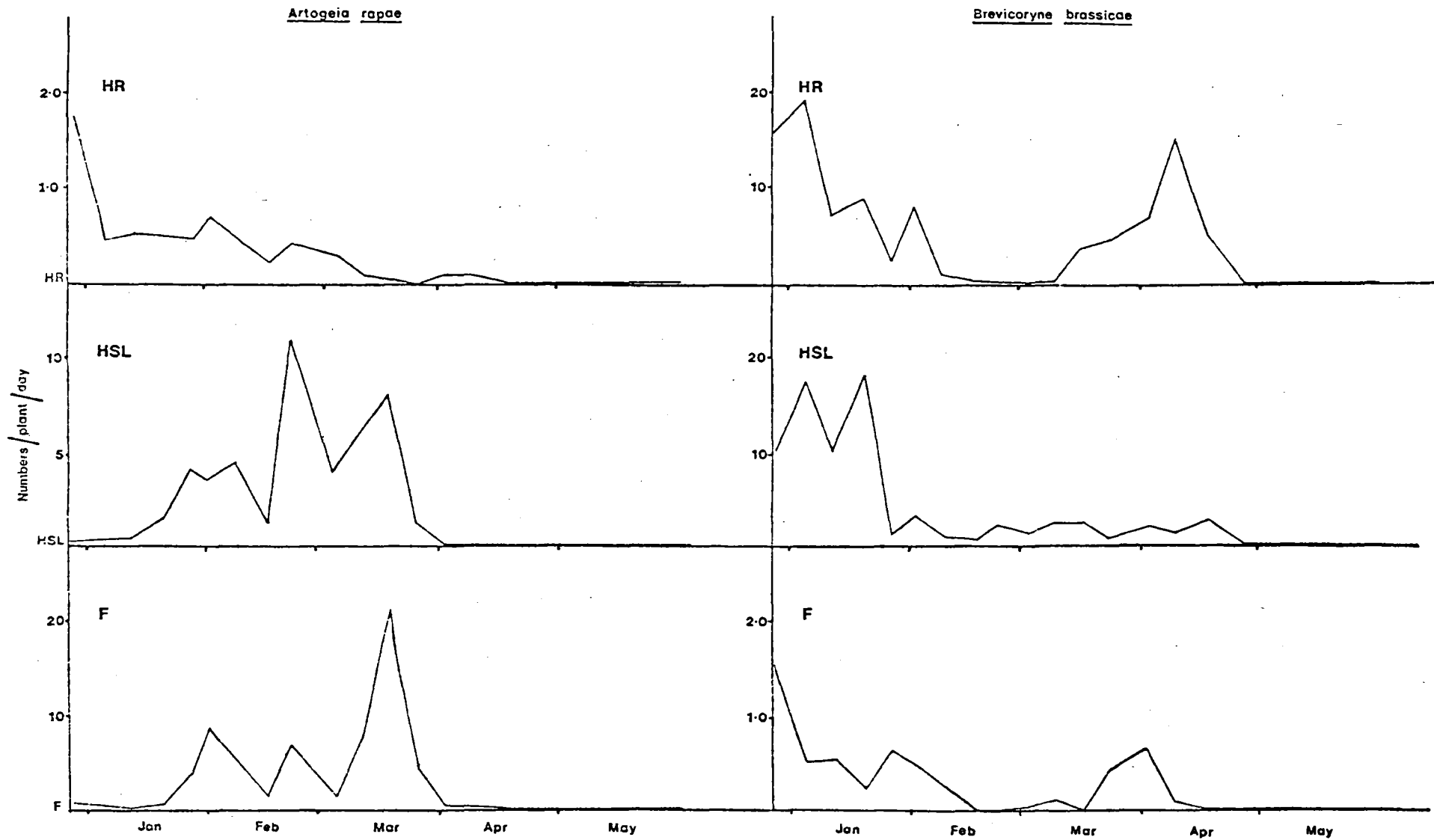


Fig. 4.3. Pattern of egg laying of white butterfly and immigration of cabbage aphid in the 1977/78 season as measured by numbers collected on trap plants at three sites.

Cabbage aphid

Greater similarities occurred between the cabbage aphid numbers recorded at each of the three sites with early peaks recorded in December and January and a second flight in March and April. This second peak was not, however, recorded at the Halswell site. It seems that these peaks correspond to the spring and autumn flights characteristic of this pest in Canterbury (Lowe, 1966). Nearly 90% of all aphids were collected at the Research Area site (Table 4.5). This may have been due to the orientation of the flying aphids towards the pattern of green plants on bare soil created by the crop (Smith, 1976) or dispersion losses from secondary flights (Hughes, 1963). Such net losses will be more likely from isolated plants than those within a crop which will also receive aphids from such local flights.

Diamondback moth

Daily suction trap catches of diamondback moth in 1979 are shown in Figure 4.4. There was considerable variation in the daily catch but weekly totals indicated a decline in flight activity from February onwards through the autumn with few adults caught after mid May.

c. Distribution on the plant

White butterfly

Examination of harvested plants in 1978 revealed that virtually all the larvae were found on the leaves

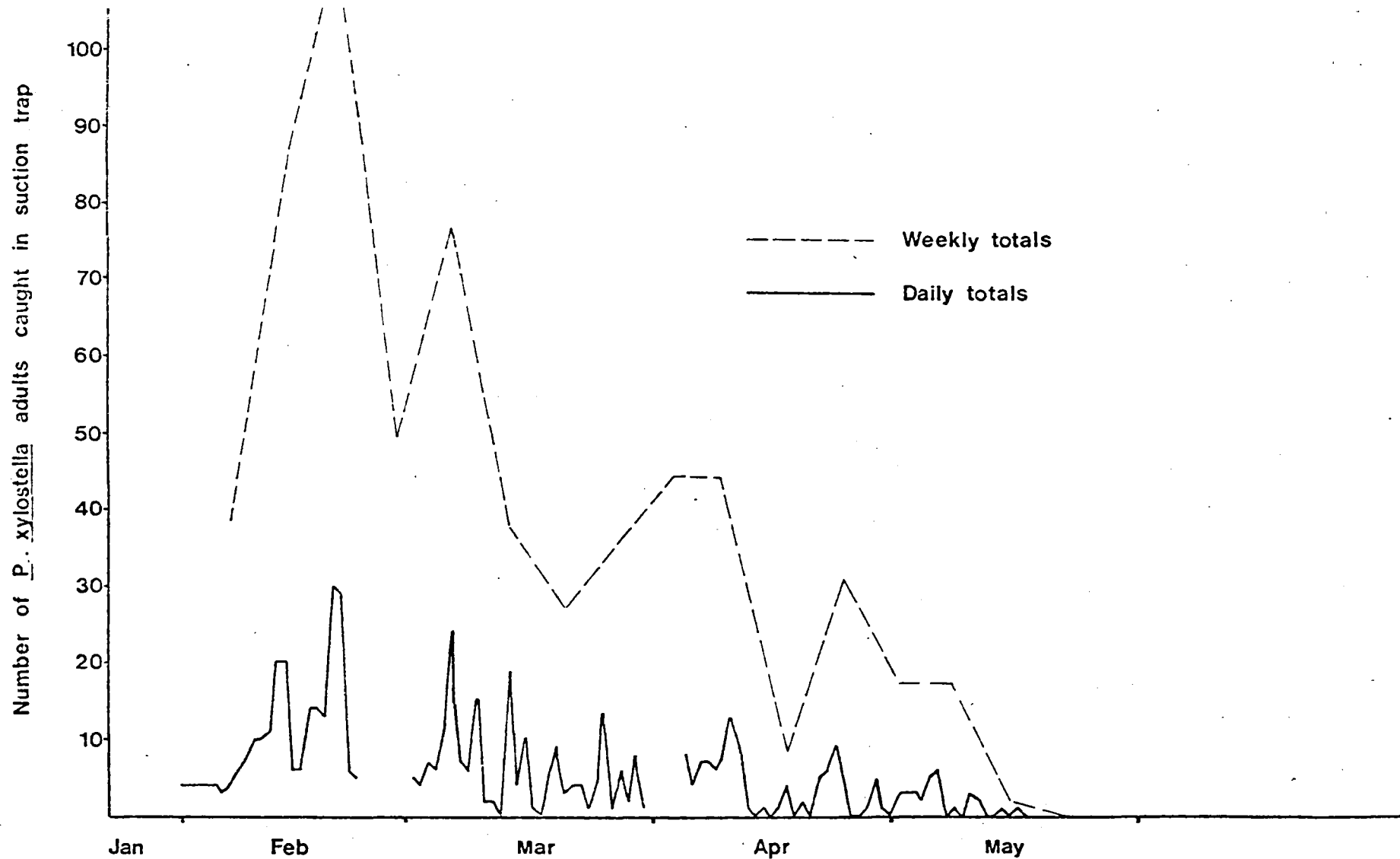


Fig. 4.4 Seasonal flight pattern of diamondback moth as shown by suction trap catches, 1979.

and that these were evenly distributed over the plant in its early growth stages but in the later part of the season tended to gather in the upper zone of the plant (Fig. 4.5). This result appeared to be caused by a preference of the larvae for the younger foliage.

Diamondback moth

Diamondback moth larvae were found predominantly in the crown of the young plants (Table 4.6). The remainder were distributed fairly evenly on the leaves although there was a tendency for greater numbers in the upper part of the plant. Later in the season, following sprout formation, the extraction technique indicated that there was a shift in the population from the leaves and the crown into the developing sprouts (Fig. 4.6).

Cabbage aphid

At the height of attack cabbage aphid colonies were distributed over the whole plant with most occurring in the middle leaf zone. After the autumn population decline colonies were found only on the lower leaves (Table 4.6). A similar change in distribution pattern throughout the season was found on Brussels sprouts in Britain by Church and Strickland (1952).

d. Seasonal population estimates

White butterfly

Seasonal trends of white butterfly egg numbers recorded by direct counts are shown in Figure 4.7. In

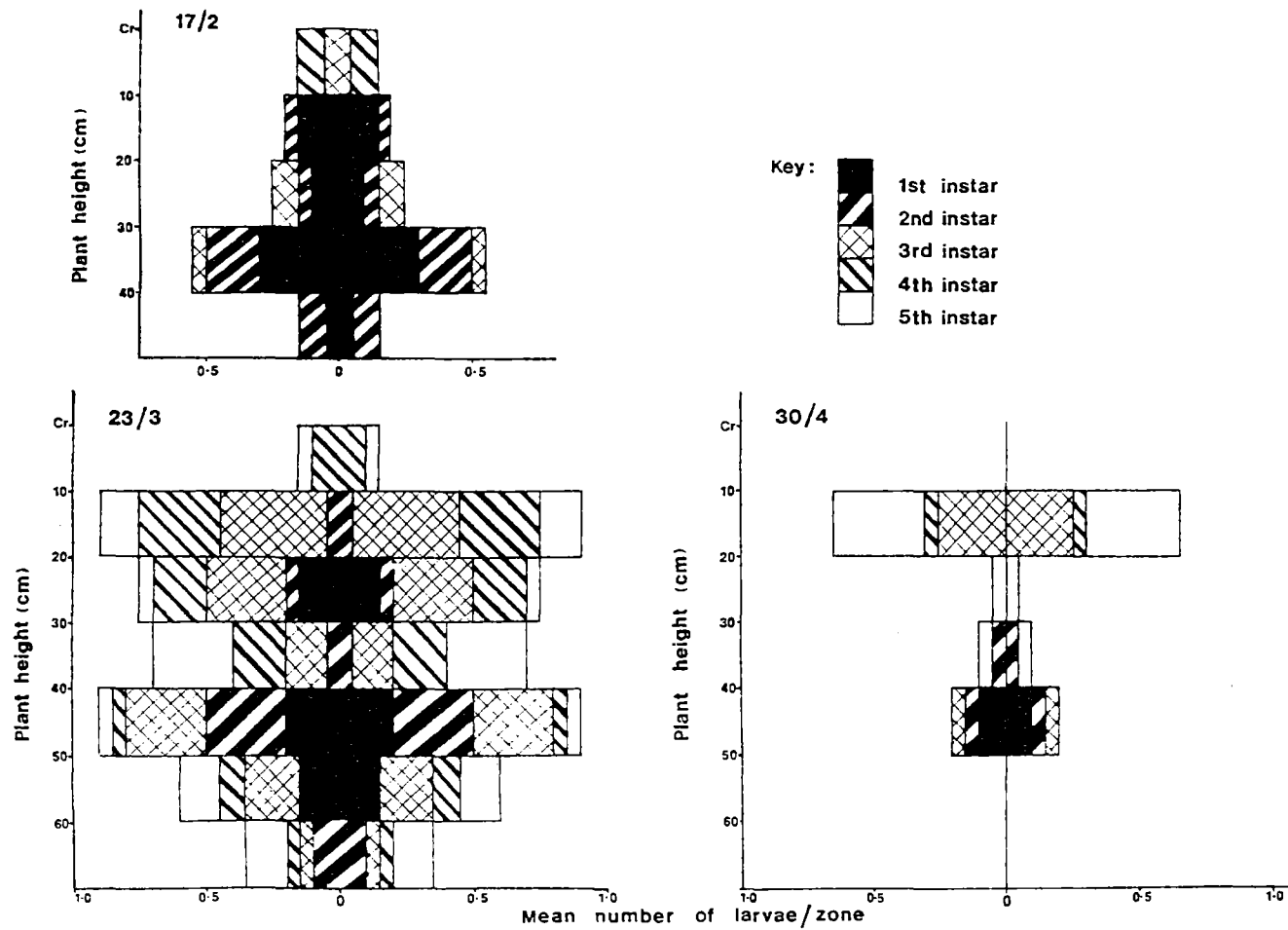


Fig. 4.5. Distribution of white butterfly larvae on the Brussels sprout plant according to leaf group at three times throughout the season, 1979.

TABLE 4.5 Total of white butterfly eggs and cabbage aphid alatae collected on trap plants at each of three sites, 1977/78.

	Research area	Halswell	Field
<u>A. rapae</u> eggs	43	329	430
<u>B. brassicae</u> alatae	727	33	57

TABLE 4.6 Distribution of diamondback moth larvae and cabbage aphid colonies on the Brussels sprout plant at two stages of growth.

	<u>P. xylostella</u>		<u>B. Brassicae</u>	
Date of examination:	17/2	23/3	17/2	23/3
Leaf group				
Crown	1.65	0.15	0.60	0
1 - 10	0.70	0.20	2.30	0
11 - 20	0.60	0.10	3.00	0
21 - 30	0.35	0.05	0.90	0
31 - 40	<u>0.20</u>	0.15	<u>0.25</u>	0.10
41 - 50		0.10		0.15
51 - 60		<u>0.05</u>		<u>0.10</u>

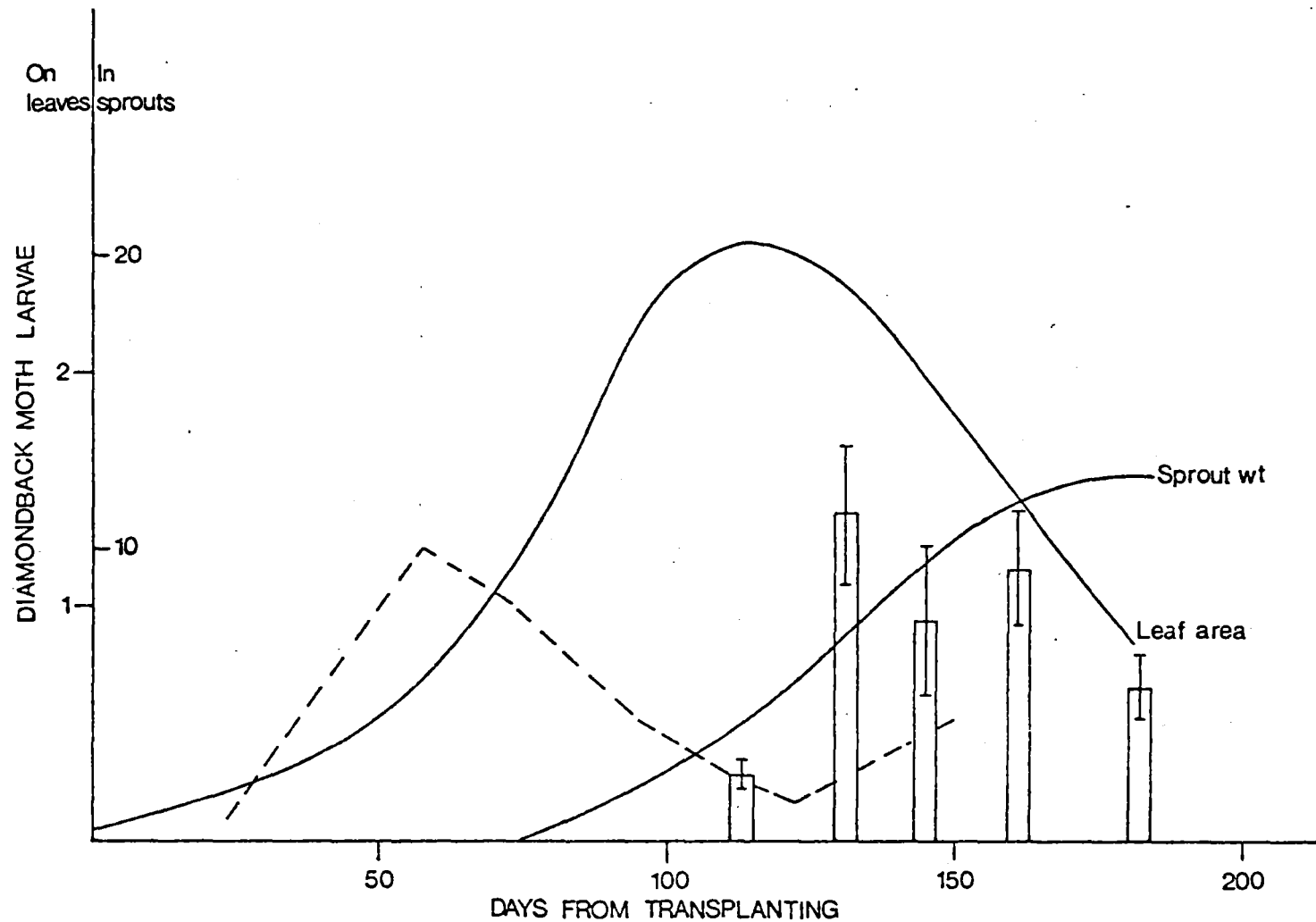


Fig. 4.6. Seasonal distribution of diamondback moth on Brussels sprouts showing the population shift from leaves to sprouts as the plant ages.

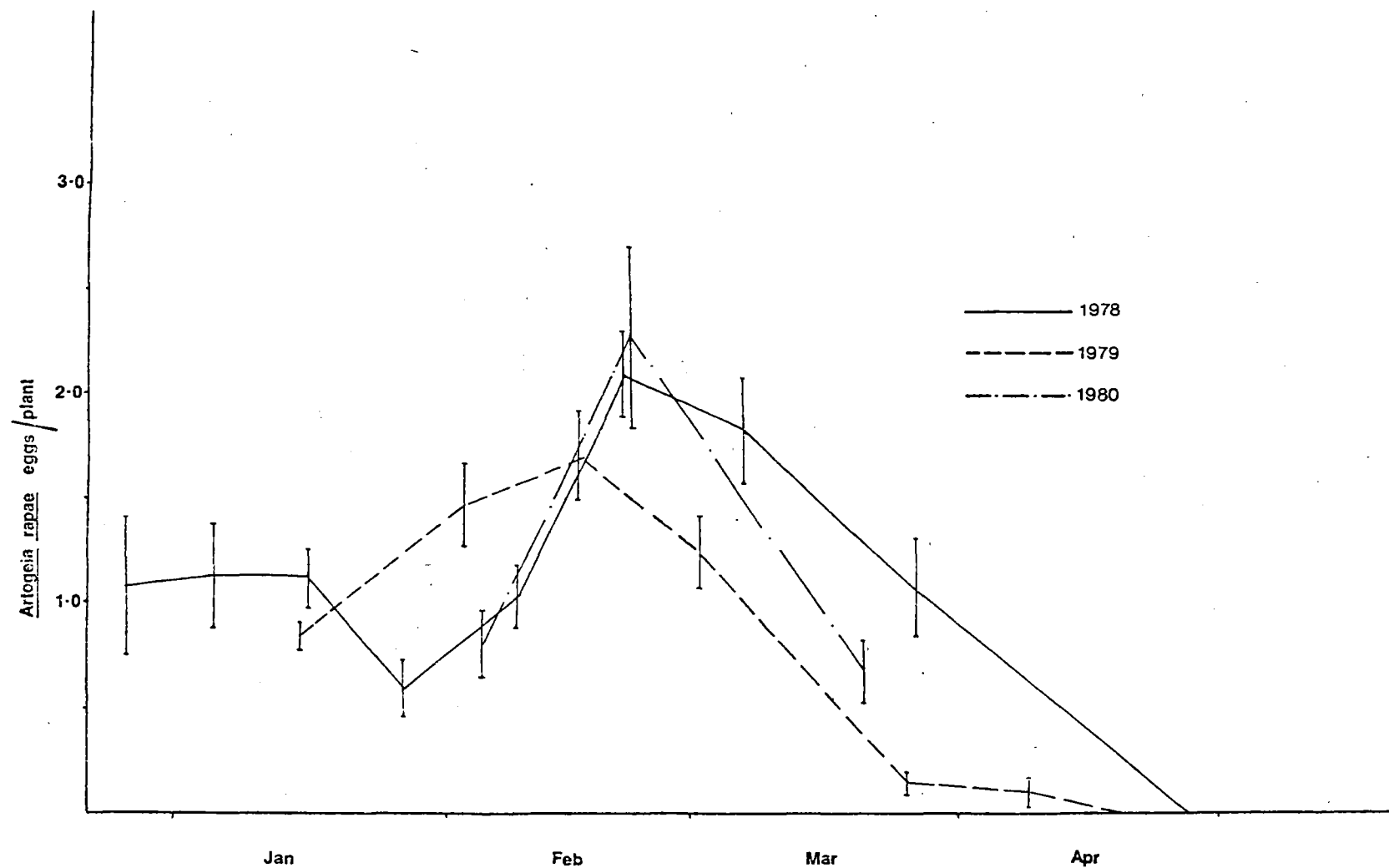


Fig. 4.7. Seasonal pattern of egg laying of white butterfly on Brussels sprouts over three seasons. Vertical lines represent standard errors.

all seasons egg numbers increased to a peak of between 1.6 and 2.2 eggs/plant in mid February followed by a gradual decline throughout March. Larvae showed a similar, but delayed, pattern (Fig. 4.8) with peak numbers of between 2.9 and 3.4 larvae/plant occurring in late March of all three years. Other studies have generally resulted in autumn population peaks (Dempster, 1968; Parker, 1970) but a different pattern occurred in New South Wales where both spring and autumn peaks were recorded (Hamilton, 1979). In contrast to the increase in egg laying in February recorded in this study, Ashby (1972) reported a decline of egg laying on September sown cabbages in mid January with few eggs laid in February. The apparent contradiction in these results may be due to the plant age or condition acting as a deterrent to oviposition (Thorsteinson, 1960).

A feature of the population curves is the regularity in both time and level of peak attack between years. Dempster (1968) and Harcourt (1966) also recorded uniformity in peak populations and Ashby (1972) suggested that this relative uniformity between years is due to pressure from a steady block of mortality factors operating in a density dependent manner. However, occasional outbreaks of white butterfly have been reported, apparently as the result of the failure of natural control by parasites (Todd, 1958).

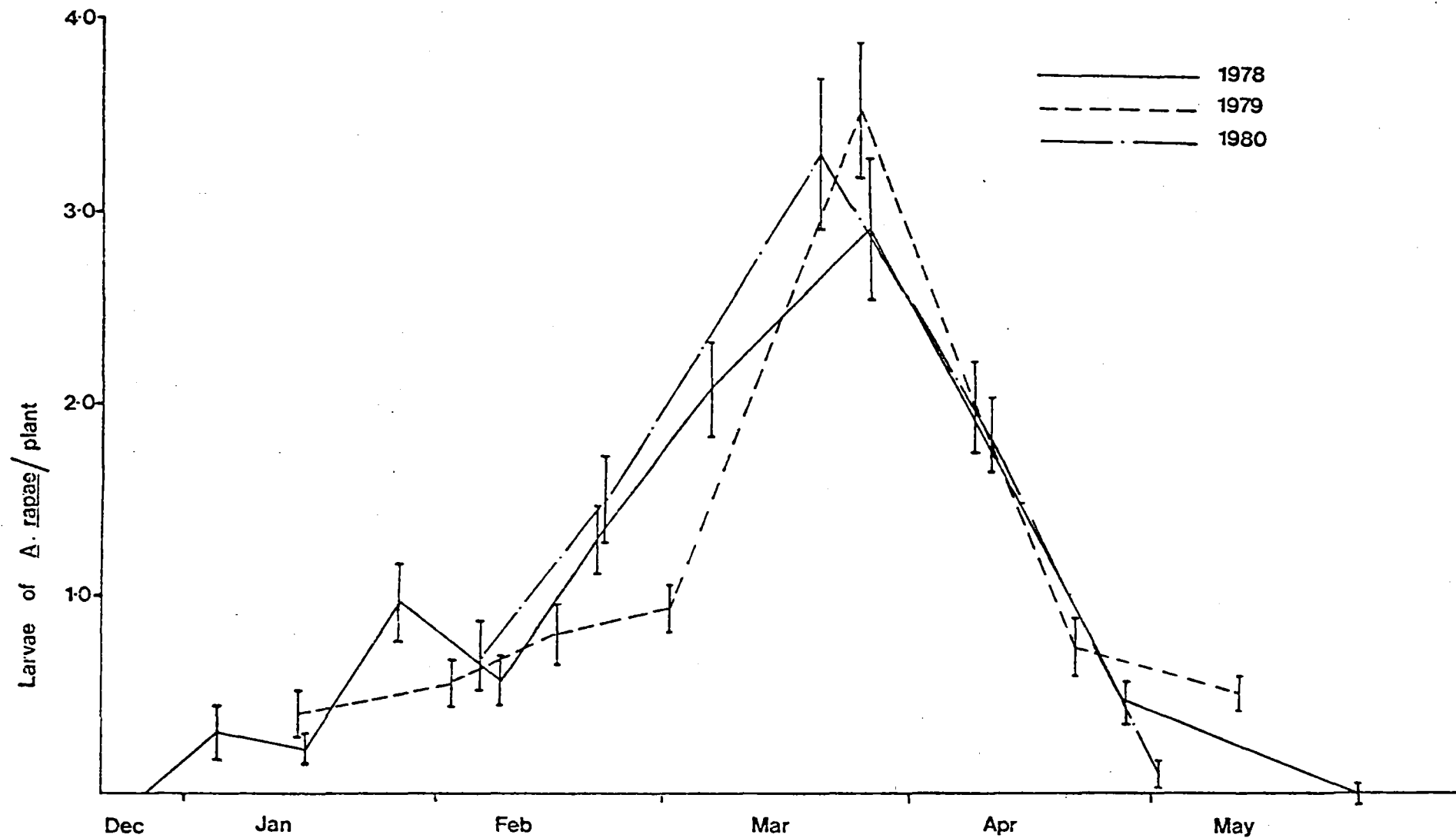


Fig 4.8. Seasonal distribution of white butterfly larvae on Brussels sprouts over three seasons, 1977/80. Vertical lines represent standard errors.

Diamondback moth

Mean larval numbers recorded from whole plant counts are shown in Figure 4.9. In 1978 larval numbers reached an early peak of 2.5 larvae/plant in mid February and then fluctuated between 1-3 larvae per plant throughout the rest of the growing season. In 1979 the population was lower, reaching a peak of only 1-2 per plant in early February and slowly declining thereafter. In 1980 high levels per plant were recorded in early February and from then they declined throughout the rest of the season.

It must be remembered, however, that these results do not represent the total population, only that portion visible on the leaves and, therefore, not those concealed in the sprouts. The latter group will increase as a proportion of the total population with the development of the sprouts from mid-February onwards. Extraction from the sprouts revealed that the population built up within the sprouts with increasing sprout size. In 1979 the number emerging reached a peak of 12.5 per plant in late April before declining in winter (Fig. 4.6). While, because of the efficiency of the sampling method, this figure closely reflects the actual population of eggs, larvae and pupae existing in the field at the time of harvesting, it should not be confused with the actual number of moths that would emerge in field conditions as considerable mortalities exist during the development of

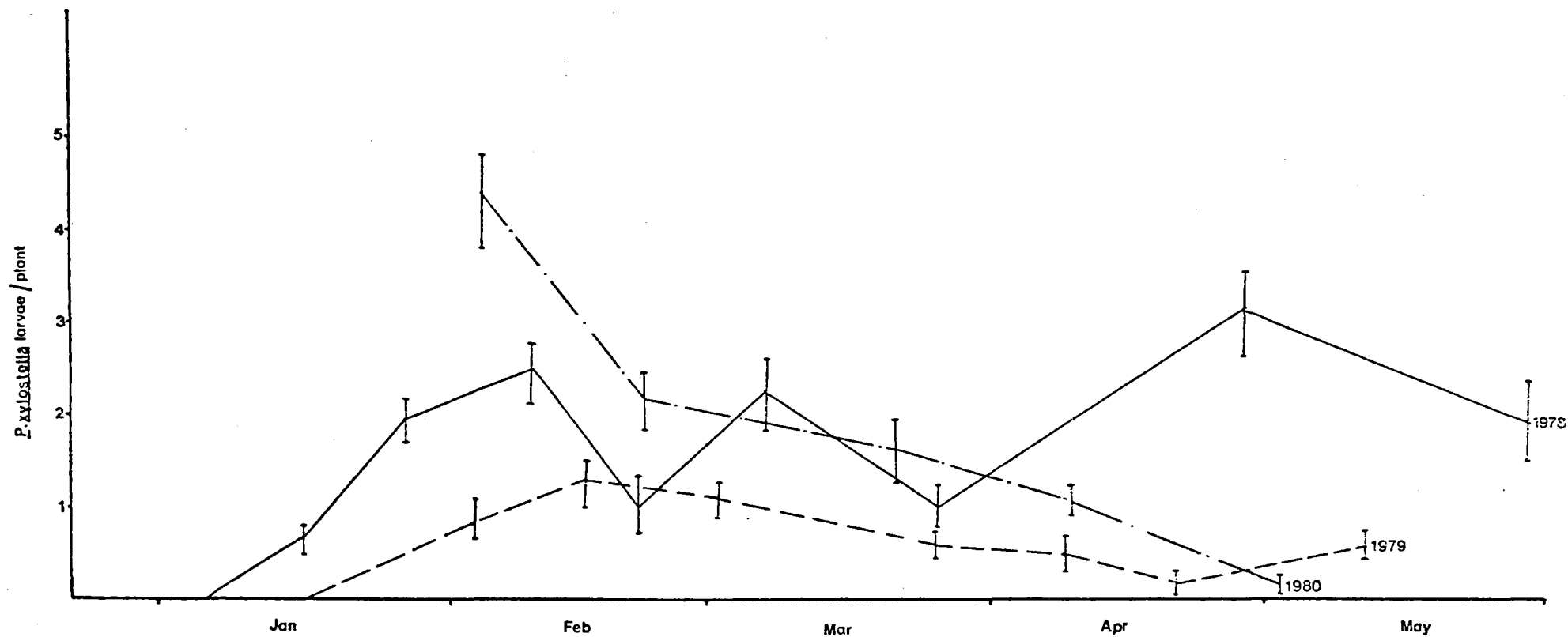


Fig. 4.9. Seasonal distribution of diamondback moth larvae on Brussels sprouts over three seasons, 1977/80. Vertical lines represent standard errors.

the insect. These were shown by Harcourt (1963) who recorded a mean larval mortality of 76% and pupal mortality of 5% over 18 generations in Canada.

Variability in intensity and pattern of attack, as shown in Figure 4.9, seem to be a characteristic of this pest. Similar sizes of peak populations were found to occur on cabbage in New South Wales but there was a considerable difference in the timing of peak attack between years (Hamilton, 1979). Even greater variability was recorded in India (Abraham and Padmanaban, 1968) and Trinidad (Yaseen, 1974). In both countries peak populations coincided with periods of hot, dry weather. However, no such relationship was found in this study, perhaps due to sprinkler irrigation applied to the crop during dry conditions.

Cabbage aphid

Cabbage aphid numbers recorded from the three seasons are shown for alatae (Fig. 4.10) and colonies of greater than 50 apterae (Fig. 4.11). While peak numbers of alatae varied only between ten and 17 per plant, the variation in numbers of aphid colonies between years was much greater. In 1978 flights of aphids into the crop shortly after transplanting led to a subsequent rise in the number of colonies with more than 0.5 per plant recorded from early January until early February. Aphid populations then declined to very low numbers in mid February and early March until a second flight of alatae

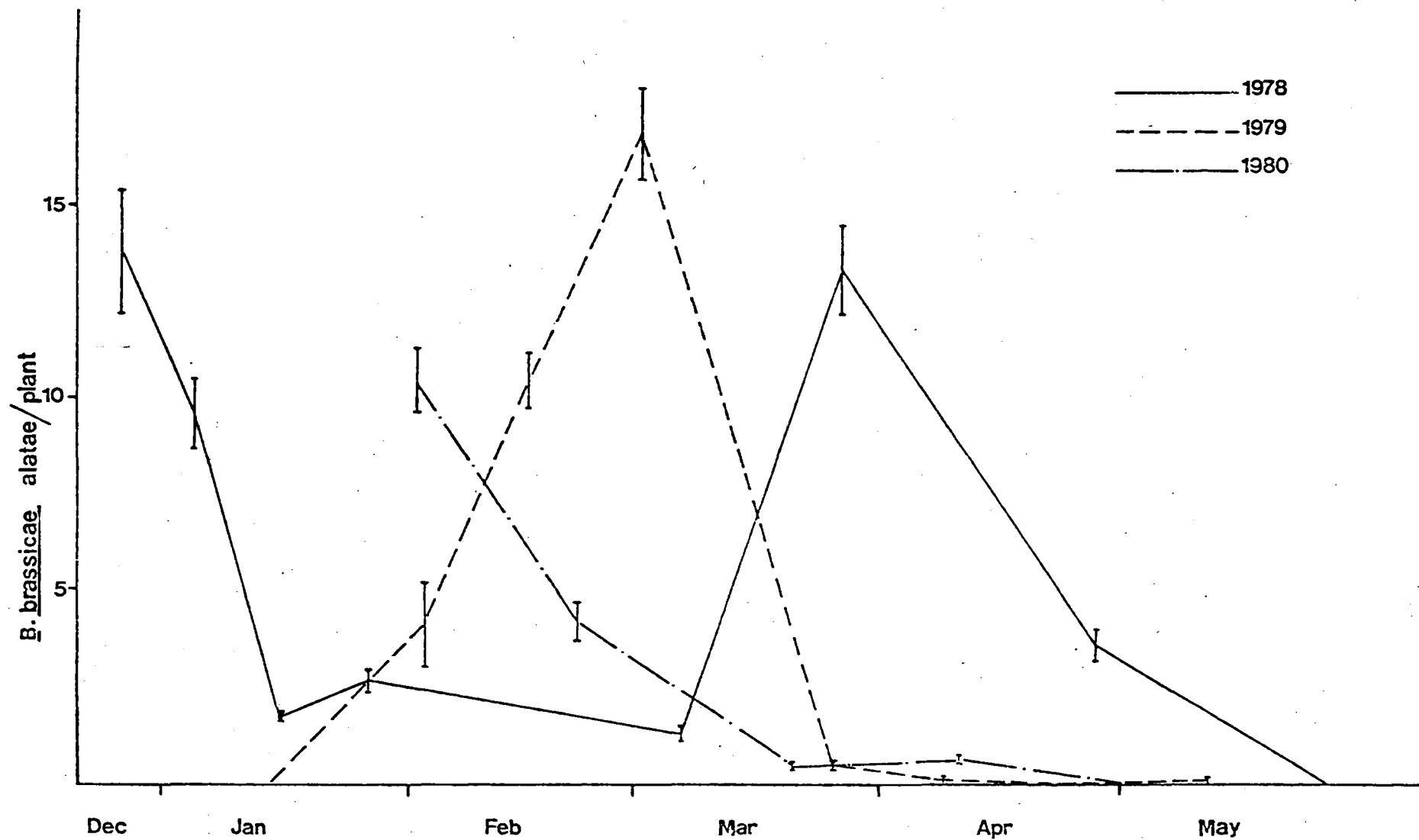


Fig. 4. 10. Seasonal distribution of cabbage aphid alatae on Brussels sprouts over three seasons, 1977/80. Vertical lines represent standard errors.

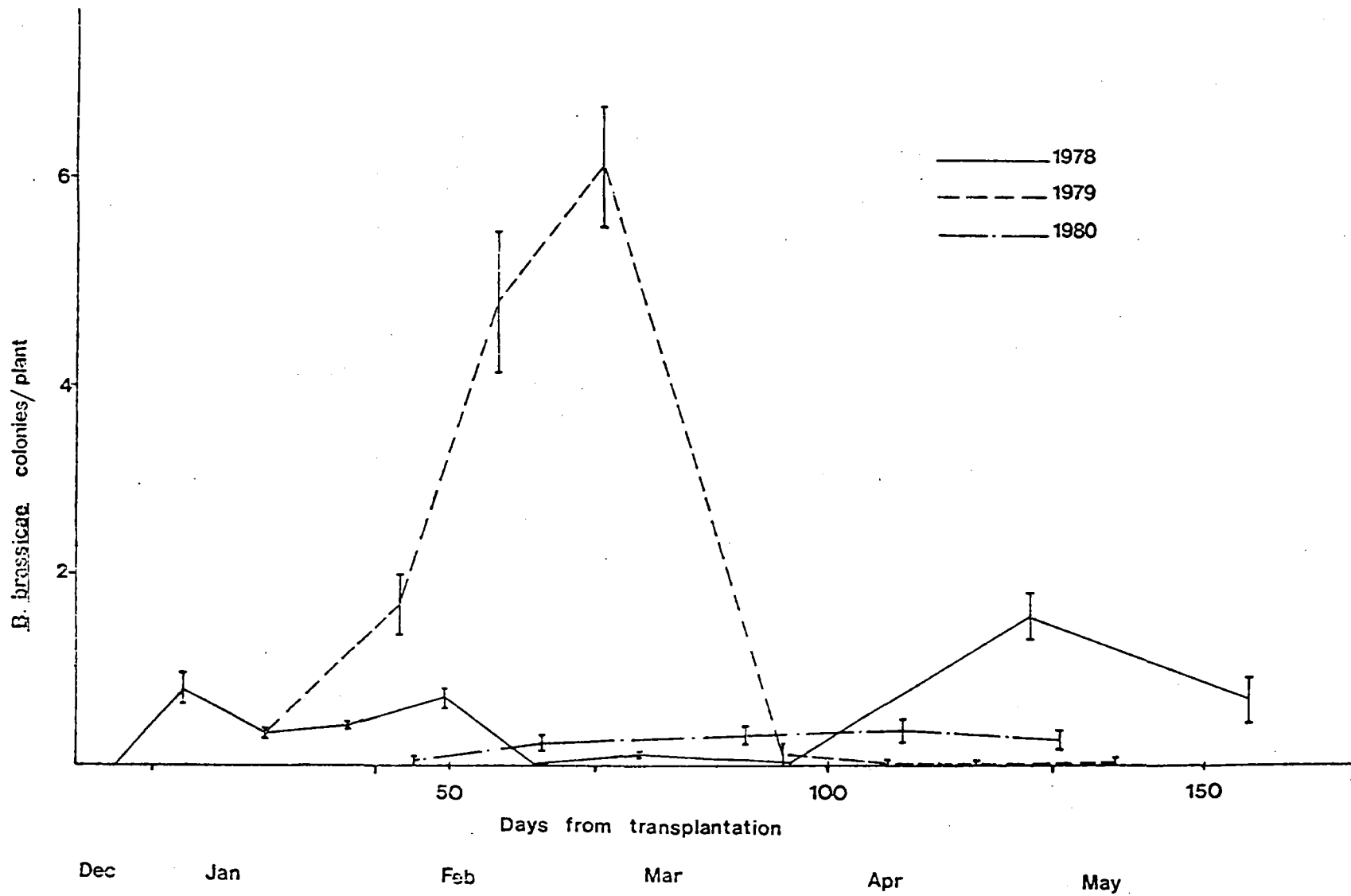


Fig. 4.11. Seasonal distribution of cabbage aphid colonies on Brussels sprouts over three seasons, 1977/80. Vertical lines represent standard errors.

in late March which resulted in a peak of 14 alatae per plant. This inflight of alatae was followed by an increase in numbers of colonies until an autumn peak was reached in April. In 1979 a different pattern emerged. Alatae numbers reached a peak of 17 per plant in early March together with colonies which reached a peak of six per plant at this time. This peak was followed by a rapid crash in the population coinciding with a period of wet weather and the spread of the fungal disease Entomophthora sp. through the colonies. Few aphids were recorded in April and May. In 1980 an early season peak of alatae never resulted in great increases in the number of colonies which remained at less than 0.5 per plant throughout the season.

Lowe (1968) recorded the flight pattern of cabbage aphid in Canterbury over an eight year period and showed that there was considerable variability in the numbers caught and the times of peak catches between years although spring and autumn peaks could always be distinguished. However, even with similar peak flights, as recorded in this study, the subsequent growth of colonies varied considerably depending on factors such as weather and predation. Studies of cabbage aphid in the U.K. have also indicated considerable variability in attack between both sites and seasons (Epsom, 1952; Strickland, 1954). Indeed the characteristic variability in both time and intensity of attack led Thomas (1948) to use cabbage aphid as an example in a discussion on the difficulties of forecasting pest attack.

4. Summary - The Characteristics of Pest Attack
in Brussels Sprouts

a. White butterfly

Females fly into the crop from the surrounding area following transplanting and commence egg laying. Thus isolated plants or small areas of crop are more likely to receive high egg numbers than those plants within an extensive crop. Each year egg numbers rose to a peak in late February followed by a decline to low numbers in April after which few eggs were laid. Larval numbers followed a similar but delayed pattern reaching a peak in late March and declining to low numbers in May. The pattern of larval distribution on the plant is apparently random in the early stages but there is a tendency for larval aggregation on the upper leaves and crown in April and May.

It appears that a characteristic of white butterfly attack is its regularity between years in both timing and intensity in crops grown with the same management practices. Thus, once the dimensions of pest attack are established for a crop in any one year the probability of a similar attack in subsequent years is very high.

b. Diamondback moth

Diamondback moth larvae were found in the crop shortly after transplanting, presumably the progeny of gravid females entering the crop from nearby brassica

crops or cruciferous weeds. Larval numbers on the leaves rose to an early peak in February followed by fluctuations presumably due to both variable mortality factors and the relatively short generation time of diamondback moth which allows a rapid population response to favourable conditions.

In the early stages of growth larvae fed on the leaves and in the crown of the plant. From mid February onwards there was a shift of the population into the sprouts as these expanded. Numbers within the sprouts rose to a maximum in May and declined in the winter months. This decline is no doubt due to the cessation of flight activity in May and the decrease in egg laying at low temperatures. While diamondback moth was present in considerable numbers in all years the population showed a marked variation in size between years which is a characteristic of attack by this pest.

c. Cabbage aphid

Unlike the other two pests there was little uniformity between years in attack by this pest. Flights of alatae into the crop came at different times between December and April and the subsequent rise in numbers of colonies also varied considerably. It seems that this variability, the causes of which are unclear, would make predictions of outbreaks of this pest difficult and thus bring into question the use of pre-emptive measures against it.

CHAPTER 5

THE FEEDING BEHAVIOUR OF
DEFOLIATING PESTS ON
BRUSSELS SPROUTS1. Introduction

The impact of a pest on a crop depends not only on population size but also on the rate of feeding of the individuals that make up the population. This will be governed by the population structure, competition and fitness as well as environmental factors, in particular temperature. However, as Waldbauer (1968) commented, little is known about the effects of environment on the rate of feeding of insects.

In this chapter the effects of developmental stage and temperature on the amount and rate of feeding by white butterfly and diamondback moth larvae are assessed.

2. Materials and Methods

a. White butterfly

Eggs of white butterfly were collected from a crop of Brussels sprouts, var. Jade Cross, and maintained at $15 \pm 1^{\circ}\text{C}$. The eggs were checked daily and after hatching, the neonate larvae were removed and placed in 50 mm diameter clip cages clamped on the leaves of six week old, glasshouse grown Brussels sprout plants (var. Jade Cross) (Plate 5.1). The clip cages were made from polyethylene



Plate 5.1 Clip cages for feeding experiments with white butterfly and diamondback moth larvae on Brussels sprout leaves.

tube and gauze, an enlarged version of the aphid cages developed by Burt et al. (1955).

The plants were then placed in constant environment cabinets at one of the following temperatures: 15°C , 20°C , 24°C , 29°C (all $\pm 1^{\circ}$), with ten larvae at each temperature. All cabinets were set to a 16L:8D photoperiod with a relative humidity of $70\% \pm 5\%$.

Larvae were examined daily to determine instar stage by head capsule width, and then moved to a fresh leaf. The leaf area consumed by the first and second instars was measured using a binocular microscope with a calibrated grid eyepiece. The areas consumed by the third to fifth instars were determined by placing the leaves above 1 mm^2 graph paper and counting the uncovered squares. Leaf weight consumed was calculated by a difference technique (Taylor and Bardner, 1968a). Fresh plants were placed in the cabinets every 2-3 days. Resulting pupae were removed, oven dried at 70°C for 48 hours and then weighed.

A further set of ten larvae was placed on three month old Brussels sprout plants in the field. The field plants were larger than the laboratory plants and the cages were moved every second day, otherwise the procedure was as described above.

b. Diamondback moth

To carry out experiments with this insect, a colony was maintained in a 20°C constant temperature chamber.

Adults were confined in a 600 x 300 x 450 mm muslin covered cage and allowed to oviposit on young Brussels sprout plants, var. Jade Cross. These plants were then removed from the cages and the resultant larvae allowed to develop on them. Pupae were returned to the oviposition cage and the colony was frequently supplemented with field collected adults. The adults were fed with a solution of honey and water.

Experiment 1. Larval feeding of diamondback moth.

Daily feeding of larvae on Brussels sprouts was examined at 25°C. Twenty neonate diamondback moth larvae were taken from the colony described above and placed individually in 20 mm diameter clip cages on the lower surface of eight week old, glasshouse grown Brussels sprout plants, var. Jade Cross. Each day the cages were removed and the area consumed, either as a mine or total leaf area, was estimated under a binocular microscope using a calibrated grid eyepiece. The larval stage was determined on the basis of head capsule width (Robertson, 1939) and the sex determined by examination of the fourth instar. Following emergence from the mine, larvae were moved each 2-3 days to a new leaf. The amount consumed in each instar and the total leaf area consumed was calculated from the sum of daily increments. On pupation, the pupae were removed and oven dried at 70°C before weighing. Due to high mortality in the early stages, a second trial

was established with 20 second instar larvae following the same procedure as described above.

Experiment 2. The effects of temperature on feeding and development of the diamondback moth.

Previous experiments had revealed that larval mortality was lower on turnips (Jackson, unpub.). Therefore, in this experiment young turnip plants were used in place of Brussels sprouts.

Ten second instar larvae were placed individually in 20 mm diameter clip cages on the leaves of eight week old, glasshouse grown turnips. var. York Globe, at each of four temperatures: 15°C , 20°C , 25°C , 30°C (all $\pm 1^{\circ}$). Each day, as in Experiment 1, the leaf area consumed was estimated, the instar determined and the larvae moved to a fresh portion of leaf. In the fourth instar sex was determined and following pupation, weight measured.

3. Results

a. White butterfly

The effects of temperature on development time, larval feeding and resultant pupal weight for white butterfly are summarised in Table 5.1. Eighty-eight percent of larvae in the experiment survived to pupation and development time was clearly inversely proportional to temperature.

As temperature increased, both leaf area and weight consumed decreased: absolute consumption at 15.5°C being

TABLE 5.1 The effect of temperature on larval development, leaf consumption and pupal weight of white butterfly. Mean \pm SE.

Temperature (T)	Development time (days)	Leaf area (LA) consumed (cm ²)	Leaf weight (LW) consumed (mg)	Pupal weight (P) (mg)
15.5	25.1 \pm 0.7 a ¹	58.37 \pm 2.59 a	212.1 \pm 12.3 a	48.4 \pm 1.2 a
19.9	17.8 \pm 0.4 b	46.05 \pm 2.35 b	151.0 \pm 9.1 b	38.9 \pm 1.3 b
24.1	11.3 \pm 0.4 c	33.19 \pm 2.61 c	136.9 \pm 9.8 c	39.8 \pm 1.8 b
29.5	8.8 \pm 0.5 d	37.62 \pm 2.82 c	140.2 \pm 13.5 bc	30.4 \pm 1.5 c
Regression equation		LA=-1.41T+77.68	LW=-4.6T+261.3	P=-1.14T+64.61
Correlation coefficient (33 df)		-0.60***	-0.55***	-0.79***

¹Numbers followed by the same letter in the same column are not significantly different (P < 0.05).

*** P < 0.001

approximately 1.5 times higher than at 29.5°C. Pupal weights were correlated with leaf area and leaf weight consumed ($r = 0.54$ and 0.62 respectively, 33 df.) and showed a corresponding decline with increasing temperature.

Food consumption may be estimated by measuring either the leaf area or leaf weight consumed. Comparison of these alternative methods showed that, particularly for the early instars, the visual estimation of leaf area removal provided the more reliable estimate of consumption (Table 5.2).

TABLE 5.2 Comparison of methods of estimating white butterfly larval food consumption showing mean leaf area and mean leaf weight consumed together with the coefficients of variation (CV) for each instar.

	Instar				
	I	II	III	IV	V
Leaf area (cm ²)	0.10	0.35	1.28	4.36	37.96
CV%	39.2	32.1	53.9	30.2	18.9
Leaf weight (mg)	0.41	1.55	3.81	15.72	138.91
CV%	190.7	81.7	46.2	41.3	22.5

At all temperatures larval feeding increased exponentially with each successive instar so that approximately 86% of the total larval consumption took place in

the fifth instar (Fig. 5.1). This relatively high consumption in the fifth instar is partially explained by a higher feeding rate but is also affected by the longer development time of this instar compared with the earlier stages. Within each instar, feeding rose to a maximum mid-way through the stage and then declined prior to ecdysis (Fig. 5.2). A similar pattern was found by Smith and Smilowitz (1976) who distinguished a post-moult recovery phase, a feeding phase and a pre-moult phase within each instar of white butterfly.

In the field plot the mean screen temperature recorded for the experimental period was 18°C. The mean field larval development time of 17 days, slightly less than expected from the laboratory work (Table 5.1), suggests that the leaf temperature was slightly higher than the recorded air temperature as has been reported for apple leaves on cool days in Canterbury (Ferro et al., 1979). The mean leaf area consumed was $269 \pm 15 \text{ mm}^2$, and the corresponding leaf weight $237.9 \pm 13.1 \text{ mg}$. This decrease in leaf area consumption in the field compared with that in the laboratory reflects the increased leaf thickness and weight/ mm^2 in the former which was more than twice that of the glasshouse grown plants. The leaf weight consumed, however, was greater than that observed in the laboratory at 18-20°C. It seems likely that this was a function of lower nitrogen levels in the leaves of the older field grown plants.

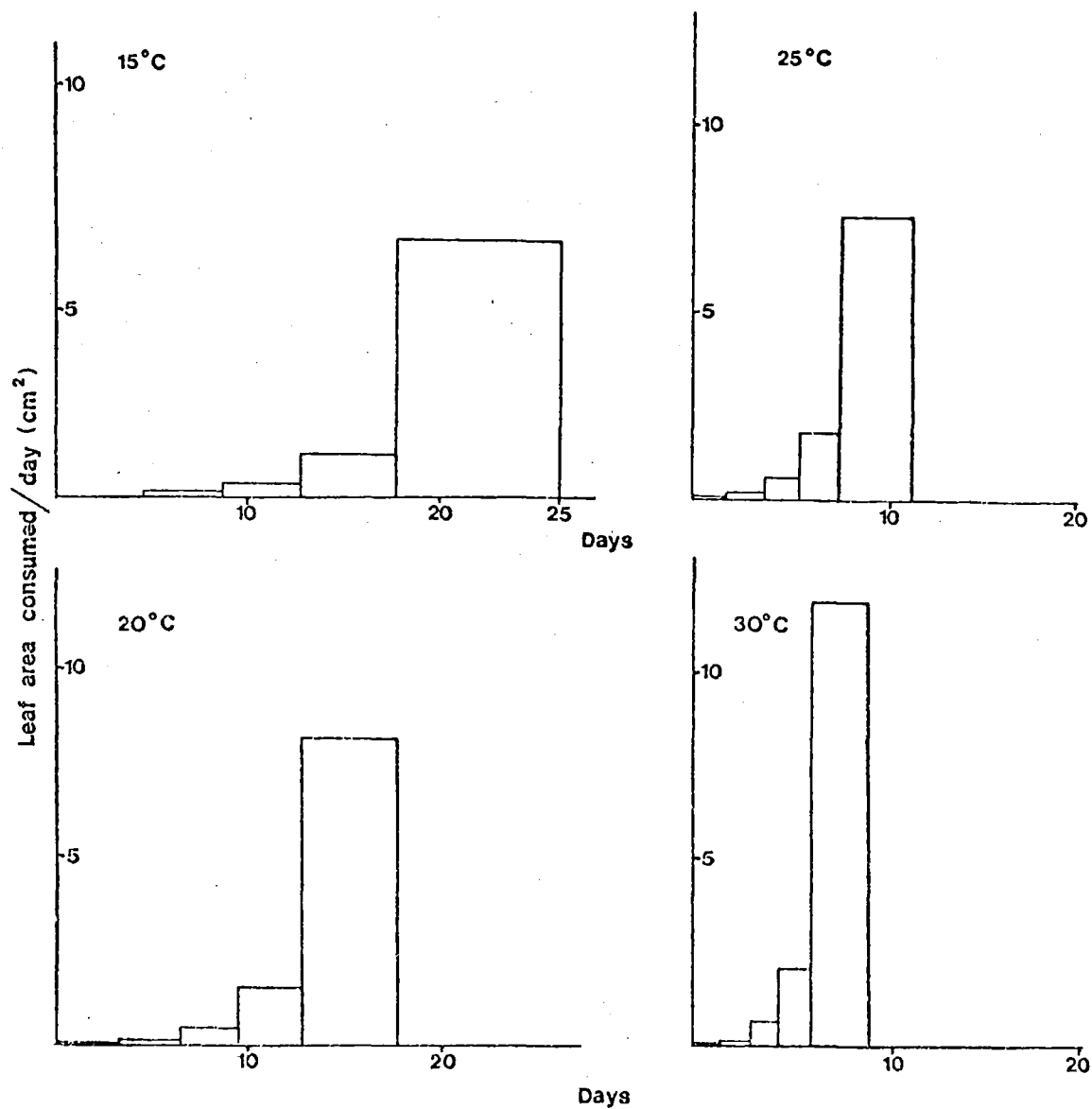


Fig. 5. 1. Leaf area consumed and larval duration at each of four temperatures for each instar of white butterfly feeding on Brussels sprout leaves.

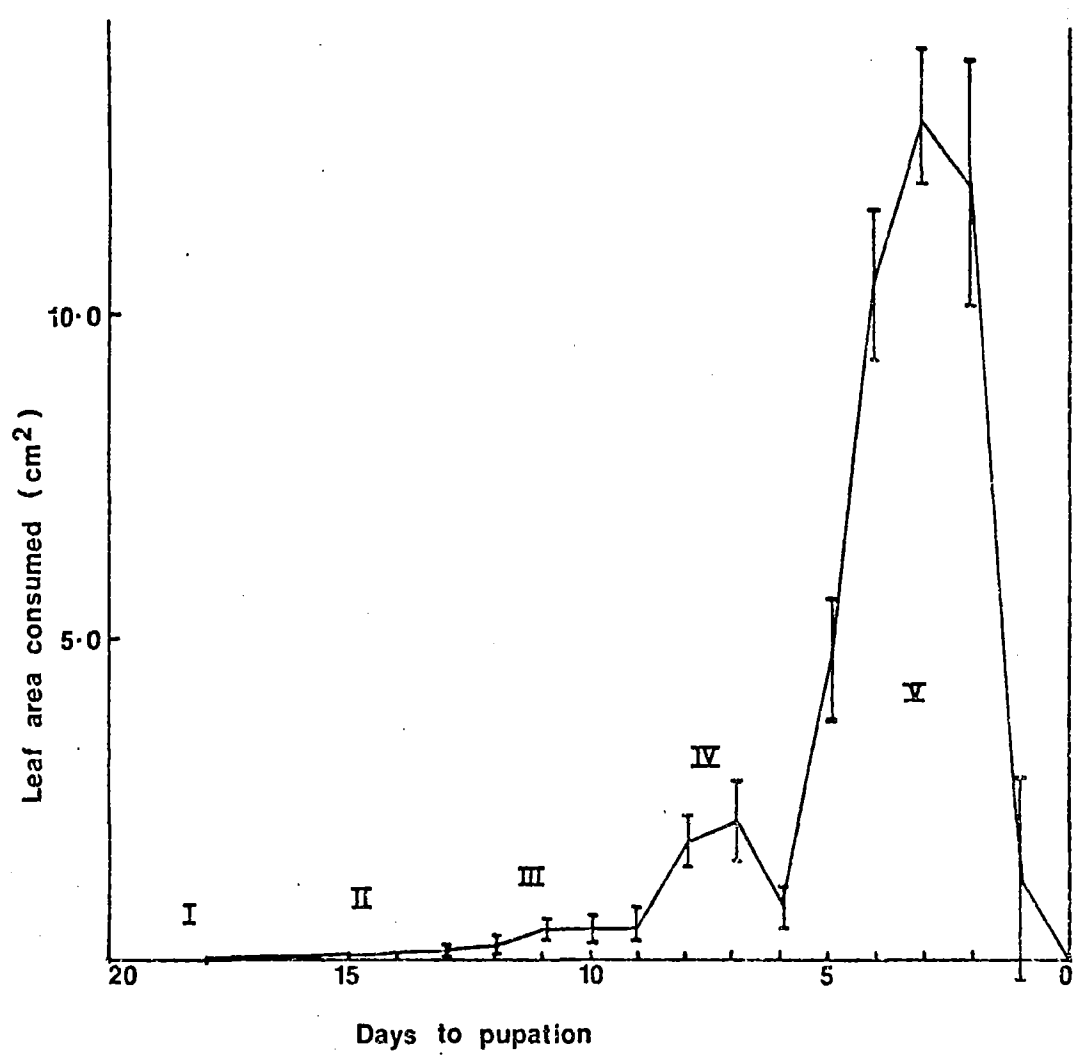


Fig. 5.2. Daily feeding of white butterfly larvae on Brussels sprout leaves at 20°C. Vertical lines represent standard errors. I - V, larval instars one to five.

Slansky and Feeny (1977) have shown that total consumption will increase from 119 to 212 mg for fifth instar larvae with decreasing nitrogen levels of fertilized collards (Brassica oleracea var. asephala). This explanation is supported by the fact that the mean pupal dry weight in the field was 43.8 ± 2.1 mg - approximately that predicted from the linear regression model for a temperature of 18-20°C.

b. Diamondback moth

The food eaten and time taken for the development of each instar on Brussels sprouts is shown in Table 5.3 using pooled data from both trials of Experiment 1.

TABLE 5.3 Development time and leaf area consumption by instars of diamondback moth feeding on Brussels sprout leaves at 25°C. Mean values \pm SE.

	Instar			
	I	II	III	IV
Development time (days)	1.9 \pm 0.04	2.6 \pm 0.26	3.0 \pm 0.34	4.0 \pm 0.27
Leaf area (mm ²)	1.4 \pm 0.3	7.7 \pm 0.8	31.0 \pm 3.9	302.8 \pm 19.6
% of total consumption in each instar	0.4	2.2	9.0	88.3

Survival of larvae in the first trial was low (40%) with most mortality occurring before the transition from leaf mining to leaf eating stage. It appeared that this high mortality was due to some qualitative factor in the leaf, possibly cuticle thickness, which also retarded the growth of the larvae because the mean development time for the first instar of surviving larvae was 1.9 days compared with 3.6 days for those that subsequently died. Survival in the second section, where larvae were placed on the plants in the second instar, was higher, 60%. The bulk of consumption took place in the final instar with female larvae consuming significantly more than the males ($P < 0.05$) (Fig. 5.3). Female pupae were also significantly heavier ($P < 0.01$) than the males, 16.5 mg and 11.7 mg dry weight respectively.

The effects of temperature on feeding and development of third and fourth instar larvae in Experiment 2 are presented in Table 5.4. Survival of larvae in this experiment was 85%. With each increase in temperature there was a significant decrease ($P < 0.05$) in the duration of the larval stage. While differences in consumption due to temperature were not significant, a trend of decreasing pupal weights emerged with increasing temperatures. The mean female pupal weight in this experiment was 1.2 times that of the males.

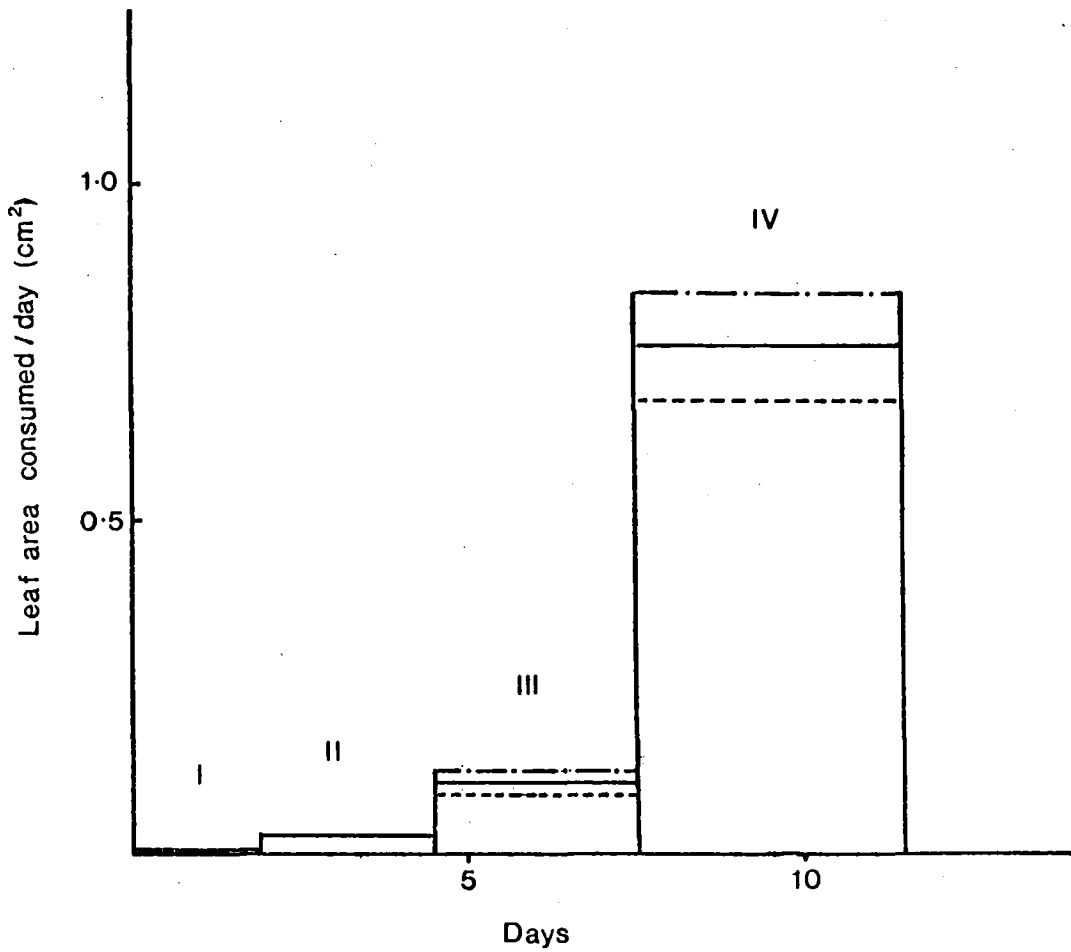


Fig. 5.3. Daily consumption of Brussels sprout leaf by diamondback moth larvae. I - IV, larval instars one to four. —, mean; ---, male; and -.-, female consumption.

TABLE 5.4 Effect of temperature on development time, consumption and pupal weight of diamondback moth feeding on turnip leaves.
Mean values \pm SE.

	Temperature			n
	Development time instars III and IV	Leaf area consumed (mm ²)	Pupal weight (fresh mg)	
15	11.7 \pm 0.33 a	387.7 \pm 44.32 a	¹ 67.4 \pm 2.98 a	6
20	7.9 \pm 0.30 b	287.8 \pm 24.18 a	63.6 \pm 3.71 ab	8
25	5.2 \pm 0.56 c	237.9 \pm 40.37 a	61.8 \pm 1.98 ab	9
30	3.9 \pm 0.23 d	329.5 \pm 20.98 a	55.7 \pm 3.09 b	10

¹Means adjusted with larval sex as covariate.

4. Discussion

a. Larval development rates

The relationship between temperature and development rate is shown in Figures 5.4 and 5.5 for white butterfly and diamondback moth respectively, using data from the experiments outlined above as well as those from earlier workers. For both insects the relationship tends to be linear except for some deviation at low temperature. However, as Wigglesworth (1974) explained, the relationship between the development of insects and temperature takes the form of a sigmoid curve with low rates or nil development taking place at both high and low extremes. The

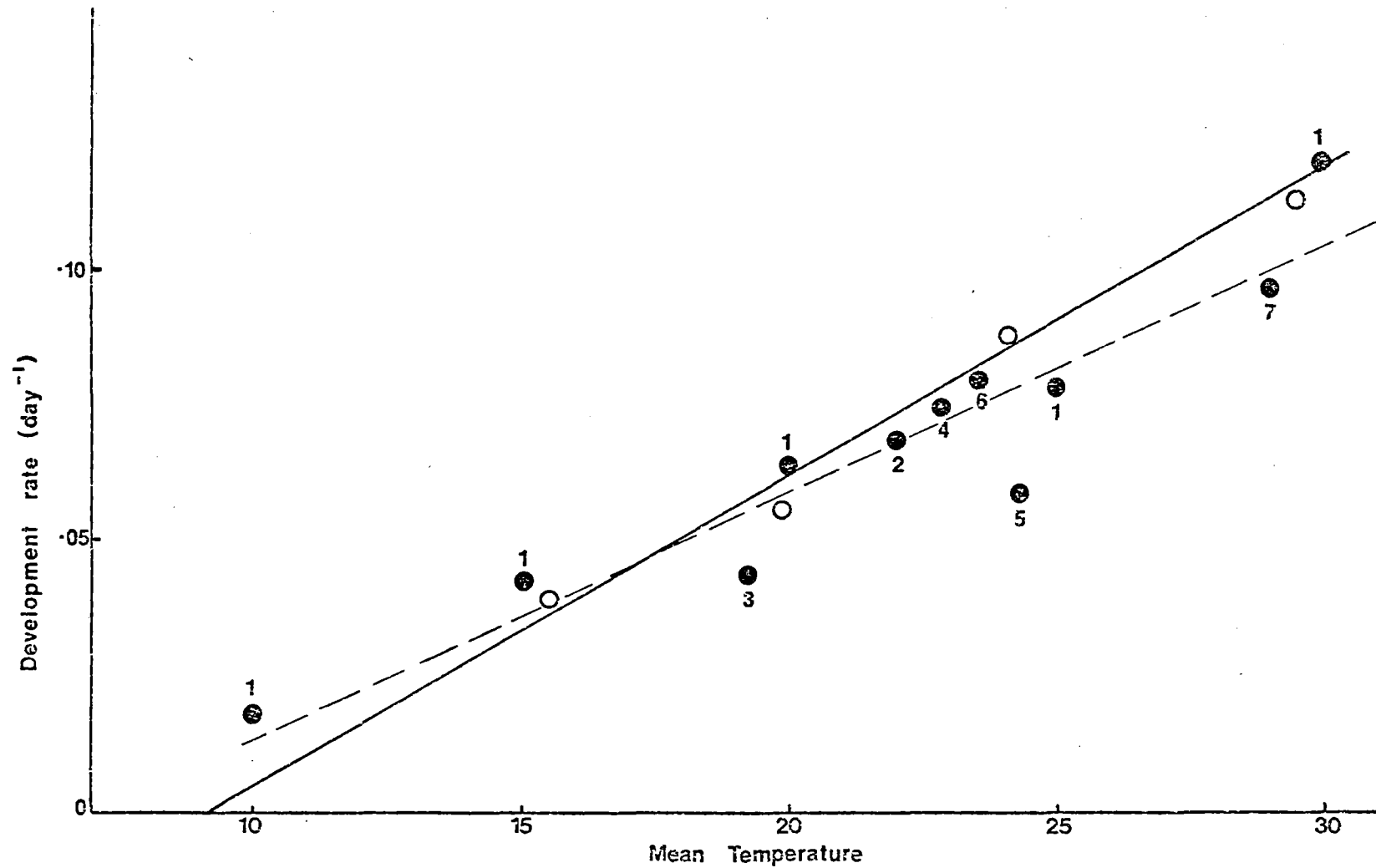


Fig.5.4. The effect of temperature on the development rate (DR) of *Artogeia rapae* larvae. O , mean results from the present study ($DR = 0.0057T - 0.0518$, $r = 0.95^{**}$). Results from earlier workers, ● : 1, Peairs (1927); 2, Given (1944); 3, Richards (1940); 4, Harcourt *et al* (1955) 5 , Rahman (1970); 6, Parker & Pinnell (1973); 7 , Smith & Smilowitz (1976). Overall regression, $DR = 0.0046T - 0.0330$, $r = 0.94^{**}$

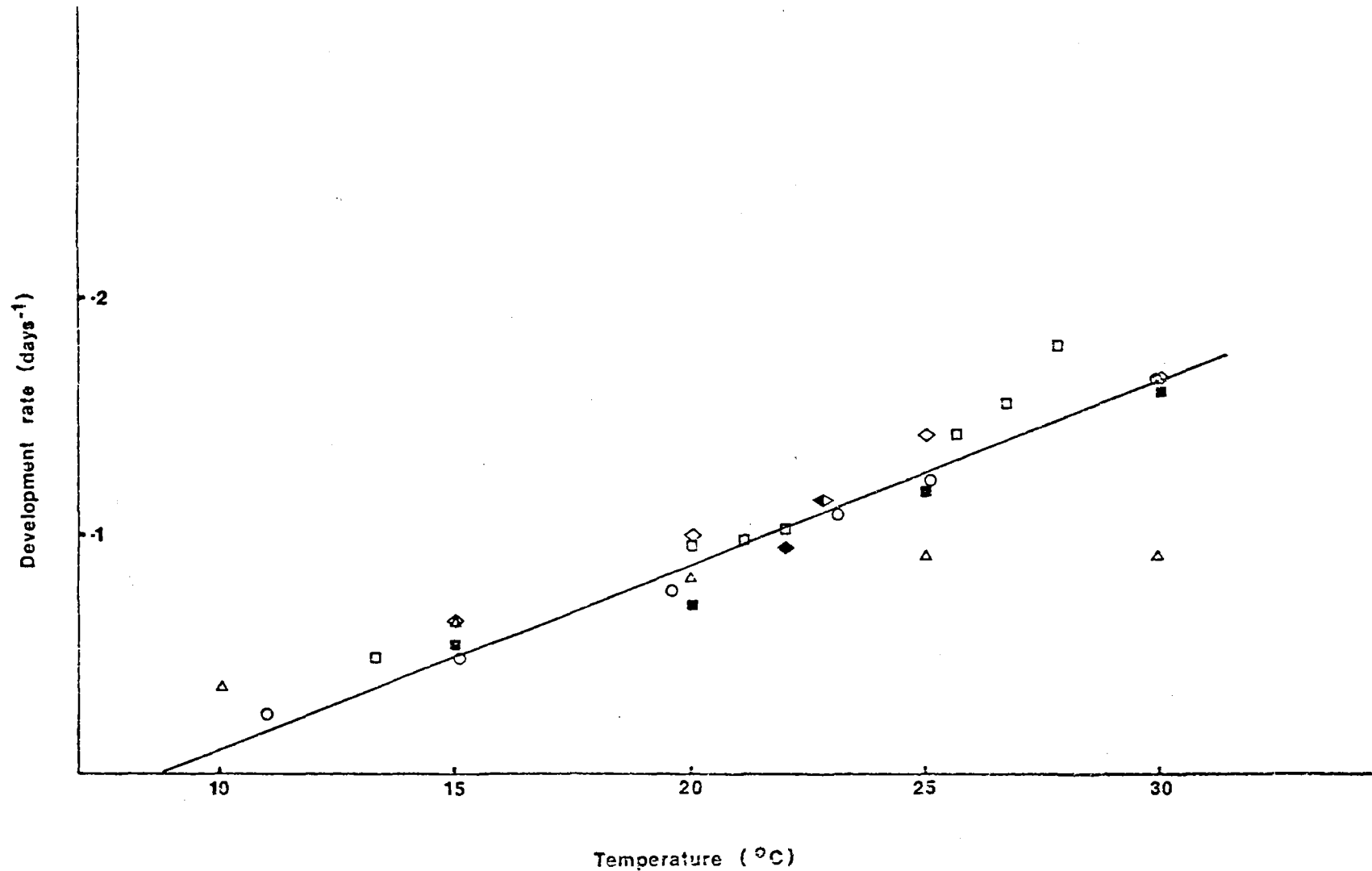


Fig. 5.5. Effect of temperature on the development of *Plutella xylostella* larvae. ■, mean results from the present study. ($DR = 0.0078T - 0.068$, $r = 0.89^{**}$). Results from earlier workers; ◇, Hardy (1938); ◆, Given (1944); □, Miner (1947); ◈, Harcourt (1966); ○, Stepanova (1962); △, Chen & Su (1978). Overall regression, $DR = 0.007T - 0.053$, $r = 0.90^{**}$.

assumption of linearity over the central portion of the curve has been utilised in the estimation of developmental threshold temperatures and the thermal constant for development (Chiang, 1978). These parameters, estimated from the present data, are 175 DD above 9.1°C and 128 DD above 8.7°C for white butterfly and diamondback moth respectively. The results are lower than those, 208 DD above 7.17°C for white butterfly and 148 DD above 6.8°C for diamondback moth calculated from all available data in Figures 5.4 and 5.5. The lower temperature thresholds obtained in both cases from the total data may be due to the inclusion of low temperature data which breaks from linearity to conform to the sigmoid relationship, although Umeya and Yamada (1973) have shown that local differences can occur in the developmental characteristics of diamondback moth. In Taiwan, Chen and Su (1978) suggested that the development rate of diamondback moth reaches a maximum at 25°C but this does not seem to be borne out in this or other experiments.

b. Larval consumption

White butterfly consumed an average of 43.81 cm^2 of the leaves of glasshouse grown Brussels sprouts. This was 12.8 times the consumption by diamondback larvae which consumed an average of 3.43 cm^2 of leaf area. Similar results were obtained by Parker and Pinnell (1973) who recorded a mean leaf area consumption by white

butterfly on cabbage of 42.68 cm^2 and Taylor and Bardner (1968a) who recorded a mean of 3.74 cm^2 turnip leaf consumed by diamondback moth larvae. Chen and Su (1978) reported feeding of the latter ranging between 3 and 12 cm^2 per larvae with the highest levels recorded at low temperatures. A similar ratio of consumption between the two pests to that in this study, 12.8:1, was found by Given (1944).

For both species consumption increased markedly with stage of development and in each over 85% of consumption took place in the final instar. In reviewing feeding studies, Waldbauer (1968) also found that the bulk of food was eaten by the later instars, particularly for lepidopterous larvae. More specifically, Parker and Pinnell (1973) reported 85% of total consumption by fifth instar larvae of white butterfly but, for diamondback moth, Chen and Su (1978) calculated only 60% of consumption by fourth instar larvae reared on cauliflower at 25°C . However, their method of calculation would tend to underestimate consumption at this stage as their experiment was terminated when only half the larvae had pupated.

Pupal weight decreased with increasing temperature, for both species. However, such variations in pupal weight according to the temperature of development are not uncommon. Danthanarayana (1975) found that pupae of Epiphyas postvittata (Walker) were lighter when reared at 25°C than at 20°C and he observed that in the field

heavier individuals occurred during cool conditions. Pupal weights of Trichoplusia ni (Hubner) were also found to vary with temperature (Boldt et al., 1975) where maximum weight occurred at 25°C corresponding to the maximum consumption of soybean foliage.

c. Larval feeding rate

In assessing the impact of a pest on a crop, absolute feeding will be of less importance than the rate of feeding in relation to the stage and rate of growth of the crop. For both pests the rate of feeding increased with increasing temperature. This is shown for white butterfly in Figure 5.6 where the feeding rate (FR) clearly increased with temperature ($FR = 0.140T - 0.092$, $r = 0.80$, 33 df), but at a lesser rate than would be expected from the development curve. If 15°C is set as a base measurement for development and feeding it can be shown that while development rate increases by three times between 15°C and 27°C the feeding rate will increase by only 1.8 times. Extrapolation of the relationship between feeding and temperature reveals a feeding threshold of 1.5°C, far below the development threshold of 9.1°C estimated earlier. This indicates that feeding continues, albeit at a slow rate, at temperatures where development is very slow or has stopped, a feature that has, in fact, been noted among larvae stored at low temperatures.

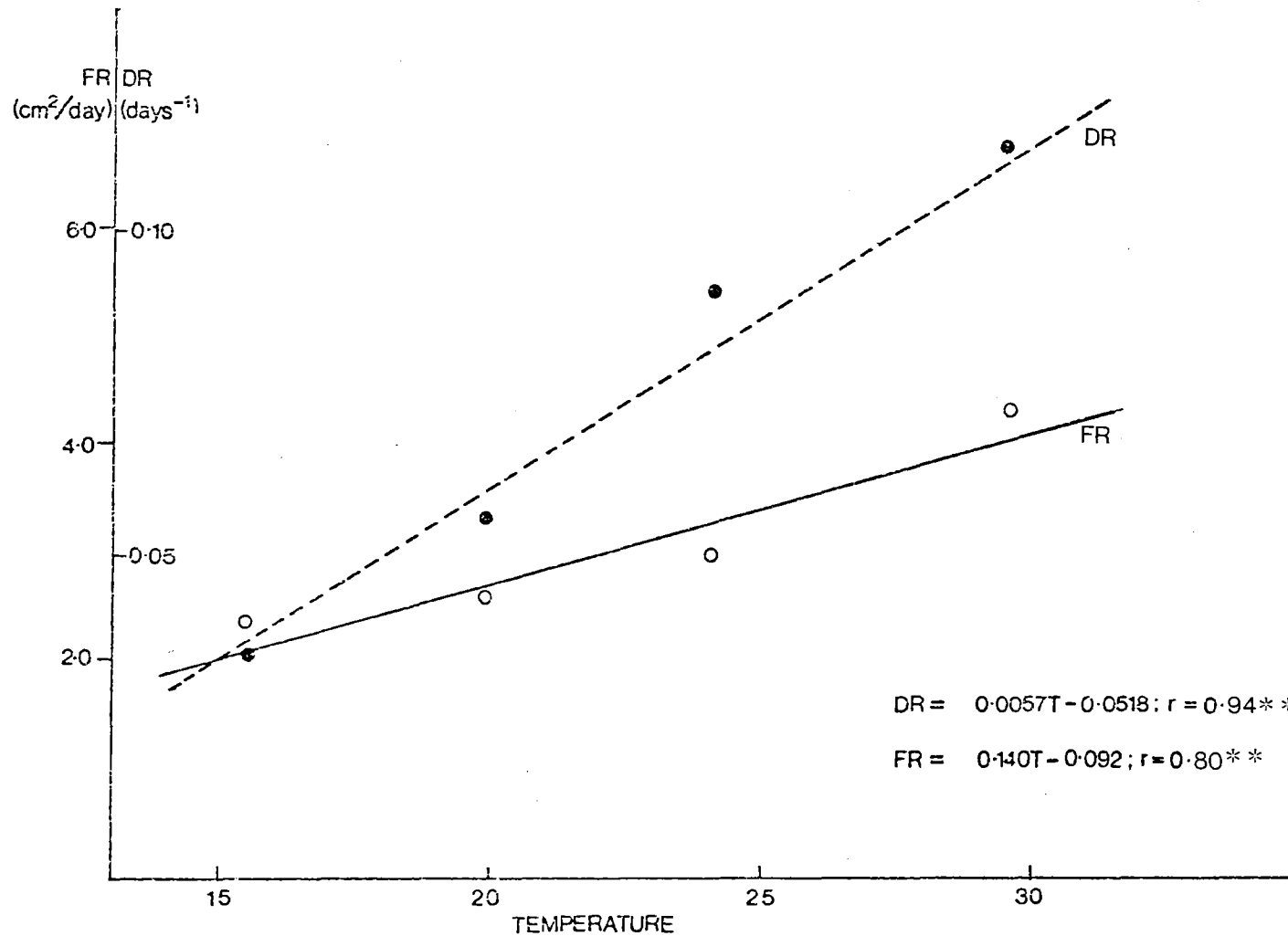


Fig. 5.6. The effect of temperature on mean feeding rate (FR) and development rate (DR) of white butterfly larvae feeding on Brussels sprout leaves. Development rate (●) and mean feeding rate (O) at each temperature.

The relationship between temperature and feeding for each instar is presented in Table 5.5. The daily feeding of a population of white butterfly larvae can therefore be represented by the model:

$$\text{Daily feeding (WB)} = N_1 C_1 + N_2 C_2 + N_3 C_3 + N_4 C_4 + N_5 C_5$$

where N refers to the number in each instar and C is the relationship between temperature and feeding for each instar given in Table 5.5. A similar model may be constructed for diamondback moth utilizing feeding rates for the third and fourth instars, where the majority of feeding occurs:

$$\text{Daily feeding (DBM)} = N_3 C(\text{DBM})_3 + N_4 C(\text{DBM})_4$$

with C(DBM) values as presented in Table 5.6.

The models thus developed may need adjustment for host plant stage and quality as well as for competition between pests but can provide a satisfactory approximation of the feeding of the larvae in normal conditions. For example, the predicted output of the feeding model for white butterfly can be compared with field collected data from Experiment 1. After adjustment for lower absolute consumption of leaf area in the field, there is a close relationship between the model output and observed values for the feeding rate of larvae during the experiment (Fig. 5.7).

TABLE 5.5 The effect of temperature on daily leaf area consumption (C) (cm²/day) of each larval instar of white butterfly feeding on Brussels sprout leaves.

Instar	Temperature (°C)				Regression equation	Correlation Coefficient (33df)
	15	20	25	30		
I	0.026	0.038	0.048	0.067	$C_1 = -0.014 + 0.003T$	0.59**
II	0.027	0.134	0.155	0.150	$C_2 = 0.050 + 0.004T$	0.46**
III	0.363	0.426	0.531	0.654	$C_3 = 0.025 + 0.021T$	0.53**
IV	1.154	1.497	1.765	2.050	$C_4 = 0.235 + 0.062T$	0.63**
V	6.856	8.190	7.563	11.790	$C_5 = 1.275 + 0.335T$	0.66**
Larval No.	8	10	8	9		(**, P < 0.01)

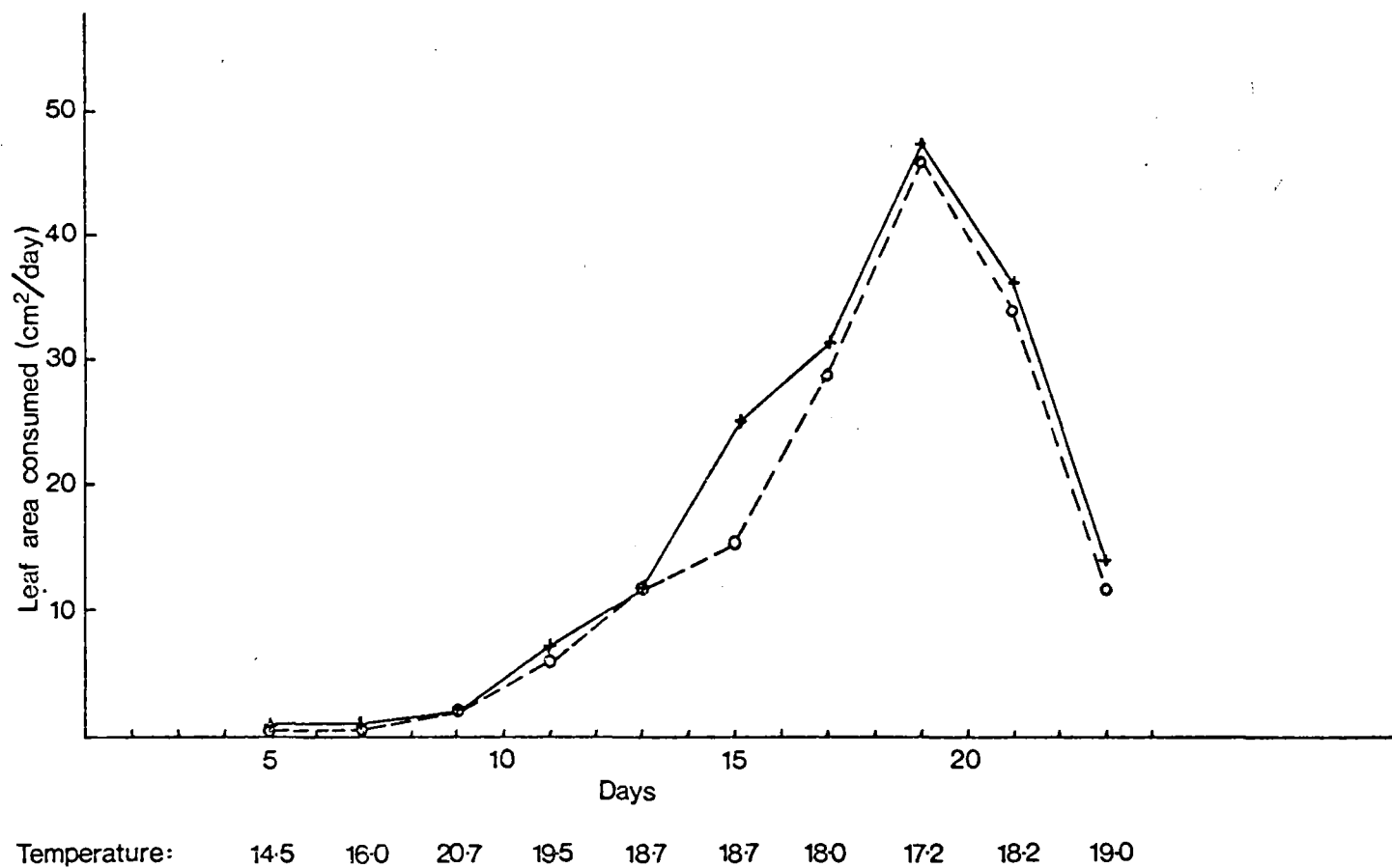


Fig. 5.7. Model output (O) and actual feeding (+) of white butterfly feeding on a field crop of Brussels sprouts.

The importance of temperature in the models can be seen in Table 5.7 where the rate of feeding of a final instar larvae of each pest has been calculated from the feeding rate curve, in relation to the mean monthly temperatures throughout the period of sprout growth. It is clear that the rate of consumption declines markedly throughout the autumn months. The use of mean temperatures in the model is also an oversimplification since even on days with mean temperatures below the threshold the daily temperature peak will often exceed it. To overcome this Poston et al. (1978) used the concept of accumulated heat in constructing a model for leaf consumption by painted lady (Cynthia cardui L.) larvae on soybeans but their model does not take into account the variations that occur in absolute feeding as a result of temperature variation or the differences that may occur between developmental and feeding thresholds. Thus while both types of model can give results that approximate feeding by natural populations their improvement depends on a better understanding of the relationship between development and feeding since the amount of feeding is clearly dependent on both the accumulation of heat and the temperature at which it accumulates.

TABLE 5.6 The effect of temperature on mean daily consumption (C(DBM) mm²/day) by third and fourth instar diamondback moth larvae feeding on turnip leaves.

Instar	Temperature (T) (°C)				Regression equation	Correlation coefficient (31 df)
	15	20	25	30		
III	7.3	6.7	12.8	17.5	C(DBM) 3 = 1.06T - 11.54	0.57**
IV	57.7	68.4	112.8	137.4	C(DBM) 4 = 7.11T - 57.87	0.64**
Larval No.	6	8	9	10		(**, P<0.01)

TABLE 5.7 Comparison of mean monthly temperatures in Canterbury with the estimated white butterfly fifth instar larval feeding rates throughout the period of Brussels sprout growth.

	Month					
	Jan.	Feb.	Mar.	Apr.	May	June
Mean temp. (°C)	16.0	15.8	14.1	11.4	8.1	5.6
Mean feeding rate (cm ² /day)	6.63	5.29	4.72	5.09	3.99	3.15

CHAPTER 6

PLANT GROWTH AND RESPONSE TO
DEFOLIATION1. Introduction

To understand the impact of pests on a crop it is necessary to be aware of the growth pattern of the plant and its responses to insect attack. The former aspect of Brussels sprout growth has been studied in Europe (Jones, 1972; Fisher and Milbourn, 1974; Fisher, 1974a, b; Berntsen, 1975) but there is little information available on the effects of insect pests on growth and yield of the crop.

Brussels sprouts are widely grown throughout Western Europe, needing both a long cool growing season and winters where frosts do not exceed -10 to -15°C (Kronenburg, 1975). They are either direct sown in spring, or, more commonly, sown in seed beds and transplanted into the field at densities ranging from $1.2 - 4.8$ plants/m² (Nieuwhof, 1969). After transplanting, leaf growth is rapid with maximum leaf area index reached in early autumn followed by the senescence of older leaves (Jones, 1972). Stopping, or removal of the apical bud, takes place in autumn approximately two months before harvesting and results in a more even pattern of sprouts on the stem (Fisher, 1974a) and can also increase yields (Berntsen,

1975). In England, the axillary bud, i.e. the sprout, starts to form in August but rapid bud growth does not begin until September (Fisher and Milbourn, 1974). The sprouts may be picked over as many as five times during harvesting (Nieuwhof, 1969) or alternatively, single destructive harvests may be made, stripping all sprouts from the stem at one time (Fisher, 1974b). Hand picking is often used for sprouts sold on the fresh market while single harvests are more common for processing sprouts. At harvest, sprout dry weight accounts for between 25 and 40% of total plant weight (Fisher and Milbourn, 1974).

In this chapter the growth pattern of the Brussels sprout plant in Canterbury will be examined as well as its response to artificial defoliation designed to simulate pest attack. Experiment 6.1 took place in the 1977/78 growing season while all others occurred in the 1978/79 season. The Brussels sprout variety Jade Cross, was used in all experiments. Experiment 6.5 also included other varieties for a comparison of growth patterns. Details of the site and management of the crop are given in Chapter 3.

2. Materials and Methods

- a. Experiment 6.1. The effects of defoliation on the growth pattern and yield of Brussels sprouts.

In this experiment the effects of defoliation on growth and yield of Brussels sprouts were examined using two sowing dates in a split-plot experiment. Main plot

treatments, i.e. sowing times, were completely randomised as were the 23 sub-plot treatments presented in Table 6.1. Treatments 1 - 13 were designed to examine the effects of three levels of defoliation, 25, 50 and 75%, at four stages of growth with a common control. Treatments 14 - 23 were designed to reveal, by sequential harvests, the growth pattern of undefoliated plants and the effects of 50% defoliation at four stages of growth on the subsequent growth of the plant. The experimental layout is shown in Figure 3.1, Beds A and B. There were three three-row plots from each sowing time, each consisting of 276 plants in sub-plots of 12 plants (3 x 4). Details of the crop growth and management were presented in Chapter 3. Defoliation was carried out by cutting alongside the leaf midrib with scissors in accordance with the procedure described by Jackson (1980) (Plates 6.1 and 6.2). At each sampling the two centre plants in each plot were removed and taken to the laboratory where each plant was divided into leaves, petioles, crown, stem and sprouts. Leaf area was measured using a Licor No. 3150 leaf area meter and component plant parts were oven-dried at 70°C to a constant weight to provide dry matter measurements.

TABLE 6.1 Treatments for Experiment 1, 1977/78, showing level and time of defoliation and time of harvesting of Brussels sprouts.

Treatment number	Defoliation		Harvest time	Treatment number	Defoliation		Harvest time
	Level	Time			Level	Time	
1	0	-	V	14	0	-	I
2	25	I	V	15	0	-	II
3	50	I	V	16	0	-	III
4	75	I	V	17	0	-	IV
5	25	II	V	18	50	I	II
6	50	II	V	19	50	I	III
7	75	II	V	20	50	I	IV
8	25	III	V	21	50	II	III
9	50	III	V	22	50	II	IV
10	75	III	V	23	50	III	IV
11	25	IV	V				
12	50	IV	V				
13	75	IV	V				

Times	I	II	III	IV	V
Sowing 1	11/1	13/2	20/3	20/4	6/6
Sowing 2	13/2	20/3	20/4	18/5	16/6



Plate 6.1 Artificial defoliation of Brussels sprouts.
50% defoliation, 16 February 1978.



Plate 6.2 Artificial defoliation of Brussels sprouts.
75% defoliation, 16 February 1978.

- b. Experiment 6.2 The effects of early defoliation on the subsequent growth pattern of Brussels sprouts, 1978/79.

In this experiment the effects of early defoliation on subsequent plant growth were examined in a randomised block design using plants from Beds A and B (Fig. 3.2). There were five blocks, each of three rows of 13 plants. Each block was surrounded by a guard row. Each row within the block was randomly allocated one of three treatments; no defoliation, 50% defoliation or 100% defoliation and defoliation took place on 14 February, 1979. Every second plant within the row was randomly allocated a sampling date at any one of three-weekly intervals when it was removed at ground level and taken to the laboratory.

In addition to the characteristics recorded in Experiment 6.1, leaf number and the number of leaf scars were recorded as well as stem height, sprout number and sprout fresh weight.

- c. Experiment 6.3. The effect of defoliation on yield of Brussels sprouts - season 2, 1978/79.

In this experiment the effects of different levels of defoliation on yield were again examined at times throughout the growing season corresponding to early, mid and late stages of growth. A 3 x 5 factorial, randomised block experiment was designed to examine

the effects of defoliation on the yield of Brussels sprouts. There were three defoliation times; 1 February, 13 March and 30 April; and five levels of defoliation; 0, 25, 50, 75, and 100%. Each of the six blocks of Brussels sprouts was divided into 15 plots of 12 plants (3 x 4) (Fig. 3.2, Beds A and B). Defoliation was carried out as in the previous season.

Intermediate harvests were not taken, but measurements of leaf number and sprout size were recorded throughout the later part of the growing season. At the final harvest, two plants were taken from the centre of each plot and, in the laboratory, sprout size in the upper, mid and lower zones was measured together with plant height and leaf area. The plant was divided into crown, leaves, petioles, stems and sprouts and oven dried as in Experiment 6.1.

- d. Experiment 6.4. The effect of leaf removal from different zones of the Brussels sprout plant.

In Chapter 4 it was shown that in the latter part of the growing season white butterfly larvae were aggregated in the upper part of the Brussels sprout plant. In order to assess the effects of defoliation in different plant zones the following 2 x 3 factorial experiment was carried out. Five sets of eight matched plants were selected from among adjacent, untreated plants in the completely sprayed plots (1) of Beds C and D in

the 1978/79 season (Fig. 3.2). The plants were divided into upper, mid and lower zones and leaves removed from individual zones or combinations of zones on 25 April. One sprout from each zone was then measured and marked with a spot of indelible ink. The marked sprouts were remeasured on the 7 May and on the 15 May the treated plants were harvested.

In the laboratory marked sprouts were removed from the stem, measured and weighed individually. Five sprouts were removed from the centre of each zone and weighed together and the total sprout weight was also recorded.

e. Experiment 6.5. Brussels sprout varieties - patterns of growth.

In 1978/79 the growth of seven varieties of Brussels sprouts, selected for differences in maturity times, was assessed in each of two beds, one under the regular spray schedule and the other unsprayed (Fig. 3.2, Beds B and E). Within each bed there were five blocks comprising seven rows by nine plants. On transplanting, varieties were assigned at random to rows within the block. To examine the growth characteristics of the varieties, leaf number and sprout size in upper, mid and lower zones were assessed in situ from Bed B. At harvest two plants were randomly selected from each row in Bed E and plant height, sprout weight and sprout number were assessed as well as damage to the sprouts which will be discussed in Chapter 7.

3. Results and Discussion

a. Pattern of plant growth. Experiments 6.1 and 6.2.

The pattern of plant growth, from both sowings in Experiment 6.1 and from the single sowing in Experiment 6.2 is shown, with curves fitted by eye, in Figure 6.1a and b (Appendices 6.i and ii). For all three sowings plant growth followed a similar pattern. An initial period of slow growth during establishment of the plant was followed by stem elongation and rapid leaf growth. The plant then entered a period of maturity when leaf growth and senescence were balanced with a rapid growth of both stem and sprouts. The final phase was one of senescence where total plant weight declined due to the loss of leaves and petioles. Data from the two sowings of Experiment 6.1 are combined in Figure 6.2 to show the general growth pattern for a Brussels sprout plant. In the first year, following early November sowing, peak leaf area occurred in March. A three week delay in sowing caused leaf area to reach a peak at the end of April. In 1978/79 initial growth was slower and leaf area reached a peak in mid April. Sprout weight increased rapidly from March onwards in both years while delayed planting delayed sprout formation. Sprout weight at harvest reached an average of 50% of the total dry weight of the aerial part of the plant in both years. This compared with 25-40% (Fisher and Milbourn, 1974) and 30-40% (Jones, 1972) in England where the total plant weight included the roots.

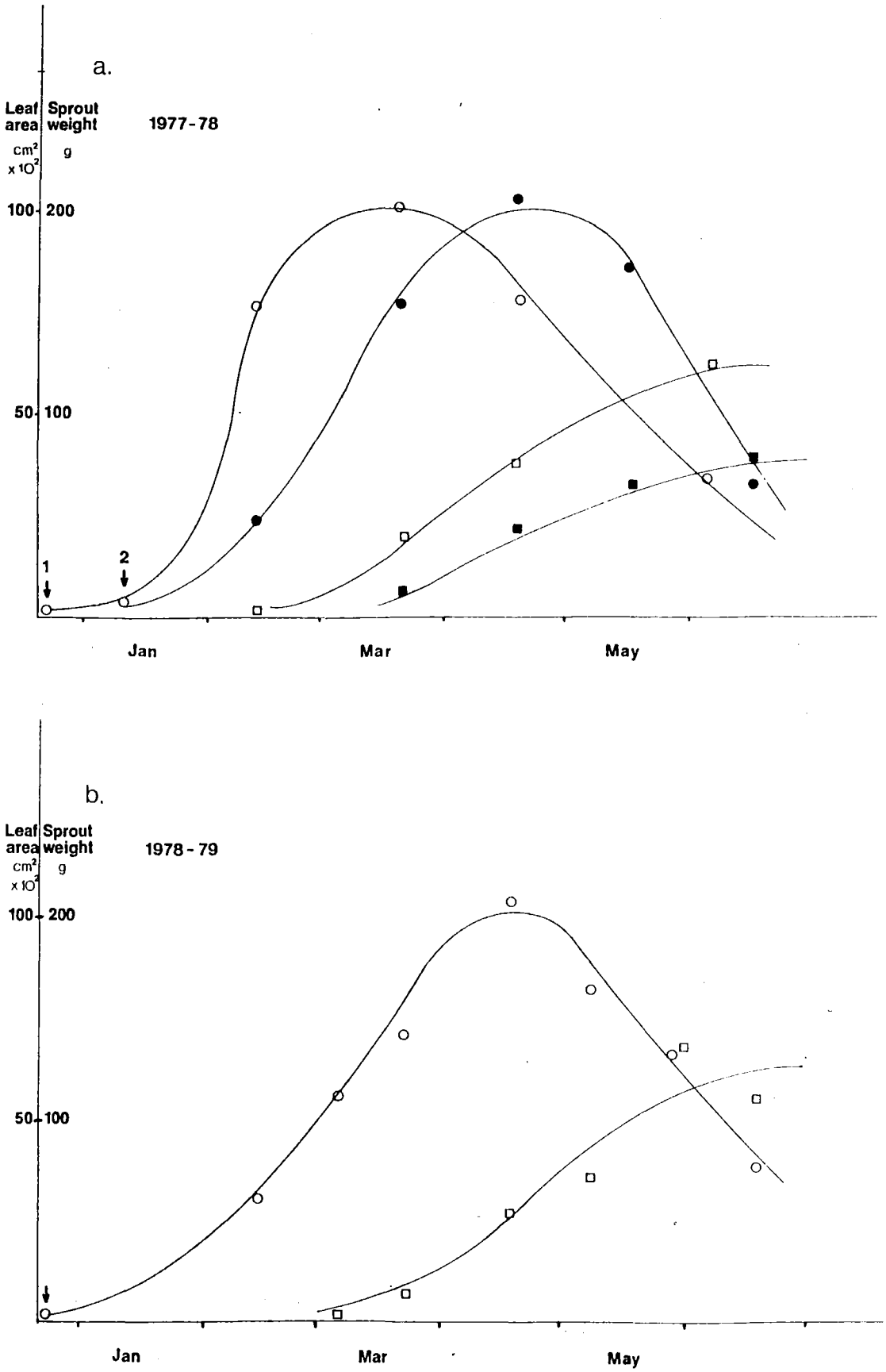


Fig. 6.1. The growth of undefoliated Brussels sprout plants.
(a) 1977/78; (b) 1978/79. (O), leaf area; (\square), sprout weight. \blacksquare 2nd sowing 1977/78. \downarrow Transplanting dates.

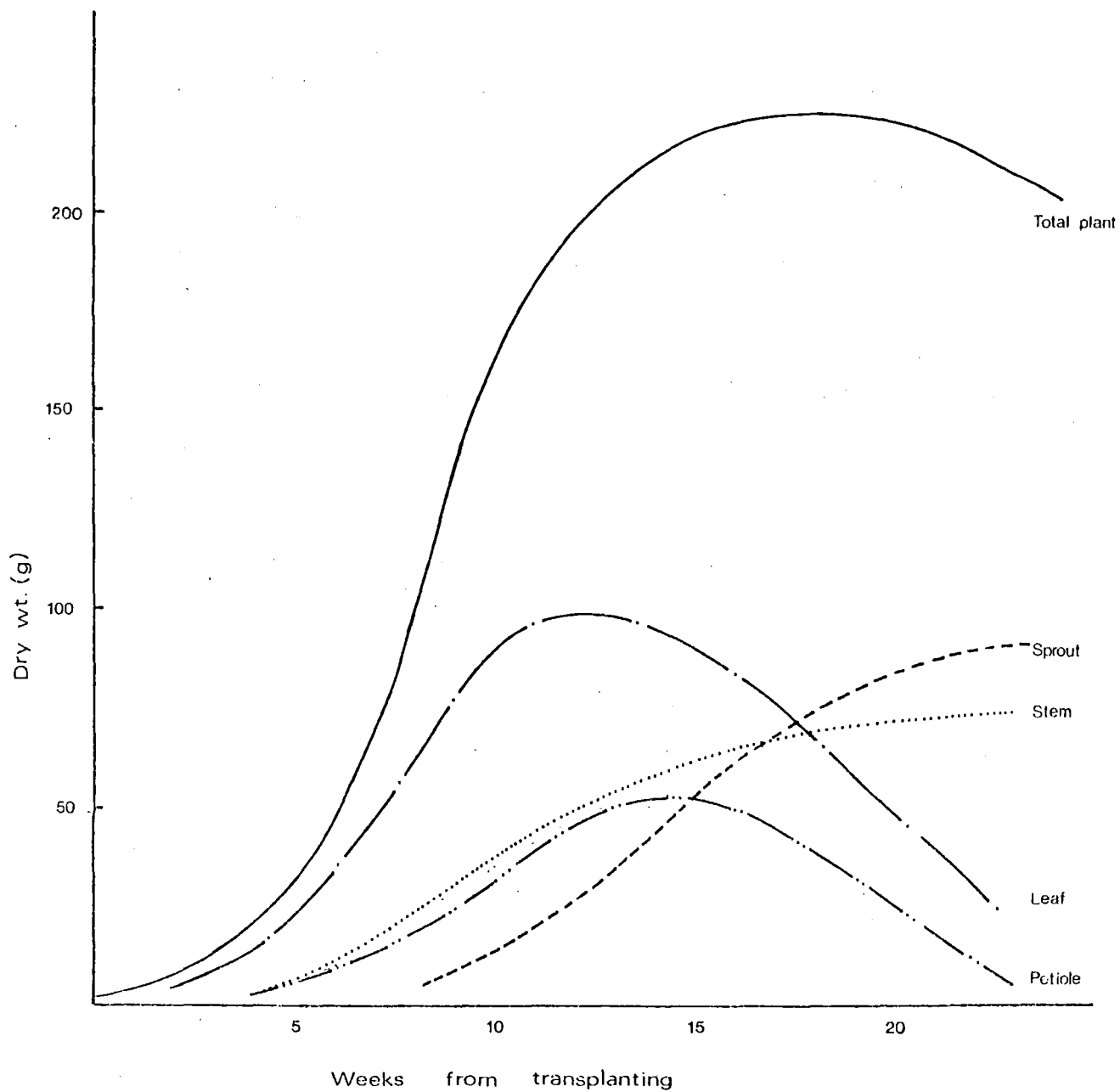


Fig. 6.2. Growth of Brussels sprout plant 1977/78 showing the accumulation of dry matter in component parts.

Fisher and Milbourn (1974) calculated that the contribution of roots to total weight was 20% at all stages throughout the plant growth while Jones (1972) calculated it as 10%. Mean yields from undefoliated plants in Experiments 6.1-3 varied from 105-111 g dry weight/plant, or approximately 700-800 g fresh weight/plant, which were higher than yields obtained for variety Jade Cross in Europe (Jones, 1972; Grainger, 1974; Berntsen, 1975).

Leaf area must be considered a major determinant of yield but its dimensions at any one time will be the results of two processes, new leaf growth and leaf senescence. The rate of leaf production reaches a maximum in late March (see Chapter 8) while senescence of older leaves seems to bear a linear relationship with time from April onwards (Fig. 6.3).

Sprout yield is the aggregate of the weight of individual sprouts borne in the leaf axils up the stem. The growth of sprouts in upper, mid and lower zones of the stem is shown in Figure 6.4. The growth of the lower zone sprouts is initiated first, followed by those in the mid zone and later in the upper zone. The result is a gradation from large to small sprouts up the stem, the characteristics of which may be altered by crop management practices such as spacing and stopping (Nieuwhof, 1969).

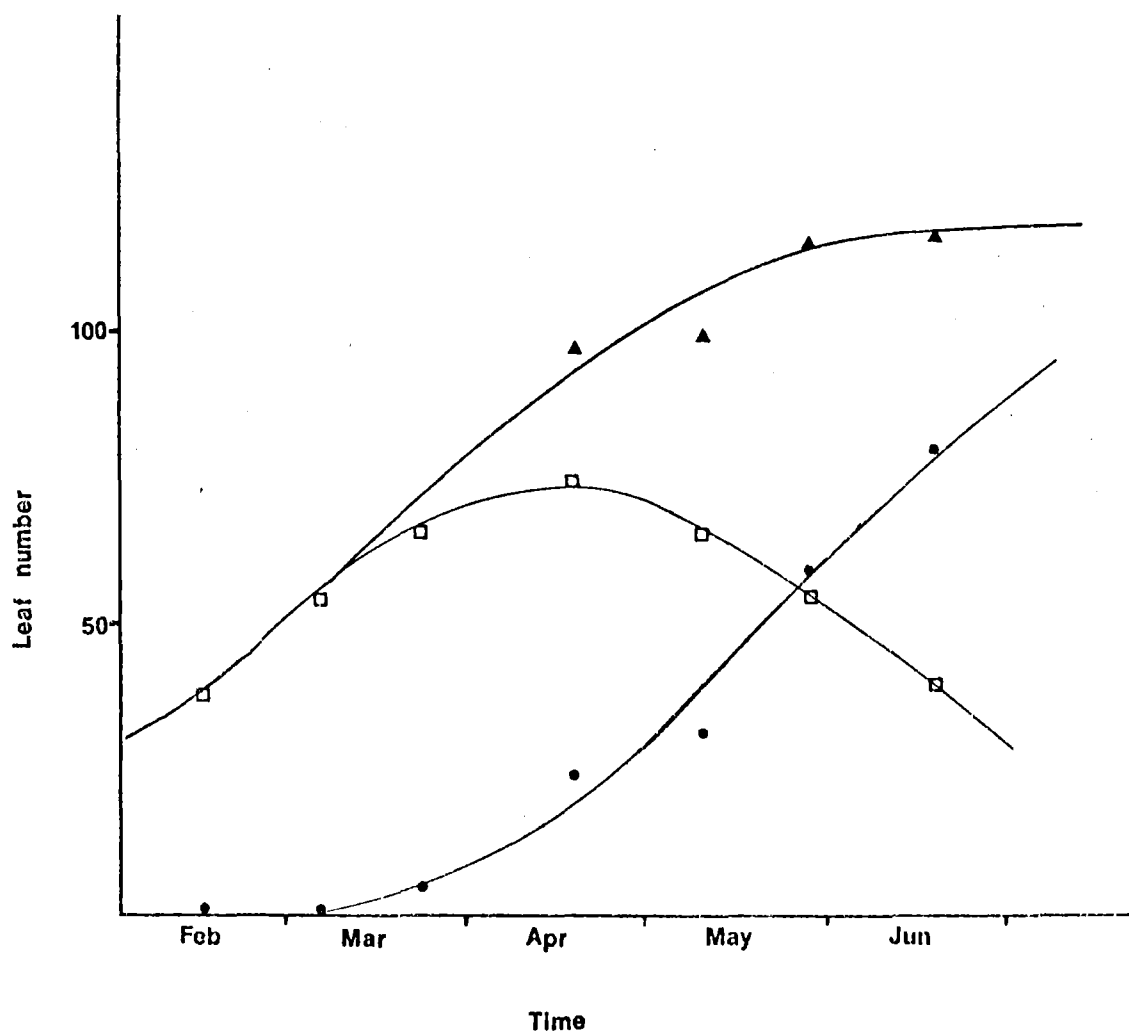


Fig. 6.3. Changes in Brussels sprout leaf number throughout the growing season. □ , actual leaf number; ● , senesced leaves; ▲ , cumulative leaf number.

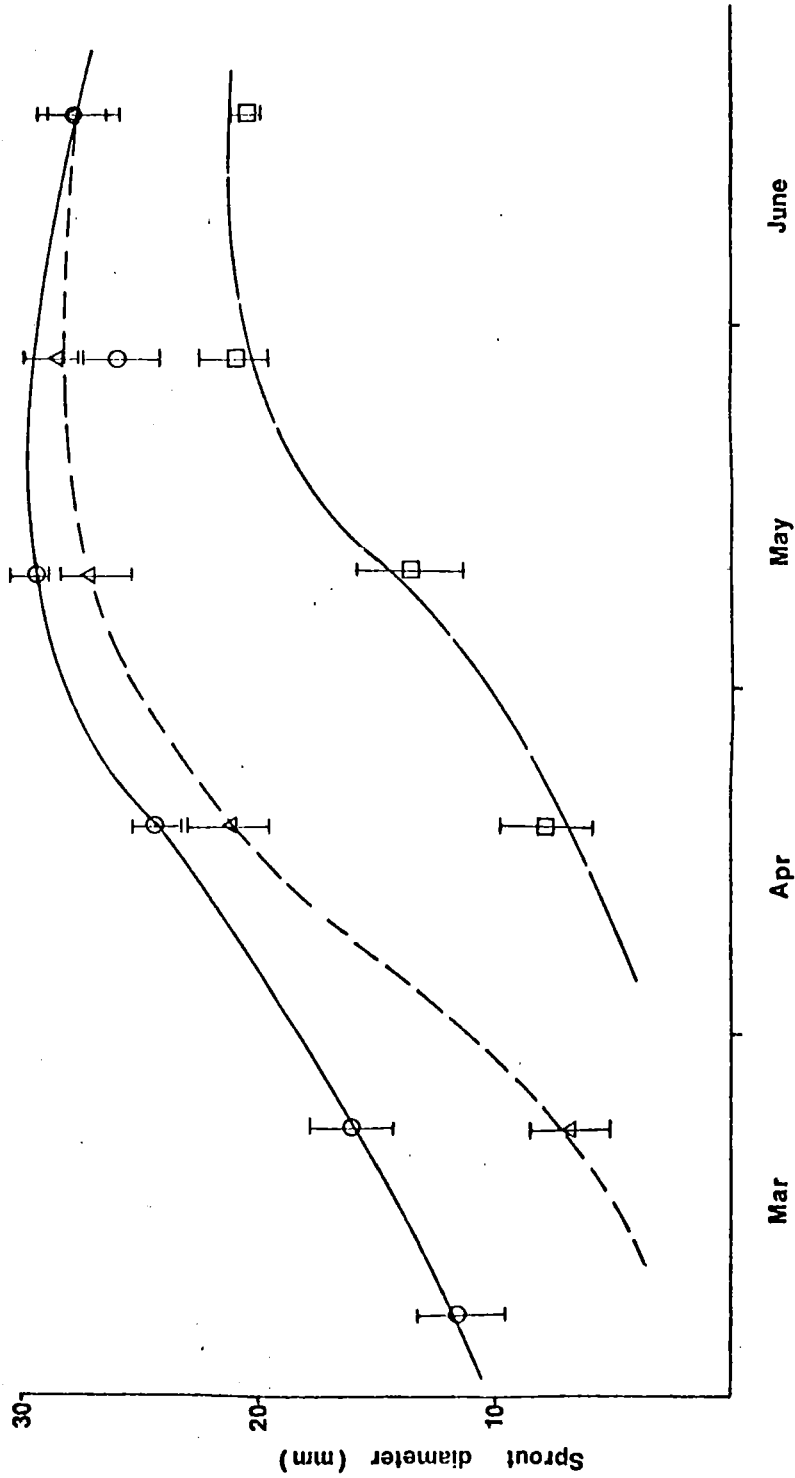


Fig. 6.4. Growth of sprouts in upper (□), mid (Δ) and lower (○) zones.

- b. The effect of defoliation on final harvest yield of Brussels sprouts. Experiments 6.1 and 6.3.

The effects of time and level of defoliation in both years are presented in Table 6.2. In Experiment 6.1 yields were significantly ($P < 0.05$) reduced following mid-season defoliation when compared to those after early or late defoliation and trend analysis (Denenburg, 1976) indicated a significant ($P < 0.05$) quadratic trend between the treatment means. At the highest level of defoliation (75%) yields were significantly lower than in any of the other treatments and trend analysis revealed a significant, negative, linear relationship between defoliation and yield. The mean yields from each level and time of defoliation are presented in Figure 6.5 and treatment means for each time of sowing in Appendix 6.iii.

In Experiment 6.3, mid-season defoliation again caused significantly greater ($P < 0.05$) yield loss than early or late season defoliation. Increasing levels of defoliation caused, in general, increased yield loss with significant linear, quadratic and cubic trends revealed by the method of orthogonal polynomials (Denenberg, 1976). The relationship between yield and the level of defoliation at each stage is shown in Figure 6.6 (Appendix 6.iv).

TABLE 6.2 The effect of level and stage of artificial defoliation on yield of Brussels sprouts. Experiments 6.1 and 6.3.

Level of defoliation	1977/78	1979/80
0	106	112
25	109	102
50	99	103
75	89	98
100	-	71
LSD(5%)	8(15) ¹	12
Linear trend	**	**
Quadratic trend	ns	**
Cubic trend	-	**

(1) LSD for comparison of common control with level of defoliation means.

Time of defoliation	1977/78		1978/79
I	105 ²	1 Feb	107
II	91	13 Mar	86
III	94	23 Apr	98
IV	105		
LSD(5%)	9		8
Linear trend	ns		-
Quadratic trend	**		-

(2) Means do not include control yield.

Footnote: The only significant interaction in 1977/78 was Time of sowing x Time of defoliation (quad.) x Level of defoliation (lin.) - 5% significant and in 1978/79 Time of defoliation x Level of defoliation (lin.) - 5% significant.

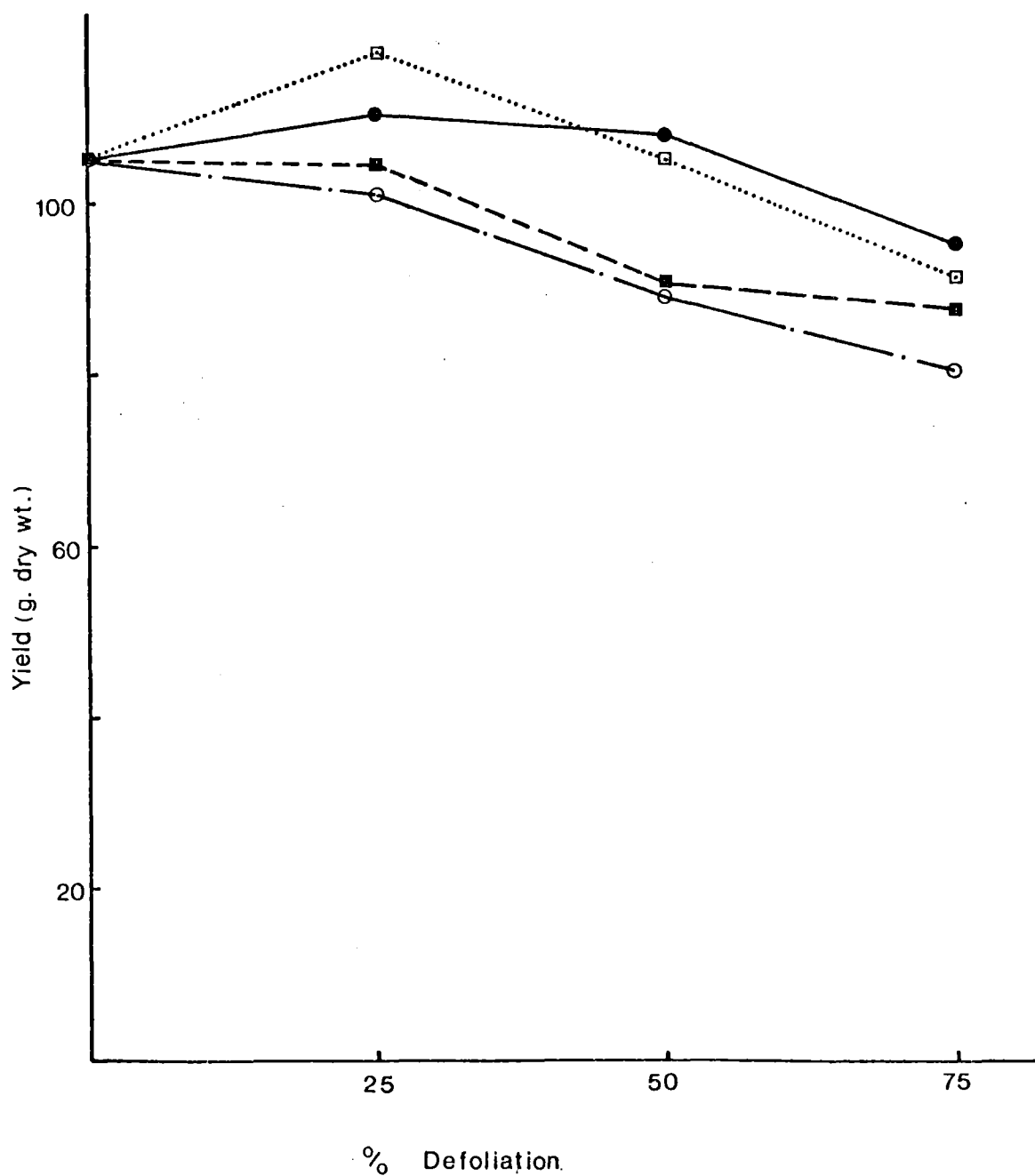


Fig. 6.5. The effect of defoliation of Brussels sprouts on sprout yield, 1977/78. (Experiment 6.1).

In each case there was a significant decrease ($P < 0.05$) in yield over the range of defoliation but it is clear that the shapes of these relationships vary between times of defoliation. Following early defoliation, trend analysis (Denenberg, 1976) indicated that the line of best fit contained a significant ($P < 0.05$) cubic element suggesting strong compensatory growth for intermediate levels of defoliation. After mid season defoliation, a significant ($P < 0.05$) quadratic trend indicates that as the level of defoliation increases the rate of yield loss increases; following late defoliation however, the relationship is best explained by a linear function ($P < 0.01$) with no significant improvement obtained by adding the quadratic or cubic terms (Appendix 6.iv).

It seems, therefore, that at the early growth stage there is high yield loss only with extreme levels of defoliation. Greatest yield loss will follow high levels of defoliation in the mid season. This has also also been found for potatoes (Cranshaw and Radcliffe, 1980) and sugar beet (Dunning and Winder, 1972) and it has been suggested that the plant is able to recover from early defoliation while for late defoliation a considerable portion of the product is already formed, hence defoliation has less effect. Following late defoliation the relationship tends to be linear but losses are low as demonstrated by its shallow slope (Fig. 6.6).

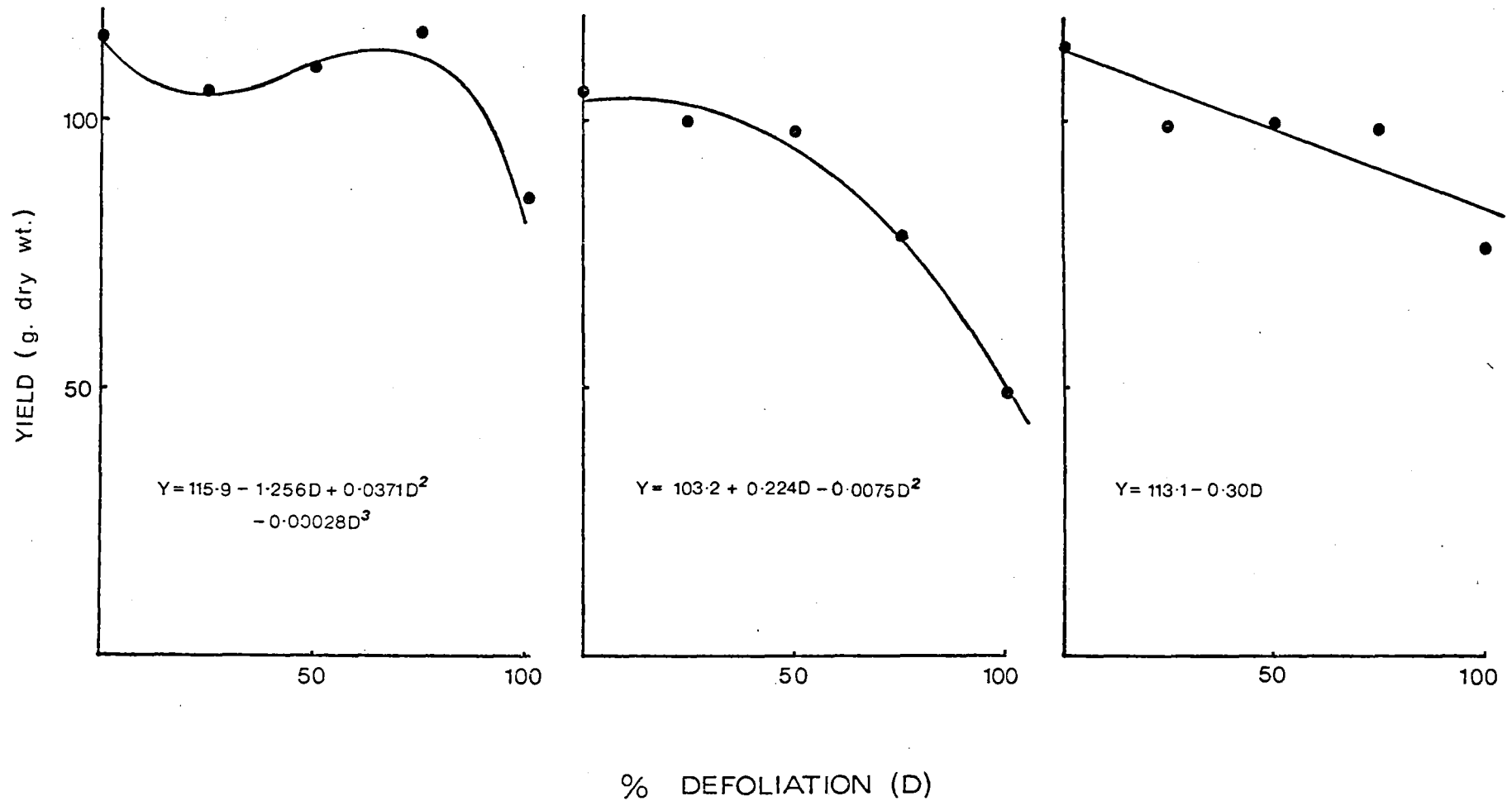


Fig. 6.6. Relationship between artificial defoliation of Brussels sprouts and sprout yield at three stages of growth. Defoliation dates; T1, 1 February; T2, 13 March; T3, 23 April 1979.

It seems clear, therefore, that defoliation can cause yield loss in Brussels sprouts but that the extent of the loss will vary with the growth stage of the plant. Thus, it is important to examine the growth of the plant to determine how defoliation interferes with the growth of the yield forming organs.

c. Effects of defoliation on the components of yield.
Experiment 6.3.

Fisher (1974b) defined the components of Brussels sprout yield to include the number of plants per metre², the number of sprouts per plant and the mean weight per sprout. In these experiments plant population was constant and set by transplanting. Hence, the effects of defoliation on sprout number and size deserve examination. The effects of time and level of defoliation on sprout number and mean sprout size are shown in Table 6.3. There was little variation in sprout numbers following defoliation and thus yield losses were the result of lower mean sprout weight following defoliation. Trends in the mean sprout weights closely reflect those from aggregate yield following defoliation (Table 6.2).

The time of defoliation has a considerable effect on the growth of sprouts from different zones. Measurements of sprout size following 0, 50 and 100% defoliation are shown in Figure 6.7. Early defoliation seems to have greatest effect on the lower and mid zones of sprout growth but with evidence of some compensation towards

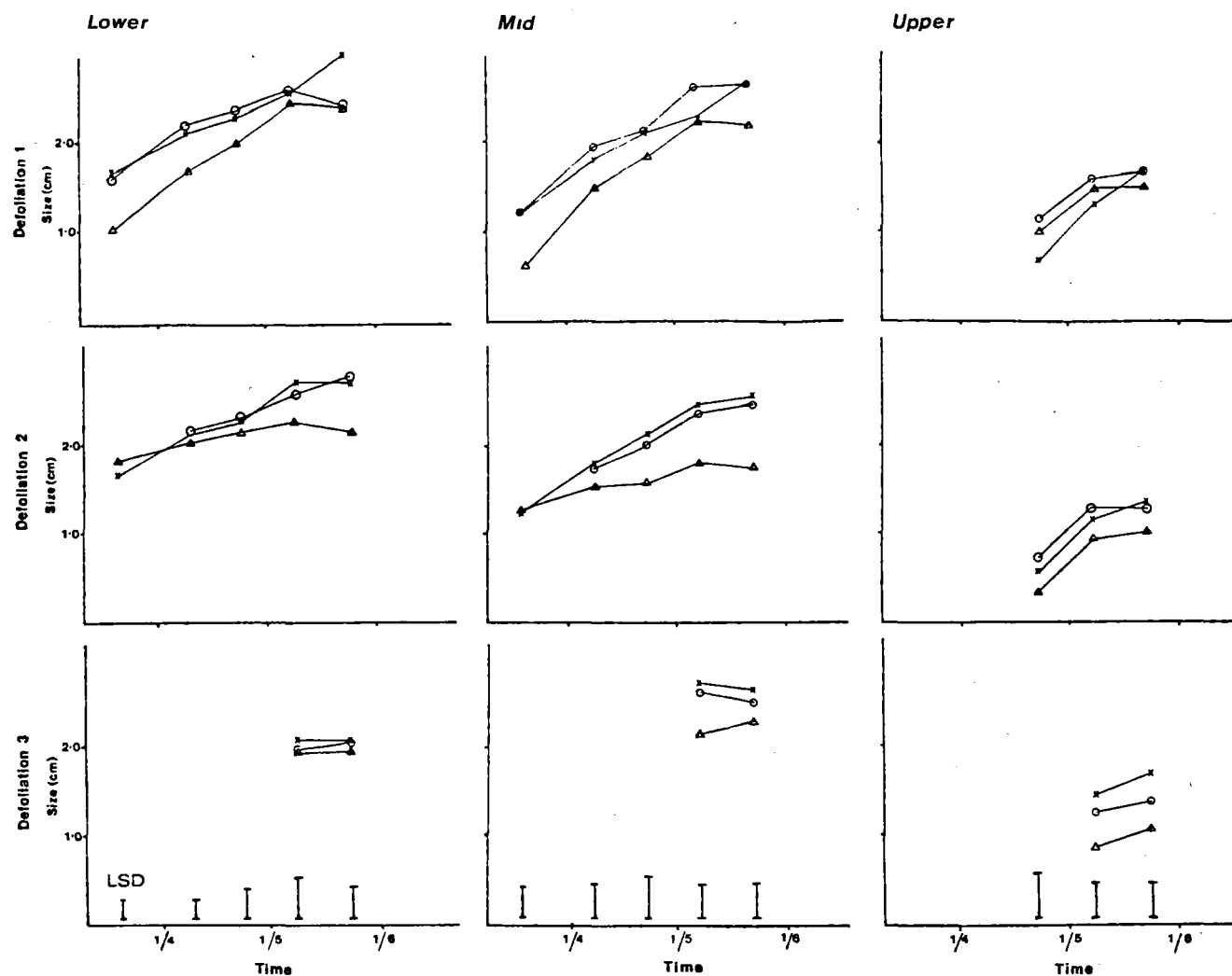


Fig. 6.7. Sprout growth in the upper, mid and lower zones following early (1 February), mid (13 March) and late (23 April) defoliations, 1979. Three defoliation levels shown; (+), control; (O), 50%; (Δ), 100%. LSD for comparison of treatment means within each time of defoliation.

harvest. Mid season defoliation affects all zones of sprouts but particularly those in the middle zone while late defoliation has apparently no effect on the lower sprouts but does reduce sprout size in the mid and upper zones.

TABLE 6.3 The effect of time and level of artificial defoliation of Brussels sprouts at three stages of growth on sprout number, and mean sprout weight (g dry wt) 1978/79.

	Sprout no.	Mean sprout weight
Time of defoliation		
2 Feb	105.8	1.01
13 Mar	103.5	0.83
23 Apr	103.0	0.95
LSD (5%)	2.8	0.07
Level of defoliation		
0	106.2	1.05
25	104.4	1.04
50	102.1	1.01
75	103.9	0.94
100	103.9	0.68
LSD (5%)	3.6	0.11
Linear trend	ns	**
Quadratic trend	ns	**

Footnote: The only significant interaction was for mean sprout weight, Time of defoliation x Level of defoliation (lin.) - 5%.

- d. The relationship between leaf area duration and yield. Experiments 6.1 and 6.2.

Yield is dependent on the amount of photosynthesis carried out in the leaves (Watson, 1971) which in turn is dependent on both the leaf area and its duration (Thorne, 1971). In these experiments plants were grown at a uniform spacing so that the leaf area duration of the plant (LAD), the integral of the leaf growth curve, will be used in the discussion. This can easily be converted to leaf area duration as defined by Watson (1956) by multiplying the number of plants/m² by 2.7.

At each time of sowing of Brussels sprouts there was a highly significant ($P < 0.01$) linear relationship between LAD and yield (Fig. 6.8). The slope of the line relating yield to LAD was obtained for each sowing time and when the slopes were compared by t-tests (Steele and Torrie, 1960) it was found that they declined significantly with delay in sowing date (Sowing 1, 1977 > 1978 Sowing > Sowing 2, 1977). This decline reflects a lower rate of growth when maximum leaf area occurs later in the growing season as it did in the later sowings. In Experiments 6.1 and 6.3 lowest yields were obtained in the after mid season defoliation and the leaf growth curves following 50% defoliation treatments in Experiment 6.1 show clearly the effects of defoliation treatment at this time in reducing leaf area duration (Fig. 6.9).

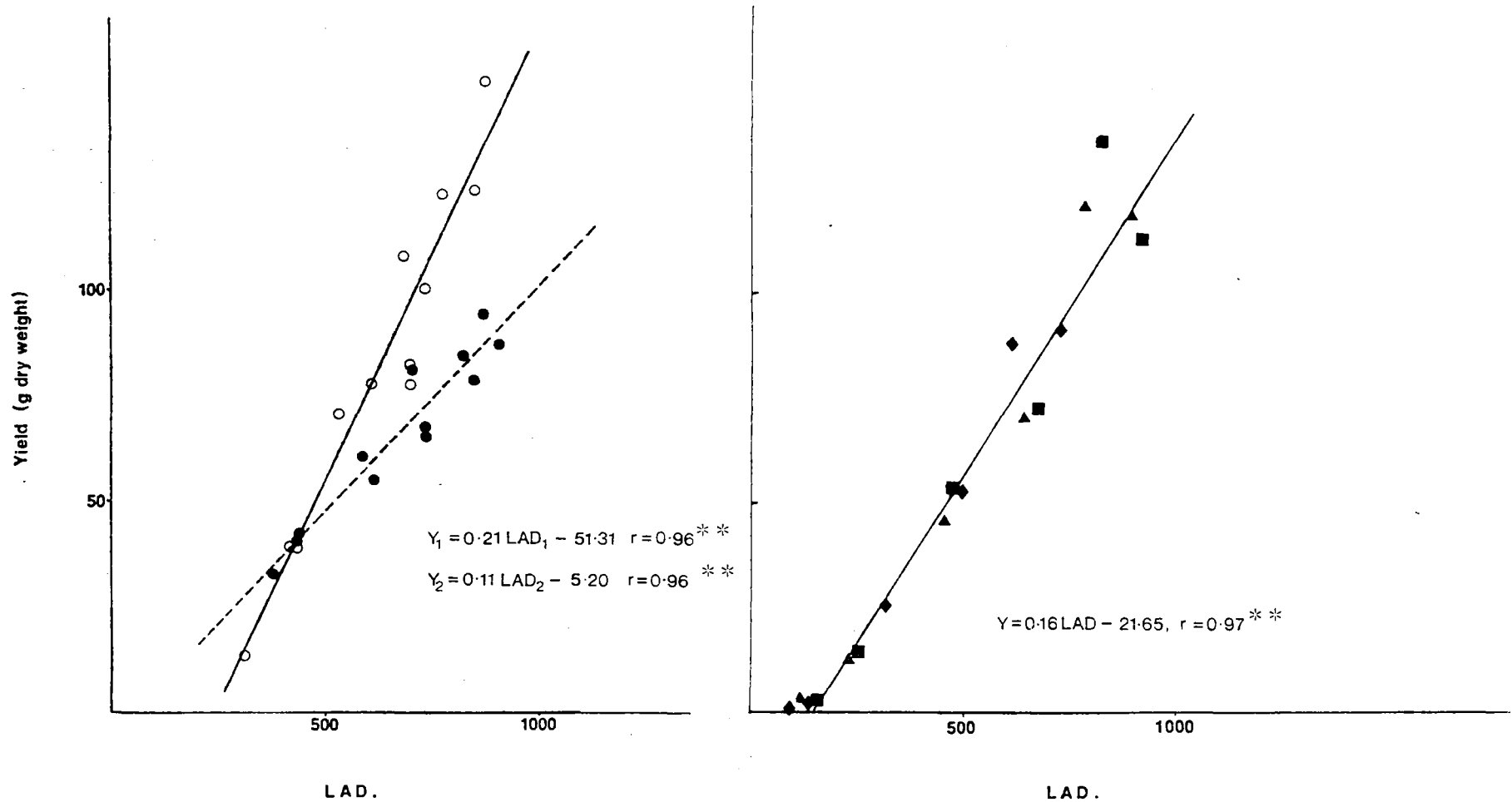


Fig. 6.8. Relationship between leaf area duration (LAD) and yield (Y) in Brussels sprouts.

a, 1977/78; (O), sowing 1; (●), sowing 2. b, 1978/79; (■), control; (▲) 50% defoliation; (◆), 100% defoliation.

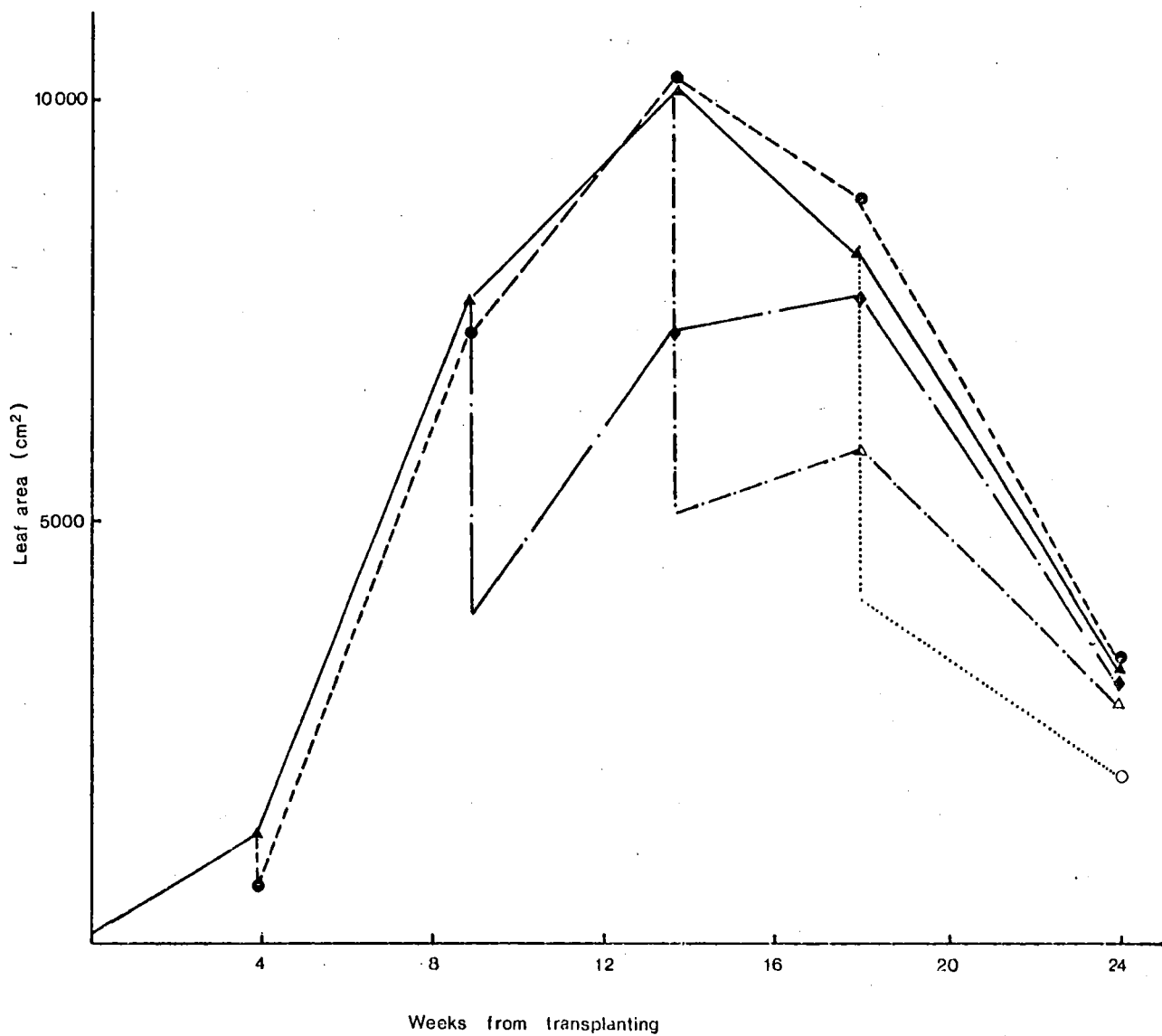


Fig. 6.9. Development of leaf area in Brussels sprouts following 50% defoliation at each of four stages throughout plant growth. ---, T1; -·-, T2; - - -, T3;, T4; —, control.

- e. Effect of defoliation of different zones of the plant on sprout yield. Experiment 6.4.

The effect of defoliation of upper, mid and lower leaf zones, either individually or in combination, is presented in Table 6.4. Factorial analysis (Bailey, 1959) revealed that removal of the mid zone leaves caused a highly significant ($P < 0.01$) yield loss. When the sprouts within each zone were examined in more detail, it was found that individual sprout size in the mid and upper zones was significantly reduced ($P < 0.05$ and $P < 0.01$ respectively) by removal of the mid zone leaves.

Factorial analysis of the weights of the five sprout samples taken from the centre of each zone indicated that in each case removal of leaves led to a decrease in harvest weight of adjacent sprouts. Sprout weight in both the lower and upper zones was also significantly ($P < 0.05$ and $P < 0.01$ respectively) reduced by removal of the mid zone leaves.

The analysis of upper zone sprout size showed a significant interaction between upper and lower zone defoliation, removal of the upper leaves decreasing the size of the upper zone sprouts only if the lower zone leaves were present. This may mean that the lower zone leaves, which were partially senescent, were acting as a sink for photosynthates at this stage and thus, if present, will act in direct competition to the growing sprouts in

TABLE 6.4 Sprout yield, size and weight in each of the upper (U), mid (M) and lower (L) zones following removal of leaves in each zone in a factorial experiment (6.4).

Zone of leaf removal	Total yield (g fresh wt)	Sprout size (mm)			Five sprout wt (g)		
		L	M	U	L	M	U
Control	630.9	27.6	25.6	18.6	51.2	38.7	17.0
U	799.5	30.2	26.8	17.2	61.5	45.0	10.8
M	560.9	28.0	24.8	15.4	47.1	36.1	9.2
L	593.6	27.6	25.0	17.6	46.9	38.3	11.1
UM	506.9	27.2	21.6	14.0	46.6	29.8	6.5
UL	638.7	28.0	24.6	17.0	49.3	40.4	13.4
LM	540.1	26.2	23.6	15.2	29.9	33.1	8.9
UML	483.8	24.6	21.2	13.2	41.3	26.1	7.0
LSD(5%)	191.2	5.1	5.4	2.5	4.2	5.0	1.0
Significance of main effects							
U	ns	ns	ns	ns	ns	ns	*
M	**	ns	*	**	*	*	**
L	ns	ns	ns	ns	*	ns	ns
Significant interactions							
	-	-	-	-	-	-	UL **
							UML *

the upper zone. A significant UML interaction was detected but reasons for it are unclear.

f. Patterns of growth of different Brussels sprout varieties. Experiment 6.5.

Leaf numbers for seven varieties counted from Bed B in the early, mid, and late season are shown in Table 6.5.

TABLE 6.5 Number of leaves/Brussels sprout plant on three dates throughout the growing season.

	Mean leaf number		
	26 Jan	26 Mar	22 June
Multima line	17.2	40.2	28.6
Jade E	25.3	62.0	28.0
Jade Cross	22.0	60.5	26.0
Lunet	15.8	55.0	36.2
Jade G	20.1	56.0	23.4
Rampart	13.4	41.5	33.8
Rasmunda	17.2	47.0	39.8
LSD (5%)	2.9	6.6	5.8

The results reveal higher leaf numbers early in the season on the Jade varieties of sprouts but leaf senescence also appears to be earlier in these varieties resulting in lower leaf numbers in late season, especially when compared to varieties Lunet and Rasmunda. Plant

height at harvest, sprout number/stem and total yields from varieties in Bed E are shown in Table 6.6.

TABLE 6.6 Growth parameters of seven Brussels sprout varieties recorded at a single harvest (6 June 1979).

	Height	Sprout no.	Sprout fresh weight (g)
Multima Line	37.6	81.2	916.8
Jade E	42.2	111.6	636.0
Jade Cross	41.4	89.6	644.4
Jade G	39.2	93.8	827.4
Rampart	40.8	72.8	444.8
Rasmunda	43.4	78.2	321.8
LSD (5%)	4.7	8.8	176.3

The total yield figures presented are results from a single harvest taken in June and, therefore, do not provide the best comparison between varieties. P. Bull (pers. comm.) reported from variety trials in Canterbury that the number of reject sprouts from variety Jade Cross was high, reaching up to 44% in some trials, while generally varieties Lunet and Rasmunda produced lower percentages of rejects. A single harvest also tends to overestimate the commercial yield from early varieties, e.g. Multima Line, which have passed their optimum harvest date so that gross yield includes many blown sprouts. Conversely, single harvests tend to underestimate the

yields of late varieties, e.g. Rasmunda, which for optimum yield should be harvested in August.

It is, therefore, of greater value to examine the pattern of sprout growth revealed by measurements of sprout diameter through the latter part of the growing season. The pattern of sprout growth for each variety in the upper, mid, and lower zones is shown in Figure 6.10. In all cases growth is initiated first among the sprouts of the lower zone, followed by the mid and upper zones. Large differences in final size between upper and lower sprouts indicate the tapering pattern of sprouts on the stems of varieties Multima Line and Jade Cross, while Lunet and Rampart show a more even size distribution. Higher growth rates in the late season are associated with those varieties that maintain their leaves, Lunet, Rampart, Rasmunda, in comparison with the early season varieties, Multima Line, Jade Cross and Jade E which all show early leaf senescence and little sprout growth in May and June.

g. General discussion; the effects of defoliation on growth of the plant.

Following transplanting of the young Brussels sprout plant, the rate of growth is initially low and the major proportion of the plant dry matter is contained in the leaves. It is during this phase that the young plant is vulnerable to soil inhabiting pests, such as the

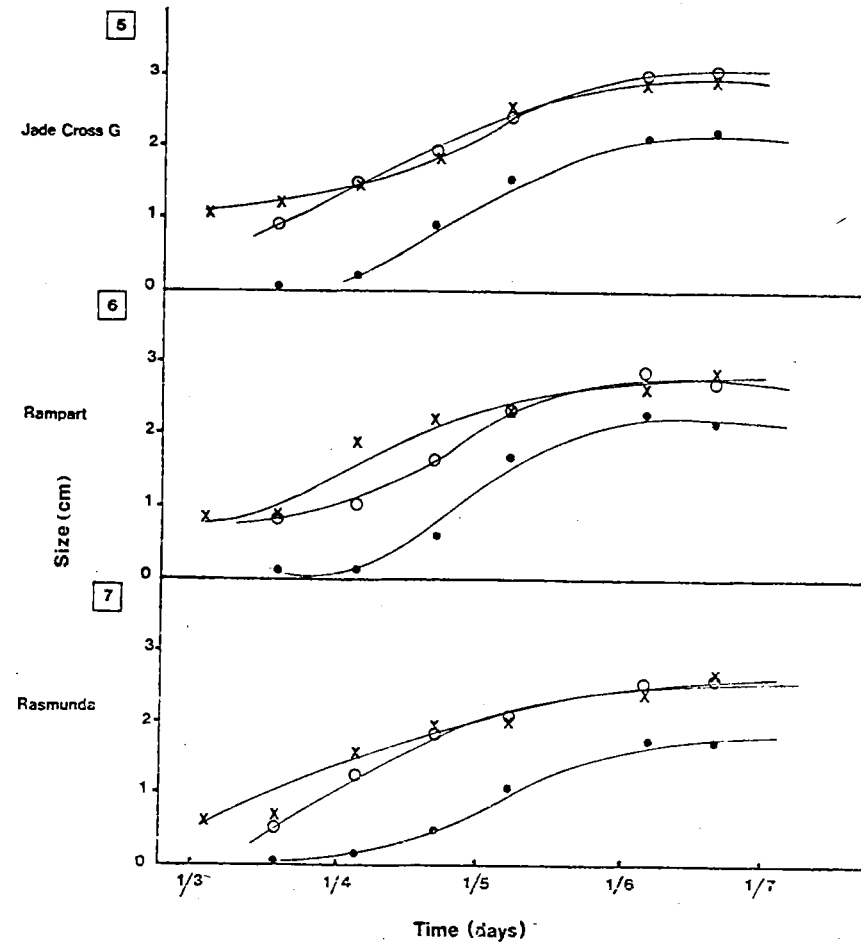
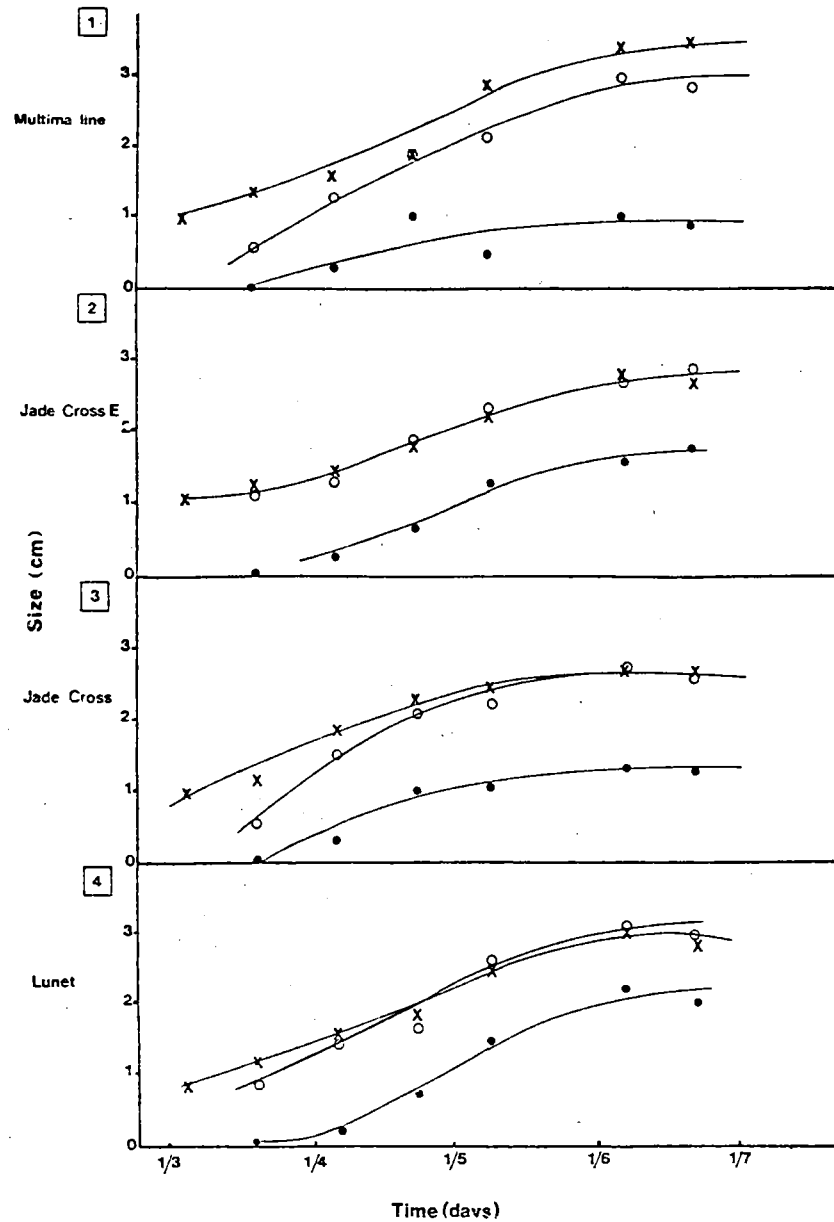


Fig. 6.10 Sprout growth in upper (●), mid (O) and lower (X) zones for seven varieties of Brussels sprouts.

cutworm, Agrotis spp., or mobile pests immigrating into the crop. There are, however, few pests present at this stage (Chapter 4), and the plants have a strong ability to compensate, with yield loss resulting only from defoliations of greater than 75%. Strong compensation in the early stages of plant growth has also been shown for sugar beet (Jones et al., 1955), flax (Hella and Stoa, 1964), rice (Taylor, 1972) and soybean (Thomas et al., 1974). This cannot, however, be viewed as a universal rule as Jackson (1980) found that radish was unable to compensate for defoliation and early defoliation resulted in the greatest yield loss. It is possible, though, that radish is exceptional, being harvested so early in its physiological growth.

Following establishment, the plant passes into a phase of exponential leaf growth. New leaves are produced rapidly and the leaf area of the plant increases to a maximum from which point senescence balances new leaf production. It is in this mid-season growth phase that losses of leaf area, when viewed proportionally, cause the greatest yield losses. Similar responses to mid season defoliation have been found with onions (Baker and Wilcox, 1965), sugar beet (Dunning and Winder, 1972), and potatoes (Cranshaw and Radcliffe, 1980). Watson (1956) found that for many crops the yield was directly proportional to leaf area duration and it seems logical, therefore, to expect a considerable yield loss at this stage when large amounts of leaf area are removed. It

seems, though, that some compensation still operates within this growth stage as there is little yield loss for 50% defoliation in Brussels sprouts.

The late stage of growth is dominated by leaf senescence together with continued growth of the sprouts. At this stage of growth the relationship between yield and defoliation tends to be linear as there is little time for compensation. However, the maximum yield losses are low as a considerable amount of yield has been formed before the defoliation took place. During the late season greatest yield losses followed mid-zone defoliation. Metcalfe (1954) reported significant yield losses with removal of the lower leaves of Brussels sprouts, but it is not recorded when the defoliation took place, while Fisher and Milbourn (1974) recorded no increases in yields after removal of the lower leaves of the plant just prior to leaf senescence.

The pattern of yield response of the Brussels sprout plant to defoliation, i.e. high levels of compensation in the early stages, maximum yield loss in the mid growth stage and a linear relationship between defoliation and loss in the later stages, can also be shown in sugar beet from data obtained by Soine (1967) following a series of defoliations to simulate hail damage (Fig. 6.11).

It seems that the growth of each sprout is the result of the translocation of assimilates from adjacent leaves but that if these are removed, assimilates may be mobilised from other areas. Sprout growth begins with

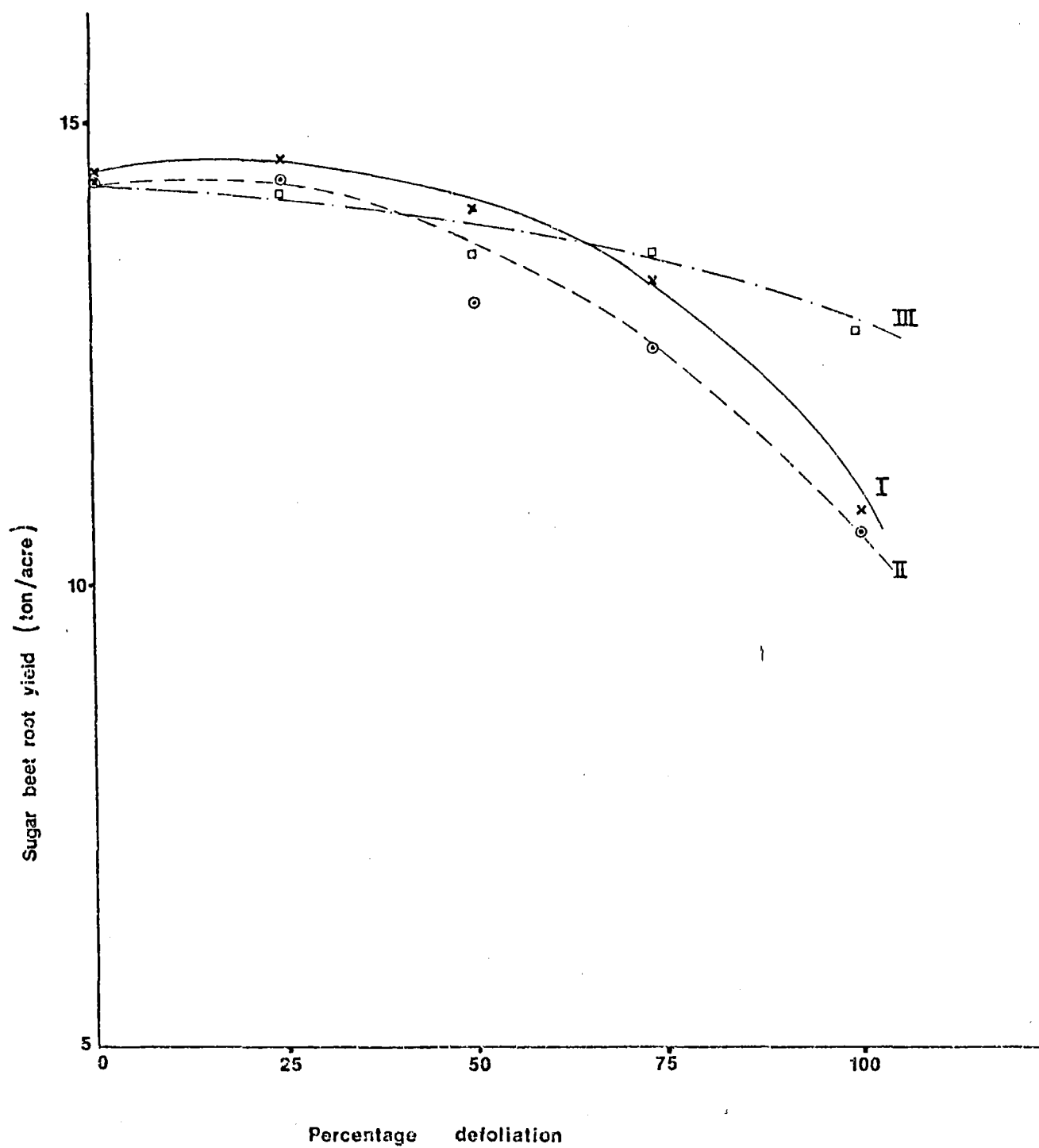


Fig. 6. 11. Effect of defoliation at early (x), mid (⊙) and late (□) stages of growth on sugar beet yield. (Prepared with data from Soine, 1967).

maturity of the older leaves and maximum growth rate is associated with maximum leaf area. The translocation of assimilates from mature leaves to the sprouts gives rise to the gradual increments in yield throughout the season in much the same pattern of yield production as described for sugar beet (Goodman, 1968). An alternative pattern of yield production has been described for crops such as sweet potato (Milthorpe, 1969), wheat (Thorne, 1971) and cauliflower (Nieuwhof, 1969), where the plants have a distinct vegetative phase followed by a yield producing phase. For cauliflowers, it has been demonstrated that curd size is directly proportional to leaf area at preheading (Salter, 1958), which indicates that protection of leaf area at this stage would be a priority rather than protection of leaf area duration throughout plant growth which must be the objective in Brussels sprout production.

It is clear that the interpretation of the results given above is based on a plant "viewpoint". It must be remembered, however, that the leaf area of the plant varies considerably throughout its growth causing a different interpretation from the perspective of the pest population, seeking to utilize the resources available, and from the perspective of the grower, seeking to minimize revenue losses. These factors will be examined further in Chapter 8.

CHAPTER 7

DAMAGE ASSESSMENT

1. Introduction

In the previous three chapters the components of the pest-damage relationship, pest numbers, feeding and plant response, have been examined individually. In this chapter the relationships between these factors are examined directly using techniques of damage assessment to relate pest numbers to yield loss. In order to assess the amount of damage suffered by the crop it is necessary to compare plants both with and without insect attack. A number of experimental methods have been developed to achieve this objective (Chiarappa, 1970) including, among others, the comparison of plants within naturally infested crops (Judenko, 1973), the use of pesticides to produce different pest populations (Wilson et al., 1969) and the use of cages to confine or exclude pests from the crop (Bracken and Butcher, 1977). Damage may be separated into two classes; indirect, where feeding on the leaves and roots causes a loss in gross yield, and direct, where the marketable product itself is attacked and there is a loss in both quantity and quality of yield (Bardner and Fletcher, 1974).

In this chapter both classes of damage are examined and experiments are described where insecticides were

used to produce both differences in pest numbers between plants throughout the whole season and to provide "pest-free" periods of growth. In some experiments cages were used to contain populations of pests higher than would naturally occur on the plants. The relationship between damage, sprout position and size was also investigated, and the effects of pests on a number of Brussels sprout varieties were evaluated.

2. Materials and Methods

a. Experiment 7.1 Damage assessment following the use of selective insecticides 1977/78.

The effects of selective insecticides on pest numbers, plant growth and insect damage were examined in a randomised block design experiment. Five treatments (Table 7.1) were applied to plots of 90 plants in each of five blocks (Beds D, E and half of C). The insecticide carbaryl (treatment II) was used for its known activity against lepidopterous larvae and demeton-S-methyl was used at two rates (treatments III and IV) as a selective aphicide. Both insecticides were combined for late season sprays to control all pests (treatment V). The insecticides were applied with a knapsack sprayer. Within each block five plants were randomly selected and marked for subsequent pest counts. Counts were made at approximately three weekly intervals and the number and species of pests on them recorded.

TABLE 7.1 Selective spray programmes applied to Brussels sprouts, Beds C, D and E 1977/78 season (Fig. 3.1).

Treatment	Rate (a.i./ha)	Spray dates						
		6/1	21/1	11/2	12/3	5/4	28/4	20/5
I Control	-	-	-	-	-	-	-	-
II Carbaryl	2.0 kg	*	*	*	*	*	*	*
III Demeton-S-methyl	0.08	*	*	*	*	*	*	*
IV Demeton-S-methyl	0.15 kg	*	*	*	*	*	*	*
V Carbaryl + Demeton-S-methyl	0.15	-	-	-	-	*	*	*

* spray application; - no spray.

At each of four monthly intervals, one plant was randomly selected in each plot, the numbers and species of pests on it were recorded, and it was then removed and taken back to the laboratory for a more detailed examination (see Chapter 4).

At the final harvest (6 June for the early sowing; 16 June for the late sowing), the marked plants were harvested and taken back to the laboratory where they were divided into leaves, petioles, stems and sprouts. The leaf area was measured and the sprouts divided into four categories:

- 1) marketable sprouts with no damage beyond the covering leaflets,
- 2) damaged sprouts with evidence of feeding into the sprouts,
- 3) "blown" sprouts with the outer leaflets open,
- 4) small sprouts less than 10 mm diameter.

Categories 2, 3 and 4 were classes that would be rejected by the processor. The component parts of the plant were oven-dried to a constant weight at 70°C.

b. Experiment 7.2 Evaluation of spray-free periods 1978/79.

To create spray-free periods in the Brussels sprout crop in the 1978/79 season, eight spray treatments, based on combinations of early, mid and late growth stages, were allocated to each of eight plots in a factorial, randomised

block design with four replicates (Fig. 3.2, Beds C and D). The insecticide dichlorvos was applied at 0.5 kg a.i./ha with a knapsack sprayer according to the spray programme (Table 7.2). Plot size was 45 plants except for treatments 2, 3 and 4, which contained 63 plants to enable extra plants to be used for the caged larvae experiments (Exp. 7.3). Counts of white butterfly and diamondback moth larvae and cabbage aphid colonies were made at three weekly intervals on two marked plants randomly selected from the centre row of each plot. To control the 1979 outbreak of cabbage aphid the selective aphicide pirimicarb was applied on the 20 February to all plants. The aphicide was applied at half the recommended rate to minimize its effects on all fauna but the aphids.

c. Experiment 7.3 Cage studies.

To study the effects of both time and intensity of pest attack cages were used to confine a range of known numbers of lepidopterous larvae on Brussels sprout plants at stages throughout the crop's growth. The cages used were cylinders, 0.5 m diameter x 0.75 m high and covered with fine cotton netting (Plate 7.1). They were placed over individual plants from plots 2, 3 and 4, Experiment 7.2, at a time corresponding to the spray-free period in that plot. White butterfly or diamondback moth larvae were then added to the cages to complete their development and, on pupation, the cages were removed.

TABLE 7.2 Dichlorvos spray programme to create early (E), mid (M) and late (L) season spray free periods in a crop of Brussels sprouts, Experiment 7.2, 1979.
0 = complete spray coverage.

Treatment		Date									
		15/1	29/1	13/2	26/2	12/3	2/4	9/4	23/4	7/5	21/5
		E				M				L	
1	0	*	*	*	*	*	*	*	*	*	*
2	E	-	-	-	-	*	*	*	*	*	*
3	M	*	*	*	*	-	-	-	*	*	*
4	L	*	*	*	*	*	*	*	-	-	-
5	EM	-	-	-	-	-	-	-	*	*	*
6	EL	-	-	-	-	*	*	*	-	-	-
7	ML	*	*	*	*	-	-	-	-	-	-
8	EML	-	-	-	-	-	-	-	-	-	-

* spray application; - no spray.



Plate 7.1 Cages for confining white butterfly or diamondback moth larvae on Brussels sprout plants to assess their effects on plant growth and yield.

White butterfly larvae were placed in cages five times throughout the season while diamondback moth larvae were placed twice (Table 7.3). Both species were placed at a range of larval densities determined by the size of the plant. For the first three trials with white butterfly, larvae were raised from field-collected eggs in a controlled temperature room at 20°C. However, low recovery of pupae from the 16 March trial led to the abandonment of reared larvae in favour of field collected larvae from an unsprayed block for the two later trials. On both occasions diamondback moth larvae were obtained from a laboratory culture.

TABLE 7.3 Date of placement and number of larvae placed on caged Brussels sprouts, Experiment 7.3, 1979.

Spray-free period	Date	Number						
<u>White butterfly</u>								
Early	24 January	0	3	6	9	12	15	
	99 February	0	4	8	12	16	20	
Mid	16 March	0	5	10	15	20	25	
	30 March	0	15	30	60			
Late	17 April	0	25	50				
<u>Diamondback moth</u>								
Early	1 February	0	8	16	24	32	40	
Mid	30 March	0	25	50	100			

For both species penultimate instar larvae were always used to ensure the maximum rate of feeding over a short period of time and thus minimize the effects of

the cage on the growth of the plant. The effects of insect attack at other times were minimized by the regular spray programme.

Before being caged, the plants were ranked according to size and their leaves counted. For the two later trials, 30 March and 17 April, plants were matched within each block to reduce interplant variation before selection and allocation of treatments.

After sufficient time had elapsed to allow for development to pupation, cages were removed and each cage and plant was searched for pupae and their numbers were recorded. Plants were checked at stages throughout their growth for sprout development and at the final harvest, sprout size, numbers, damage and weights were recorded.

d. Experiment 7.4 Relationship between sprout position and damage.

A series of small experiments were carried out to examine the relationship between the position of the sprout on the stem and insect damage.

(i) Relationship between sprout zone and diamondback moth attack

In 1979, 20 Brussels sprout plants were harvested each three weeks from the unsprayed bed (E) and sprouts were divided into those from the upper, mid and lower zones. The sprouts were then placed in extraction

boxes (Chapter 4) and placed in a constant temperature room at 25°C for 21 days. The boxes were then removed and the diamondback moth adults removed from the Tac trap on the lid.

- (ii) The relationship between sprout position and damage

In order to determine the characteristics of sprouts under attack, three harvests of 15 plants were made (1 May, 1 June, 22 June 1979). Groups of five sprouts were removed at 10 cm intervals up the stem, measured and examined for signs of damage which was categorised as new or old, depending on the characteristics of the feeding hole. The proportion of damaged sprouts in each position on the stem was then calculated.

- (iii) The position of egg laying by diamondback moth.

To examine the effect of oviposition in determining larval numbers in different zones 50 moths were placed in each of five cages, of the same design as in Experiment 7.3, covering a single Brussels sprout plant. After one week, the cages were removed and the whole plant harvested. Groups of sprouts, each with their associated leaf where appropriate, were removed at 10 cm intervals up the stem of the plant and examined for the presence of eggs.

e. Experiment 7.5 Relationship between sprout
 size and attack by diamondback moth

As the size of sprouts appeared to be an important parameter determining damage in 1979, ten untreated Brussels sprout plants were harvested mid-season in 1980 (24 April) and all sprouts were removed. Individual sprouts were measured, placed into categories corresponding to 1 mm increments in diameter and examined for damage.

In a further experiment, sprouts were removed from the stem of untreated plants from each of three zones - upper, medium and lower. Thirty-two sprouts from each zone were then measured and placed individually into small plastic pottles. A neonate first instar diamondback moth larvae was then added to each pottle, the pottle sealed and placed in a controlled temperature cabinet for one week at 25°C after which larval survival was assessed.

f. Experiment 7.6 Estimates of yield loss caused
 by cabbage aphid using the analytical method

Following the outbreak of a cabbage aphid attack in January 1979 each of 70 plants, from two blocks within the unsprayed Bed E, was graded into one of the following categories dependent on the severity of aphid attack:

- I Aphid free
- II Aphids present in low numbers
- III Aphids present in distinct colonies
- IV Aphid colonies causing leaf curl and
chlorosis
- V Serious stunting of the plant
- VI Death of the plant

The plants were revisited at approximately ten day intervals for the next six weeks and regraded at each time. Following a crash in aphid population levels in mid March the procedure was discontinued. The plants were harvested in late May. Crop loss was then estimated using the method of Judenko (1973). For each time of assessment, the proportion of plants in each grading was calculated together with the mean sprout weight of that grade. The difference between the average sprout weight over all grades and the mean of insect-free plants, or those within the lowest grade of attack, was then calculated and expressed as a percentage of the latter as an estimate of yield loss due to the insect attack in the crop.

g. Experiment 7.7 Evaluation of the response of seven varieties of Brussels sprout to insect attack

This experiment uses the seven Brussels sprout varieties in the sprayed and unsprayed beds (B and E, Fig. 3.2) described in Chapter 6. Insect counts on

the varieties in the unsprayed bed were made on the 7 February to determine pest populations. Three plants were counted from each variety in each of the five blocks. In early March the aphid population in the sprayed bed built up between spraying dates. Plants within this bed were examined for the presence of aphids and colonies of more than 50 were counted. In late March the varieties in the unsprayed bed were graded for aphid attack according to the scale presented in Section f. They were also graded on a 1-5 scale according to feeding severity by lepidoptera larvae.

At the final harvest one plant, randomly selected from each row in each of the five blocks, was taken to the laboratory where the sprouts were removed and divided into those from upper, mid and lower zones before being examined for signs of insect damage and weighed. Two randomly selected sprouts were taken from each zone of each sampled plant and examined to determine the number of senesced leaflets at the base of the sprout.

3. Results

a. Effects of selective insecticide spray regimes on pest populations and yield loss in Brussels sprouts. Experiment 7.1, 1977/78.

(i) Pest population

The seasonal mean numbers of each pest species and each stage recorded are presented in Table 7.4 and show

TABLE 7.4 Effect of five different spray regimes on mean pest population levels/plant in Brussels sprouts, Experiment 7.1, 1977/78.

Treatment		<u>A. rapae</u>		<u>P. xylostella</u>		<u>B. brassicae</u>	
		Eggs	Larvae	Larvae	Pupae	Alatae	Colonies
I	Unsprayed	0.76	0.88	1.41	0.10	2.29	0.33
II	Carbaryl	0.65	0.26	0.48	0.04	3.47	0.30
III	Demeton-S-methyl, full rate	1.05	1.21	2.10	0.20	1.58	0.06
IV	Demeton-S-methyl, half rate	1.16	1.32	1.78	0.10	0.95	0.05
V	Demeton-S-methyl and carbaryl, late spray	0.67	0.85	1.38	0.16	2.40	0.14
	LSD (5%)	0.42	0.44	1.02	0.11	0.91	0.12

clearly the effects of the selective spray programme. Lowest numbers of lepidoptera larvae were recorded in the carbaryl treatment (II). There were significantly ($P < 0.05$) less white butterfly larvae in this treatment than in any other and significantly less diamondback moth larvae than in either of the demeton-S-methyl treatments (III and IV). Both demeton-S-methyl treatments resulted in significantly ($P < 0.05$) less cabbage aphid colonies than the control (I) or carbaryl (II) treatments.

The effects of each treatment on the seasonal trends of each of the damaging stages of each pest is shown in Figure 7.1. White butterfly larval numbers were significantly ($P < 0.05$) lower in the carbaryl treatment (II) than in all other treatments throughout the mid-season period. Diamondback moth larvae were also significantly ($P < 0.05$) lower in the carbaryl treatments (II) than the control (I) at each of the population peaks. High numbers of diamondback moth larvae were present in the demeton-S-methyl treatments (III and IV) towards the end of the season but these were not significantly higher than those in the control.

The application of demeton-S-methyl kept cabbage aphid populations at low levels in treatments III and IV throughout the experiment. In the carbaryl (II) treatment, however, significantly ($P < 0.05$) more cabbage aphid colonies were recorded than in the control (I) at the time of the first population peak, late January-early

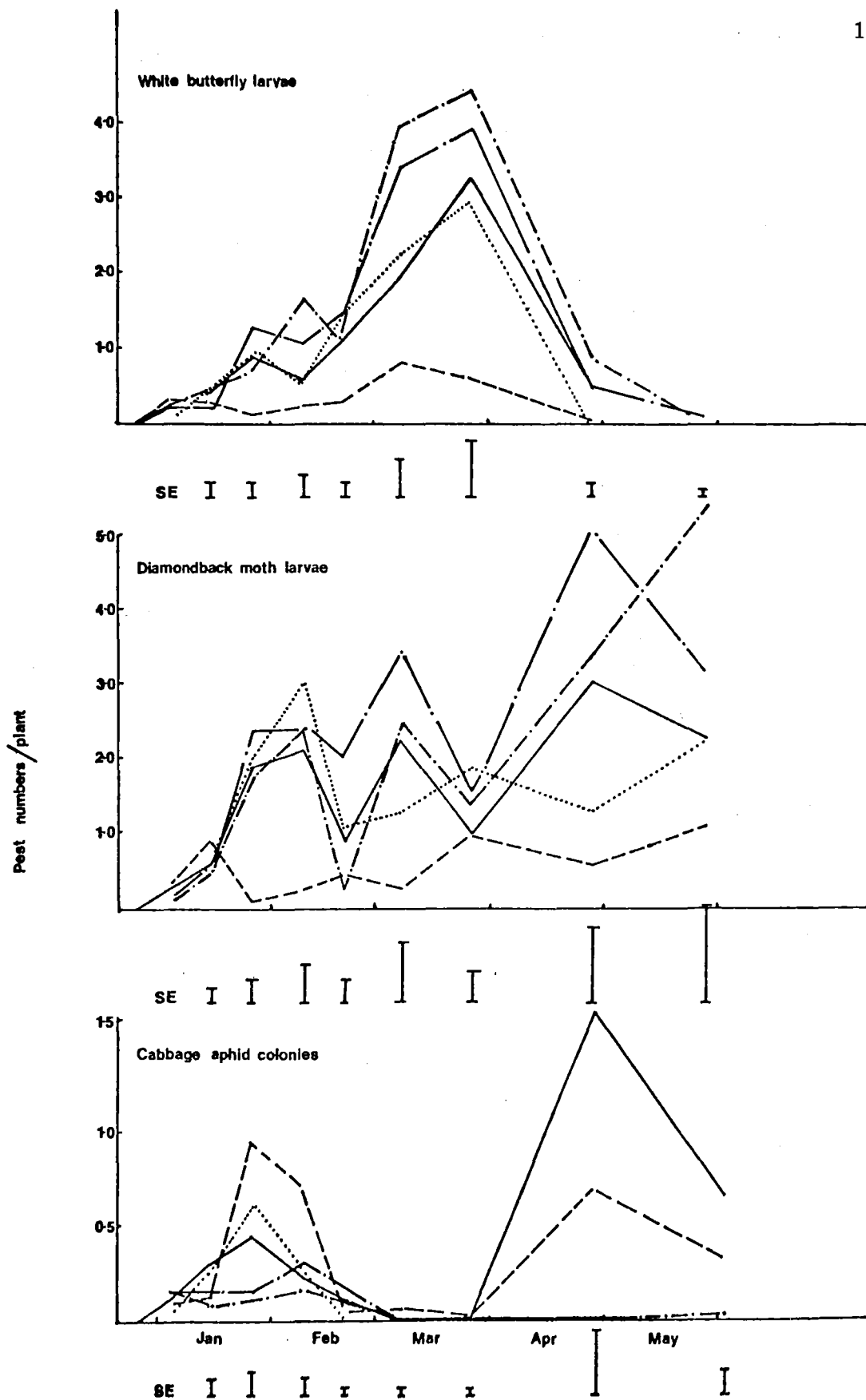


Fig. 7.1. The effect of five insecticide spray regimes on numbers of white butterfly larvae, diamondback moth larvae and colonies of cabbage aphid on Brussels sprouts.

(—), control; (---), carbaryl; (---), demeton-S-methyl full rate; (---), demeton-S-methyl half rate; (.....), late spray. SE. Standard errors.

February. The application of late sprays of carbaryl and demeton-S-methyl (V) maintained all pests at levels lower than those in the control (I) in the late season.

(ii) Sprout yields and damage

Sprout yields may be reduced indirectly, by pests feeding on the leaves reducing the flow of assimilates to the sprouts, or directly, by feeding on the sprouts themselves. White butterfly larvae and cabbage aphid colonies were found primarily on the leaves while diamondback moth not only feed on the leaves but also bore into the sprouts making them unmarketable (Plate 7.2).

In this experiment total sprout yield in the carbaryl treatment (II) was significantly greater than in the control (I) although no greater than in the demeton-S-methyl treated plots (III and IV) (Table 7.5). Only a portion of the total sprout yield is marketable. Sprouts are unmarketable for a number of reasons; they may be damaged by insects; become "blown" through opening of the bud; or may be too small for marketing. Marketable yield was significantly ($P < 0.05$) higher in the carbaryl treatment (II) than in any other and the weight of damaged sprouts in this treatment was the lowest of all treatments but not significantly less than the control (I). Significantly ($P < 0.05$) higher damage levels occurred in the demeton-S-methyl treatments (III and IV) than in the control (I) or carbaryl (II)



Plate 7.2 Direct damage to Brussels sprouts caused by diamondback moth larvae.

TABLE 7.5 The effect of five different insecticide spray regimes on total yield and yield components of Brussels sprouts, Experiment 7.1, 1977/78. (g dry wt)

	Total yield	Marketable yield	Damaged sprouts	Blown sprouts	Small sprouts
I	88.2	50.5	17.9	14.4	5.5
II	106.2	71.8	10.9	17.1	4.0
III	94.3	35.3	35.9	20.2	4.8
IV	104.8	41.0	40.0	18.2	5.7
V	90.6	49.9	18.5	18.3	4.0
LSD (5%)	16.0	17.9	13.5	7.2	2.1

treatments probably reflecting the high number of diamondback moth in the former. There was little difference in the weights of blown or small sprouts between treatments. Despite late sprays of carbaryl and demeton-S-methyl in treatment V there was neither an increase in yield nor less damage in this treatment than in the control (I).

- b. Effects of insecticide spray-free periods on insect populations and Brussel sprout yields, Experiment 7.2, 1978/79.

In Experiment 7.3 populations of diamondback moth and white butterfly in the unsprayed plots followed the same seasonal trends as in the unsprayed bed (E) with populations of diamondback moth approximately half those of the 1977/78 season. The numbers of white butterfly and diamondback moth in each treatment throughout the season are shown in Figure 7.2 and indicate effective control by dichlorvos in each of the sprayed periods.

The effects of treatments on plant height, sprout numbers, and sprout weight are shown in Table 7.6. Plant height and sprout number, indicators of the general vigour of the plant, appear to be little affected by spray free periods. Sprout yield, though, is significantly ($P < 0.05$) reduced following the mid spray-free period and the effects of an early spray-free period only just fail to reach significance at the 5% level. There was also a significant EL interaction indicating that where

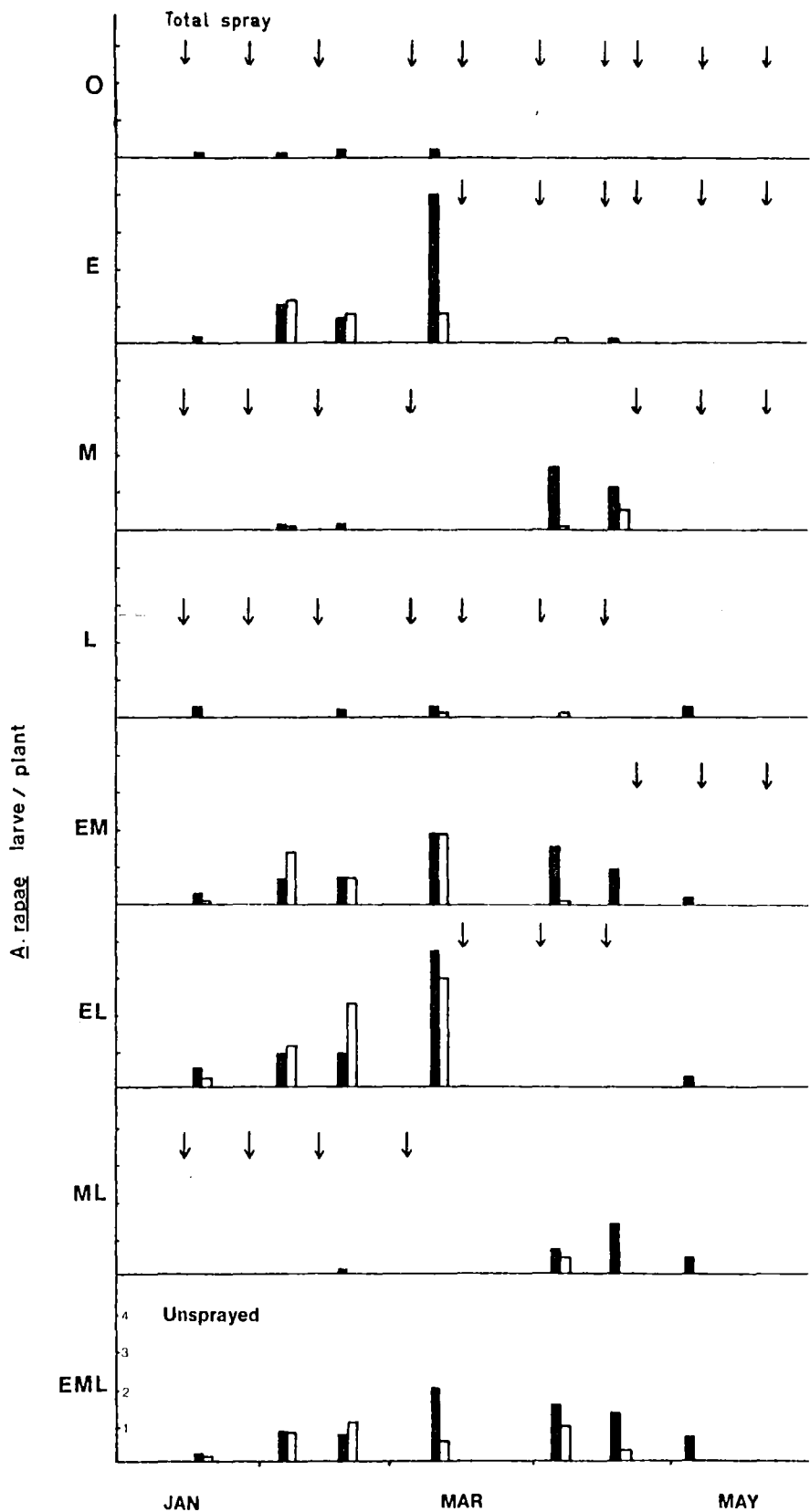


Fig. 7.2. The effect of early (E), mid (M) or late (L) spray-free periods on white butterfly (■) and diamondback moth (□) larval numbers on Brussels sprouts, Experiment 7.2. O, whole-season spray coverage.

TABLE 7.6 Effect of early (E), mid (M) or late (L) spray-free periods on plant height, sprout number and sprout weight in Brussels sprouts.

Treatment	Plant height (cm)	Sprout number	Sprout dry weight (g)
0	36.5	96.4	93.9
E	37.8	97.4	101.1
M	37.3	97.8	83.8
L	36.3	99.5	103.5
EM	35.5	94.6	90.9
EL	36.4	91.7	85.0
ML	35.1	95.6	92.7
EML	35.5	94.7	75.6
LSD (5%)		6.7	21.0
Significance of main effects			
E	ns	ns	ns
M	ns	ns	*
L	ns	ns	ns
Interactions	-	-	EL*

spray had not been applied early in the season a late spray-free period caused a reduction in sprout weight.

The effects of spray-free periods on levels of damage in the upper, mid and lower zones were also examined and the results are presented in Table 7.7. The early spray-free period resulted in a significant increase in damage only in the mid sprout zone. The mid spray-free period resulted in a significant ($P < 0.05$) increase in all zones and the late spray-free period a highly significant ($P < 0.01$) increase in all zones. There were no significant interactions following transformation ($\ln (x + 1)$) of the data.

It appears, therefore, that each spray-free period will contribute to an increase in the level of damage. The early spray-free period had least effect on damage levels in the sprouts which was expected as it occurs before the development of the sprouts.

Considerable damage was caused in the middle period but the greatest increase in damage resulted from the late spray-free period which corresponded to the peak of diamondback moth numbers in the sprouts together with the maximum number of sprouts susceptible to attack.

TABLE 7.7 Total damaged sprouts/plant (transformed $\ln(x + 1)$) and numbers in each of the upper, mid and lower zones following combinations of early (E), mid (M) and late (L) spray-free periods. Raw data in parenthesis.

Treatment	Damaged sprouts/ plant	Damaged sprouts in each zone		
		Upper	Mid	Lower
O	0.21(0.25)	0.07(0.08)	0.07(0.08)	0.08(0.09)
E	0.35(0.42)	0.04(0.04)	0.16(0.19)	0.16(0.19)
M	0.63(1.00)	0.27(0.38)	0.32(0.42)	0.18(0.21)
L	0.59(0.88)	0.34(0.46)	0.12(0.13)	0.24(0.29)
EM	1.00(1.79)	0.37(0.50)	0.62(0.92)	0.30(0.38)
EL	1.31(2.68)	0.86(1.46)	0.59(0.84)	0.30(0.38)
ML	1.54(3.56)	0.91(1.50)	0.94(0.94)	0.37(0.46)
EML	1.91(5.54)	1.25(2.75)	1.03(1.88)	0.63(0.92)
LSD (5%)	0.44	0.41	0.32	0.26
Significance of main effects				
E	**	-	*	-
M	**	*	**	*
L	**	**	**	**
Interactions	-	-	-	-

- c. Effect of pest species and time of attack on yield loss in Brussels sprouts, Experiments 7.1 and 7.2.

Spray programmes such as those in Experiments 7.1 and 7.2 affect the yield of sprouts indirectly by controlling the pests on the plant but it is not clear from the results of these experiments just which pests are responsible for yield loss and when this occurs. To investigate these aspects further, correlations were made between insect numbers, yields and damage in both experiments.

In the first season, Experiment 7.1, pests were monitored throughout the season and for each of the two sowings the mean number of pests per plot was correlated with both mean yields and mean weight of damaged sprouts. The results are presented in Table 7.8. There was no significant correlation between the numbers of any of the pests and sprout yields from the first sowing while in the second sowing white butterfly larval numbers were significantly ($P < 0.05$), negatively correlated with yield and the correlation between diamondback moth numbers and the weights of damaged sprouts.

In the second season, Experiment 7.2, mean pest numbers of each treatment were correlated with yield and numbers of damaged sprouts but no significant relationships were found. When larvae were divided into those present in early and mid periods there was a highly significant ($P < 0.01$) correlation between numbers of

TABLE 7.8 Correlations between pest numbers, yield and damage in Brussels sprouts.

- a. Correlations between overall mean pest numbers, yield and damaged sprouts, Experiment 7.1 (21 df.).

	White butterfly	Total yield Diamondback moth	Cabbage aphid	Damaged sprouts Diamondback moth
Sowing 1	0.29 ns	0.25 ns	0.01 ns	0.56**
Sowing 2	0.41*	0.37 ns	0.07 ns	0.49**

- b. Correlations between mean numbers of diamondback moth in early and mid periods of sprout crop growth, yield and damage, Experiment 7.2 (6 df.).

	Early	Mid
Total yield	0 ns	0.53 ns
Damaged sprouts	0 ns	0.92 **

ns, not significant; *, $P < 0.05$; **, $P < 0.01$.

diamondback moth present in the mid stage and numbers of damaged sprouts but no correlation between those present in the early stage and the number of damaged sprouts. There were few pests present at the late stage so no correlations were attempted.

White butterfly feed on the leaves of the sprout plants and therefore the negative correlation between larval numbers and yield may be the result of this feeding indirectly reducing sprout yield. Diamondback moth also feed on the leaves and in addition can cause yield loss by feeding directly on the sprouts. In both sowings of Experiment 7.1 there was a significant ($P < 0.05$) correlation between mean diamondback moth numbers and damaged sprouts. In Experiment 7.2, when insects were separated by insecticide sprays into discrete periods, there was no correlation between numbers and damage in the early stage but a highly significant ($P < 0.01$) correlation in the mid stage indicating the importance of pest attack at this time.

- d. The effects of caged white butterfly and diamondback moth larvae on yield of Brussels sprouts, Experiment 7.3.

After seven to 14 days the cages were removed from the plants and a thorough search was made for pupae. Recovery of white butterfly pupae ranged from 60 to 80%

of the added larval numbers with the exception of the trial started on the 16 March when disease caused a high mortality leading to a recovery of only 30% of the pupae. The feeding levels were correspondingly low and consequently this trial was abandoned. Numbers of diamondback moth larvae were not recorded as their smaller size and often concealed position made searching for them impractical without damaging the plants.

The relationships between white butterfly larval numbers, introduced at stages throughout the growing season, and yield are presented in Table 7.9 together with the relationship between estimated defoliation and yield. While the analyses indicate a negative relationship between larval numbers and yield this only reached significance ($P < 0.05$) in the earliest trial (24 January). In each case estimated defoliation was more closely correlated to yield than pest numbers placed on the plant, probably due to different rates of survival and different positions of feeding among the larvae. Scattergrams of the relationship between yield and defoliation are shown in Figure 7.3, together with the fitted functions. It is evident that in the early stages of growth very high yield losses occurred at the extremes of defoliation. By the mid stage, 30 March, maximum losses were low as the level of defoliation never exceeded 50%. While there is some hint of curvature in the relationships there was no significant improvement by the addition of a quadratic term to any of the functions.

TABLE 7.9 Relationship between white butterfly numbers, estimated defoliation and yield of Brussels sprouts. Cage studies 1979.

	Larval numbers	Estimated % defoliation (D)	
24 Jan	$Y = 629.4 - 25.2 N, r = 0.43^*$	$Y = 690.8 - 4.9 D, r = 0.58^{**}$	22 df
9 Feb	$Y = 642.8 - 5.2 N, r = 0.16 \text{ n.s.}$	$Y = 750.9 - 4.7 D, r = 0.49^*$	22 df
30 Mar	$Y = 603.3 - 1.8 N, r = 0.47 \text{ n.s.}$	$Y = 602.1 - 3.4 D, r = 0.58^{**}$	14 df
17 Apr	$Y = 704.3 - 0.33 N, r = 0.05 \text{ n.s.}$	not recorded	10 df

* - $P < 0.05$;

** - $P < 0.01$

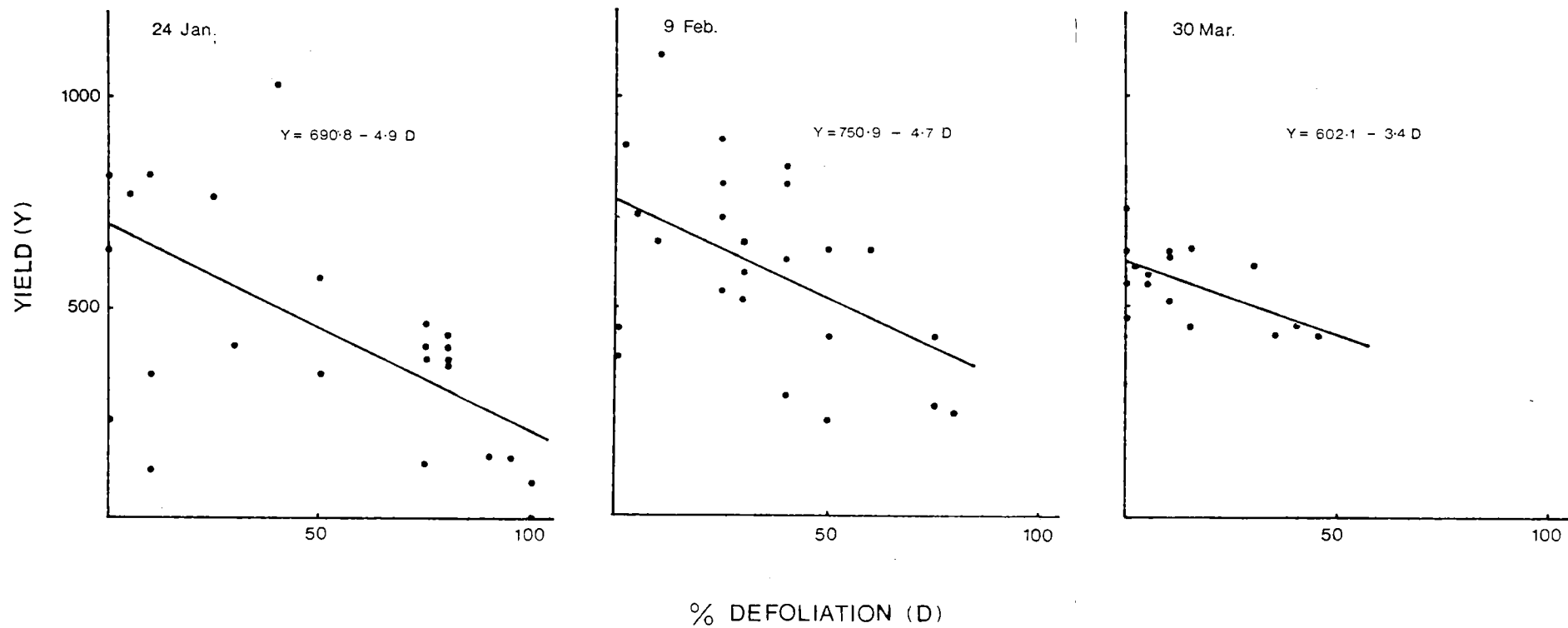


Fig. 7.3. The relationship between defoliation by white butterfly larvae caged on Brussels sprout plants and sprout yield at three stages throughout the crop's growth.

The results from these defoliations with white butterfly larvae apparently contradict those from the artificial defoliation study (Chapter 6) where mid season defoliation resulted in most yield loss. In these trials, however, it was not possible to achieve a complete range of defoliations, especially in the mid stage, due to the size of the plant. Thus it appears that for the 30 March trial only the upper part of the yield response curve is showing which corresponds to the portion of the curve below 50% defoliation in the artificial defoliation study.

No relationship was found between diamondback moth numbers and yield at either stage of introduction but this may have been because few of the introduced larvae fed at the crown of the plant where most feeding occurs naturally among field populations.

When the sprouts were examined for damage a different pattern emerged (Fig. 7.4). In early February neither the addition of white butterfly nor diamondback moth had any effect on the damage levels recorded in the sprouts. In late March however, there was a significant increase ($P < 0.01$) in the numbers of damaged sprouts with increased diamondback moth larval numbers. Even as many as 60 white butterfly larvae per plant still had no effect on the damage levels recorded in the sprouts.

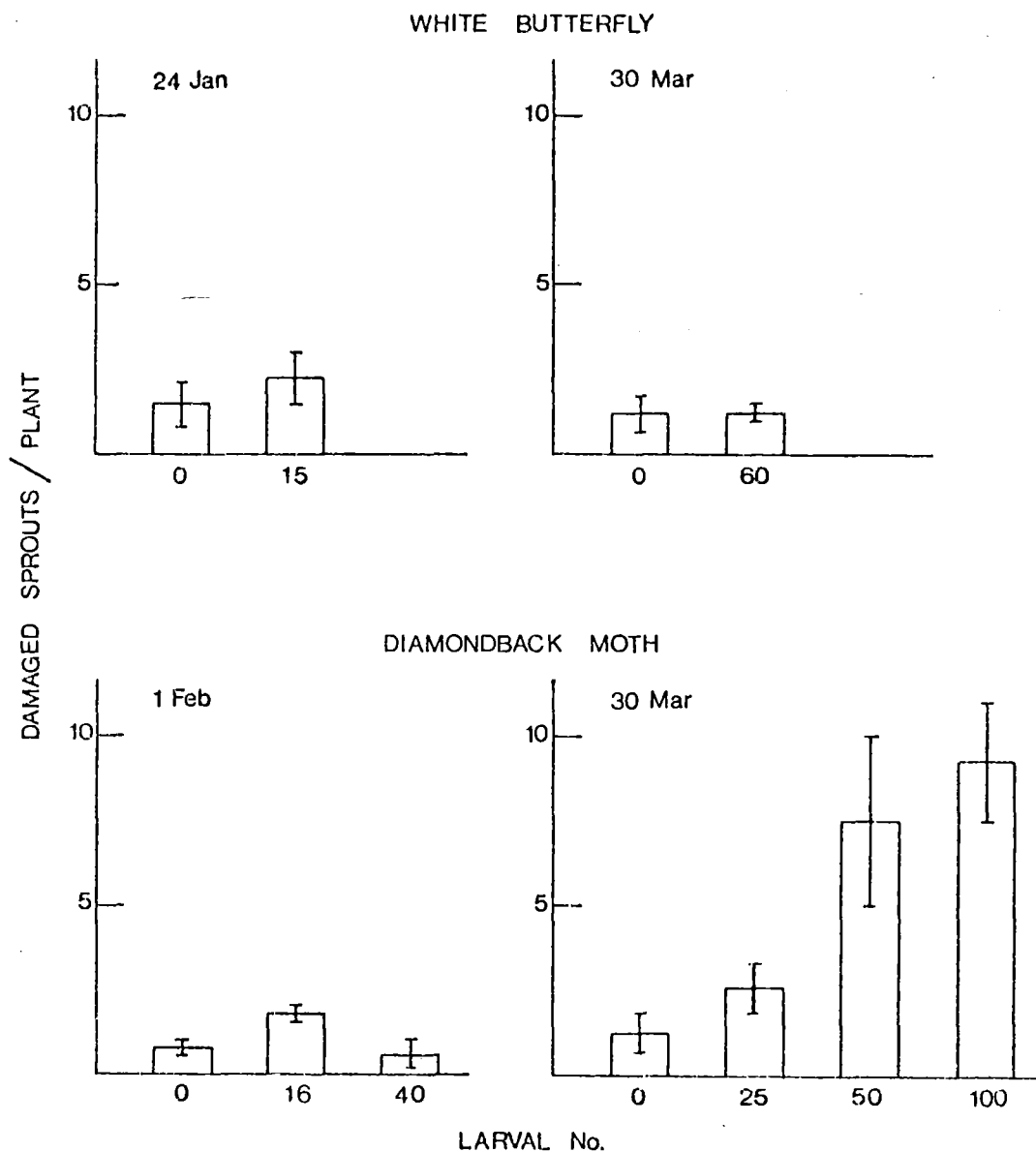


Fig. 7.4. Relationship between caged white butterfly and diamond-back moth larval numbers and direct damage to sprouts at two stages in the growth of a Brussels sprout crop.

- e. The effects of position of sprouts growth and size on damage, Experiments 7.4 and 7.5.

Extraction of diamondback moth from different zones of the stem revealed that the greatest number are associated with the mid zone and that there was a shift upwards over time (Chapter 4).

Direct examination of sprouts on the stem also showed that most damage occurred in the mid zone. The high proportion of newly damaged sprouts on 1 May indicated that most damage occurred at that time and the presence of the bulk of damage in the upper part of the plant in the later harvests suggests a shift in the larval population up the stem as the season progresses.(Fig. 7.5). There was also a reduction in the levels of damage in the lower part of the stem in the late sampling.

Examination of sprouts from heavily damaged plants in 1980 revealed that most damage occurred in the larger sprouts and there was a size threshold, of 7 mm diameter, below which few sprouts were damaged (Fig. 7.6). The movement towards the upper part of the plant is, therefore, in part explained by the availability of resources as sprout growth up the stem takes a greater number across the 7 mm threshold but it is also affected by adult oviposition and larval survival. When adult moths were caged over mature plants it was found that 82% of eggs were laid on the upper half of the plant (Fig. 7.7). Larval survival was also affected by the position of the

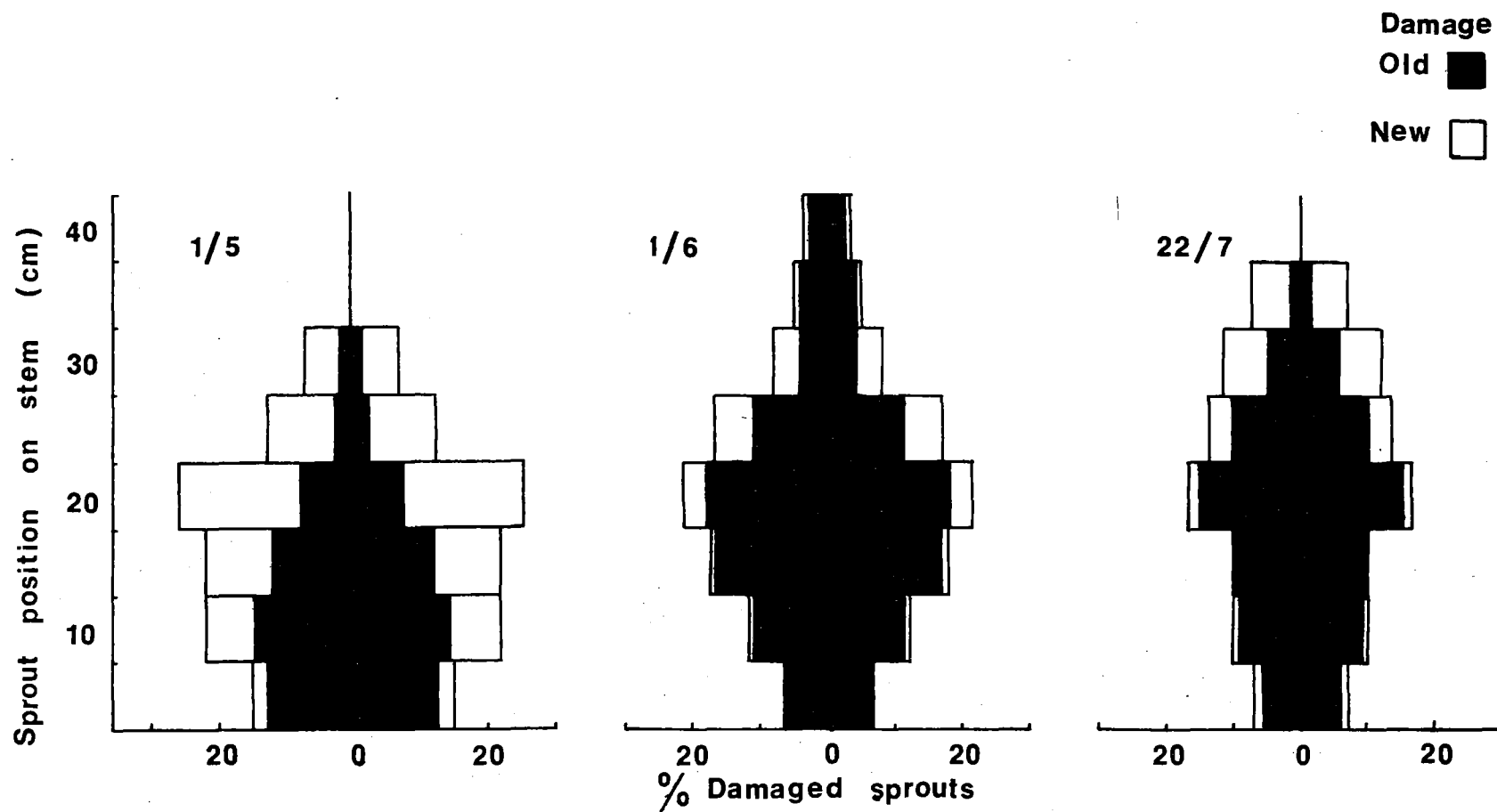


Fig. 7.5. The proportion and position of damaged sprouts on the stems of Brussels sprout plants taken from an unsprayed crop at three times during the latter part of the growing season, 1979.

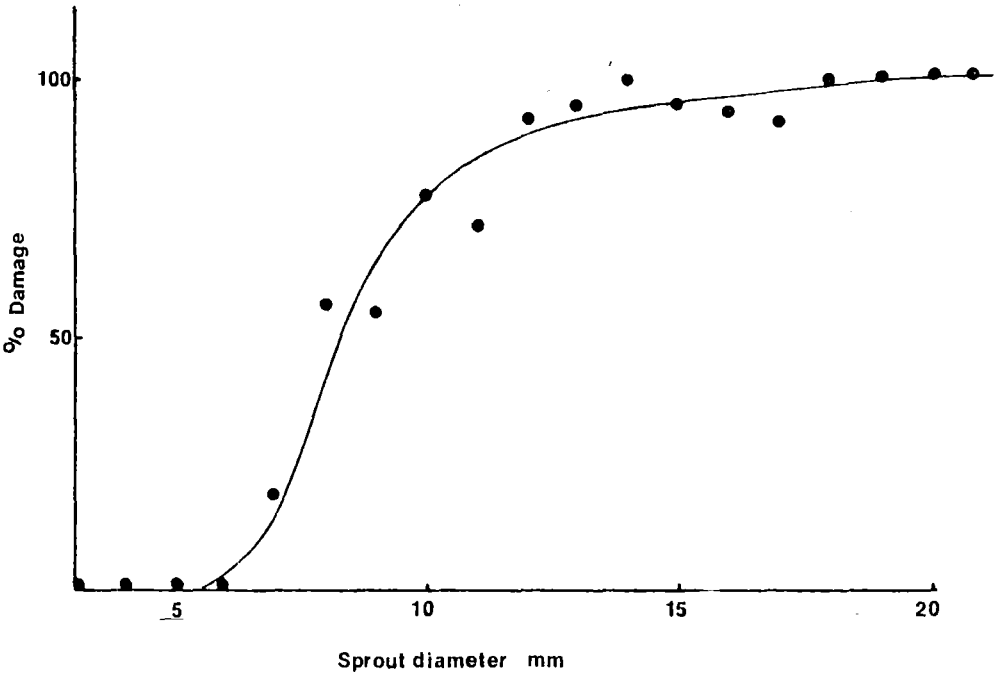


Fig. 7.6. Relationship between sprout size and damage by diamondback moth. Assessed by direct examination of sprouts, 20 March, 1980.

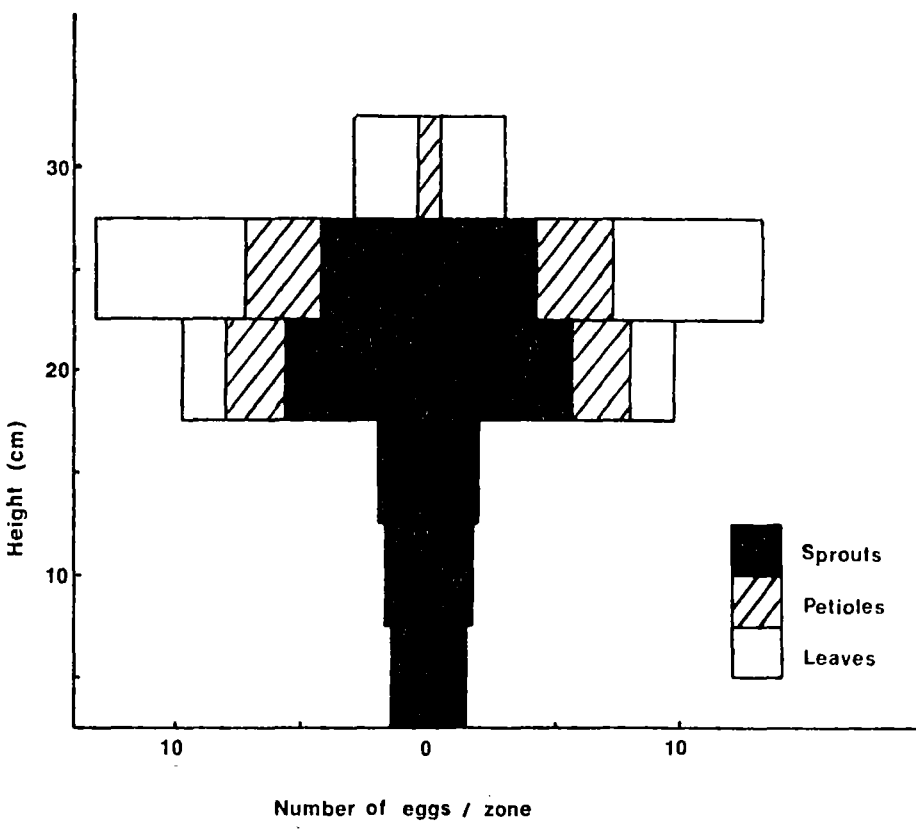


Fig. 7.7. Position of egg laying by diamondback moth caged on Brussels sprout plants.

sprouts on the stem as shown by the results of attempting to rear larvae on individual sprouts from different zones in pottles (Table 7.10). This showed clearly that larval survival was highest among the upper zone sprouts and decreased markedly in the mid and lower zones.

Close examination of the sprouts in this study revealed that the average penetration by larvae into the sprouts was 4.1 leaflets although the range was from 2-8 leaflets.

TABLE 7.10 Survival of first instar diamondback moth larvae on sprouts from each of the upper, mid and lower zones of the Brussels sprout plant.

	Upper	Mid	Lower	LSD
% Survival	93.8	62.5	50.0	11.8

f. The effects of cabbage aphid on yield of Brussels sprouts, Experiment 7.6.

The growth of the 1979 aphid population recorded in Figure 4.11 was reflected in an increase in the mean grading of aphid attack as the season progressed among those plants monitored in the unsprayed block. By mid March, aphids were present on all plants but none had been killed by the aphid outbreak; class VI was therefore removed from the analysis. Following harvest, yield figures were grouped according to aphid grading for

each time of assessment and the results (Table 7.11) show little yield loss in the lower classes of attack but considerable loss within the higher classes. There were, however, few plants in the two higher categories, hence overall yields were little affected. For example, at the first assessment, yield losses of 50 and 84% were recorded from plants in attack classes IV and V respectively, yet total yield loss was estimated at only 11%. Estimates of overall yield loss ranged between 11 and 19% depending on the time of assessment, with a mean of 15.2%.

The results in Table 7.11 suggest that the earlier a plant comes under heavy aphid attack the greater will be the yield loss. This was substantiated by multiple regression analysis using times of grading as variates with yield where step-down procedures (Zar, 1974) selected gradings on day 49 as making the greatest contribution to yield loss ($P < 0.01$) although attack at peak population, on day 77, also significantly ($P < 0.05$) affected yield.

g. Varietal differences in Brussels sprouts' susceptibility to pest attack, Experiment 7.7.

The mean numbers of pests per plant on the variety trial sampled in the unsprayed bed (E) on 7 February are shown in Table 7.12. Although the sampling occurred early in the season, before the peak of pest attack,

TABLE 7.11 Mean yields (g fresh wt) of Brussels sprouts in relation to severity of aphid attack. Yields are grouped according to the class of aphid attack assessed at five stages through the 1979 outbreak. Yield loss estimates by Judenko's (1973) method.

Time of assessment (days from transplant- ing)	Class of attack					Estimated yield loss (%)
	I	II	III	IV	V	
39	617.9+38.1 (36)	663.3+32.7 (27)	514.6+59.4 (19)	307.1+39.2 (16)	101 (2)	11
49	667.0 (3)	652.5+35.6 (50)	557.2+52.2 (21)	393.0+47.8 (18)	218.2+42.0 (8)	16
63	- (0)	655.4+34.1 (55)	524.0+46.7 (23)	404.0+55.0 (14)	191.0+23.4 (8)	16
70	- (0)	696.5+94.2 (15)	614.8+43.0 (35)	541.4 (35)	278.0+67.4 (15)	19
77	- (0)	-	636.5+38.0 (55)	527.7+31.5 (32)	237.1+39.4 (13)	14

TABLE 7.12 Mean numbers of insects/plant from seven varieties of Brussels sprouts in a trial counted on 7 February 1979.

	White butterfly		Diamondback moth	Cabbage aphid	
	Eggs	Larvae	Larvae	Alatae	Colonies
Multima line	3.2	0.6	1.5	3.2	0.7
Jade E	2.1	0.5	0.2	4.0	2.0
Jade Cross	1.8	0.9	1.8	2.5	0.4
Lunet	1.5	0.4	2.4	2.1	0.1
Jade G	2.4	0.3	2.2	4.8	0.3
Rampart	2.5	0.5	1.6	3.8	0.5
Rasmunda	1.9	0.7	1.7	2.3	0.1
LSD (5%)	1.2	0.7	1.4	1.7	1.2

some differences emerge. There was little difference between numbers of white butterfly eggs or larvae between varieties but numbers of diamondback moth larvae were significantly lower on variety Jade E. The lowest numbers of cabbage aphid *alatae* occurred on varieties Lunet and Rasmunda while Jade E had significantly ($P < 0.05$) more aphid colonies than any of the other varieties at this time. The results of gradings and counts made in March for both sprayed and unsprayed blocks are shown in Table 7.13. In the sprayed plot high numbers of aphid colonies were present on varieties Jade E and Jade Cross and every plant of Jade E had aphids present, at least in low numbers. This contrasted with variety Lunet where only 20% of the plants held aphids and there were none with colonies (Plate 7.3). In the unsprayed block a similar pattern emerged with the grading of the varieties according to pest attack. The highest gradings for aphid attack were those for variety Jade E and the lowest on variety Lunet. Conversely lowest levels of feeding damage occurred on variety Jade E and the highest on varieties Lunet and Rasmunda.

The susceptibility of the plant through its growth is not necessarily related to the amount of direct damage that will occur at harvest. The variety trial was harvested on 7 June and the results of sprout examination are shown in Table 7.14. There was little difference



Plate 7.3 Differential responses among sprout varieties to cabbage aphid attack. Varieties Jade Cross and Jade E in the centre with Lunet in the right foreground.

TABLE 7.13 Percentage of plants infested with aphids with mean number of aphid colonies/plant from the sprayed block (5 March 1979) and mean grading for aphid attack and feeding injury in the unsprayed block (19 March 1979).

	Sprayed		Unsprayed	
	% plants with aphids present	Mean no. of colonies/plant	Aphid attack	Feeding injury
Multima line	40	0	2.93	1.80
Jade E	100	2.3	3.13	1.27
Jade Cross	80	1.9	2.13	2.00
Lunet	20	0	1.53	2.07
Jade G	80	0	2.27	1.87
Rampart	60	0.2	1.40	1.80
Rasmunda	70	0.4	1.87	2.07
LSD (5%)		1.2	0.52	0.61

in the overall levels of damage between the varieties but a tendency did exist for greater damage in those with later maturity. This effect was even more pronounced when the presence of aphids or their detritus was considered. On careful examination of the sprouts from each zone for damage it was found that new damage was generally confined to the upper zone which was also where the highest levels of damage were located. The apparent recovery of sprouts in the lower zones from damage, as indicated in section e, may be explained by leaflet senescence. In section e it was recorded that the

average penetration by diamondback moth larvae was 4.1 leaflets. The results of examination of the Brussels sprout varieties for senescence of leaflets are shown in Table 7.15. It can be seen that the earlier maturing varieties, in general, showed greatest senescence particularly in the lower zones. When number of damaged sprouts was plotted against senescence in the mid zone (Fig. 7.8) a significant ($P < 0.05$) inverse relationship emerged and it can be seen that leaflet senescence was probably an important factor in reducing damage levels in some varieties.

4. Discussion - The Relationship Between Pests and Damage in Brussels Sprouts

The results show clearly that, in specific circumstances, each of the three pests can cause damage to the crop. White butterfly and cabbage aphid were both found to be responsible for loss of gross yield indirectly by feeding on the plant, while diamondback moth caused losses both by foliage feeding and feeding directly on the sprouts. Direct damage by diamondback moth was related to the seasonal mean numbers and, therefore, the losses in unsprayed plots were high in 1978 and 1980, 21% and 14% respectively, and low in 1979 with 6% of the sprouts damaged.

TABLE 7.14 Mean percentage of sprouts at harvest damaged by diamondback moth or containing aphids or aphid detritus from a comparison of seven different Brussels sprout varieties.

	Diamondback moth damage	Aphid contamination
Multima line	7.7	3.26
Jade E	8.9	1.54
Jade Cross	8.3	0.54
Lunet	10.6	2.34
Jade G	6.3	1.90
Rampart	10.9	6.98
Rasmunda	19.5	4.98
LSD (5%)	6.6	2.6

TABLE 7.15 Relationship between sprout leaflet senescence and numbers of damaged sprouts from each of three zones among seven Brussels sprout varieties.

	Mean no. of senesced leaflets/sprout			Mean no. of damaged sprouts/plant		
	Upper	Medium	Lower	Upper	Medium	Lower
Multima line	0.8	4.4	10.3	3.0	3.2	1.0
Jade E	0.1	4.4	6.3	8.4	1.6	0.4
Jade Cross	0	5.9	9.6	9.4	0.4	0
Lunet	0	2.5	4.5	6.4	3.6	0.8
Jade G	0	4.5	8.4	2.6	2.4	1.6
Rampart	0	1.3	2.5	5.4	2.0	0.8
Rasmunda	0	0.1	1.1	10.2	6.2	2.0
LSD(5%)		1.6	2.1	5.9	3.4	1.8

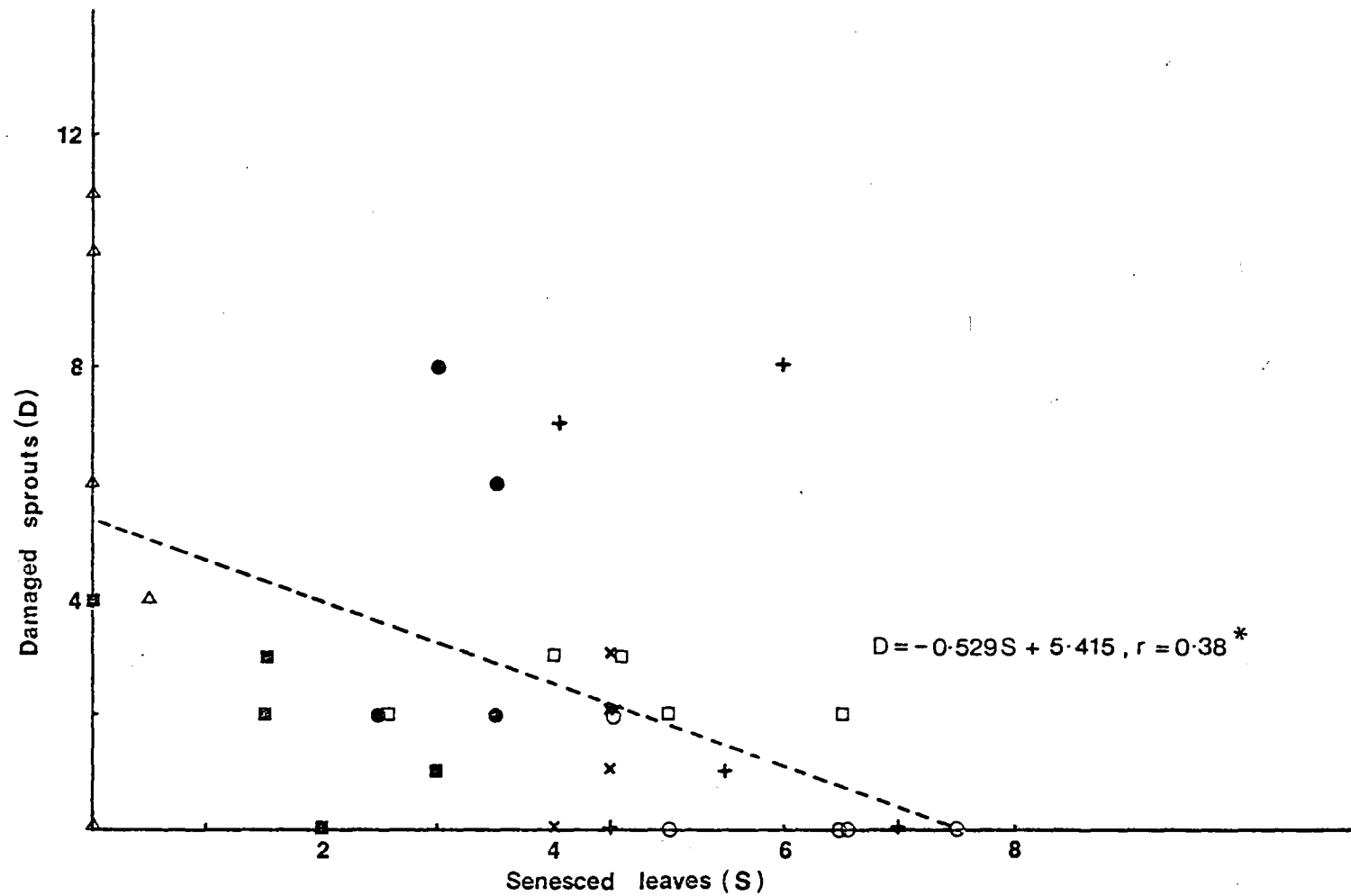


Fig. 7.8. Relationship between sprout leaflet senescence and numbers of damaged sprouts in 7 varieties. + , Multima line; x , Jade E; O , Jade Cross; ● , Lunet; □ , Jade G; ■ , Rampart; Δ , Rasmunda;

The use of schedules of different insecticides and examination of harvest yield in 1978 allowed the effects of the major pests to be identified, in particular with the reduction of larvae and the subsequent reduction of damage in the carbaryl treatment. The use of selective insecticides, however, resulted in increased numbers of non-target pests. Carbaryl promoted an increase in the cabbage aphid population, as had been previously noted by Pimentel (1961) and Root and Selsey (1969). The former author considered that increased aphid numbers were the result of predator mortality while the latter authors proposed that decreased herbivore competition was the most important factor. In this experiment up to six dead coccinellids were noticed under each plant in the carbaryl treated plot thus tending to support the former argument. In the demeton-S-methyl treated plots levels of damage caused by diamondback moth were significantly higher than in other treatments as were diamondback moth numbers in those plots but the causes of this are unclear.

While selective insecticides used in the 1977/78 season allowed identification of the effects of the major pests they gave little indication of the dynamics of the pest-crop interaction. Division of the crop growing season into three phases of treated or untreated periods in 1978/79 showed that sprout yield was reduced when insecticides were omitted in the mid season. The number of damaged sprouts was greatest following a late spray-free

period but omission of sprays in either the early or mid periods also led to an increase in damage.

The effects of attack at specific times were examined by confining known numbers of larvae of white butterfly and diamondback moth on individual plants in cages. The results indicated that white butterfly could cause considerable yield loss by feeding on the foliage while diamondback moth, more commonly, caused direct damage to the sprouts. In these cage experiments white butterfly were found to have greatest effect on yield at early growth stages. Similar effects were found for defoliator attack on cabbages (Prasad, 1963) and wheat (Pickford and Mukerji, 1974). When natural populations were studied (Experiment 7.2) there was, however, little yield loss following insect attack at early stages. This was probably due to the few pests present (Figs. 4.7-11) and the ability of the plant to compensate for defoliation in the early stage (Chapter 6).

In Experiments 7.1 and 7.2 yield losses occurred after attack by relatively low numbers of pests in comparison to those required to cause yield loss in the cage experiments. The apparent differences in the results may be due to the fact that losses caused by natural populations are dynamic and will accumulate over time while caged populations are confined to one time period. It is interesting to note that the majority of cage studies of insect damage have led to the conclusion

that field populations do not cause yield loss (e.g. Mueller and Engross, 1980). The relationship between time of attack and damage will be examined further in Chapter 8.

Direct damage to the sprouts was caused by feeding of the diamondback moth larvae. When white butterfly larvae were confined at levels of 60/plant there was no increase in damage levels over the control plants. Cabbage aphid were occasionally found in the sprouts, causing contamination, but this was a relatively minor problem. Diamondback moth larvae feed on the leaves and in the crown of the plant in the early stages of growth but later in the season were mainly found in the developing sprouts. The larvae do not feed on the very small sprouts and thus there was a threshold of 7 mm below which they did not, or could not, enter the sprouts. This, therefore, confined their ability to damage the sprouts to the latter part of the season when the sprouts had exceeded this size and the use of spray-free periods (Experiment 7.3) confirmed that, in fact, most damage occurred in the mid and late periods. Among the lower sprouts there appears to be some tolerance of damage as these sprouts will naturally shed the outer leaflets before harvest. Differential leaflet shedding between varieties may help to explain some of the differences in varietal susceptibility that were found in this study.

In the early part of the season there were no

clear differences between varieties with regard to attack by diamondback moth or white butterfly although Jade E did have lower numbers of diamondback moth and a lower grading for feeding damage. At harvest the later maturing varieties had the greatest number of damaged sprouts. Clear differences were evident for aphid attack with variety Lunet consistently supporting the lowest number of aphids. The leaves of this variety were relatively flat as opposed to curled in some of the other varieties which may, in part, explain the differences in numbers of aphids (Dunn and Kempton, 1971).

At harvest it is the late maturing varieties that have the most contaminated sprouts. This may be due to the low shedding of leaflets prior to harvest in these varieties. It is clear, therefore, that variations in response to pest attack, particularly aphid attack, are evident between currently grown commercial varieties of Brussels sprouts and that the use of tolerant or resistant varieties should be examined further as a means of reducing insecticide use in this crop.

CHAPTER 8

MODELLING AS AN AID TO THE UNDERSTANDING
OF YIELD LOSSES CAUSED BY DEFOLIATING
PESTS IN BRUSSELS SPROUTS

Norton (1976a) proposed that our understanding of pest problems could be improved by examining key relationships through the use of simple models which could be either simply descriptive or mathematical in form.

Many of the simple models for pest-yield interactions are static in relation to time and as Ruesink (1975) pointed out, implicit in the use of these models is the assumption that no leaf growth occurs during defoliation. Hence static models are most appropriate to those pests which are present in the crop for short periods only, e.g. locusts. For pests present through a considerable period of the crops' growth, like the brassica pests in this study, dynamic models of pest-crop interactions are more appropriate.

In this chapter, Section 8.1, a dynamic-deterministic computer model (Ruesink, 1975) is developed to elucidate the relationship between plant growth and defoliation. In Section 8.2 simple graphical models are developed to show the relationship between pest population, feeding and insecticide use. The computer model is then used (Section 8.3) to assess the effects of white butterfly feeding on yield loss and the optimal timing of insecticide sprays.

1. Plant Growth and Response to Defoliation

The model described below is developed from data gathered in Experiments 6.1 and 6.2 and output is then compared with the results from Experiment 6.3.

a. Model development

For construction of even a simple model data is needed on the growth pattern of the plant and the development of yield in the crop. In Chapter 6 it was shown that leaf area duration over the whole season was the major determinant of yield. Leaf area at any one time is the result of two processes, the growth of new leaves and the senescence of old. The former can be represented by a logistic curve while the latter seems to follow a linear relationship (Fig. 8.1).

The effects of early defoliation on leaf growth and leaf senescence are shown in Figure 8.1. In each case the leaf growth follows a logistic function with a similar asymptote (assume $K = 155$). Leaf senescence appears to occur at the same rate in all three treatments following defoliation. The apparently high senescence on 18 April, following 100% defoliation, is in fact due to the removal of more than 40 leaves from this treatment which were then considered senesced. Yield is a function of leaf area duration (Ch. 6) and therefore, with this information a simple simulation model of plant growth was constructed using Fortran as the programming language.

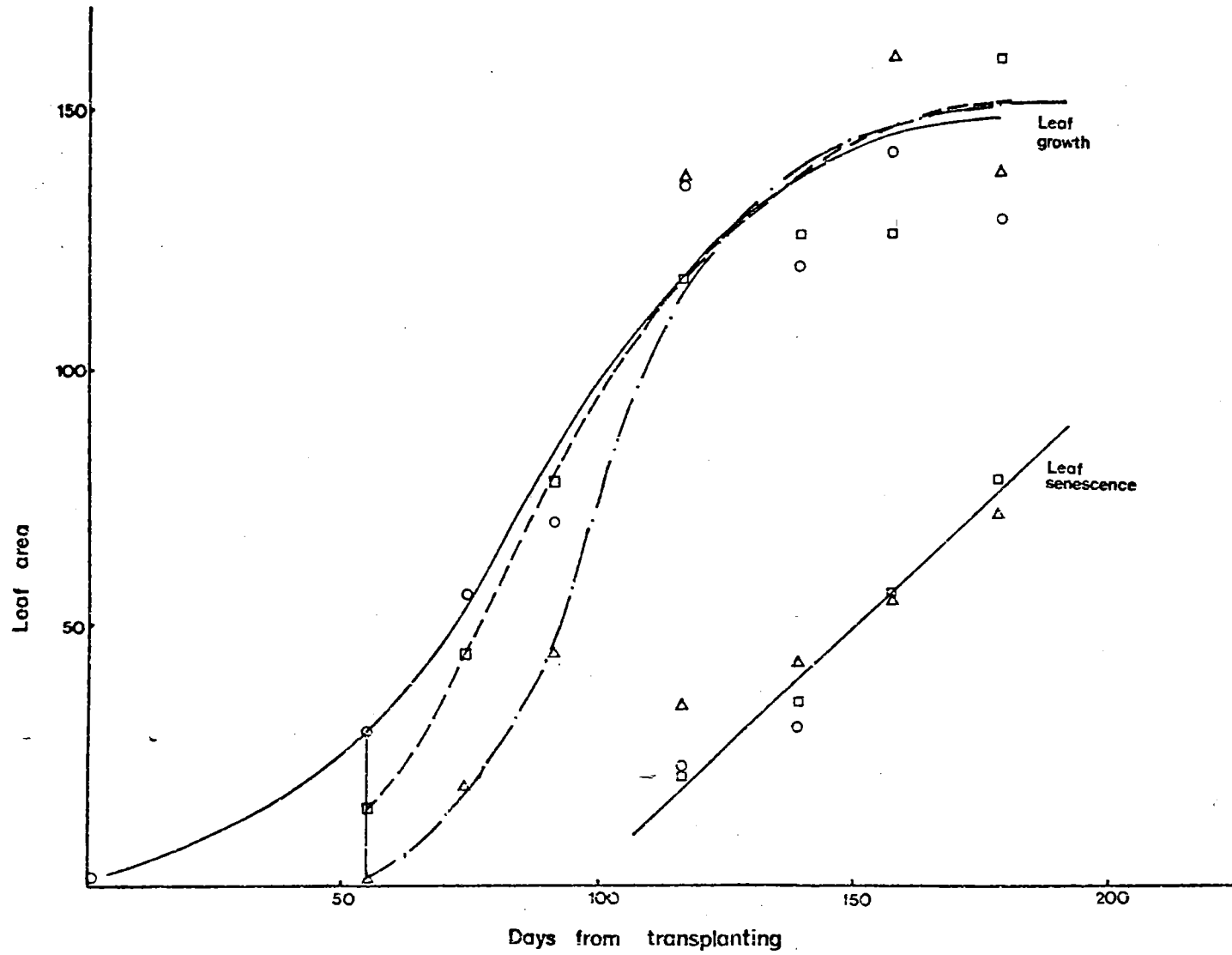


Fig. 8. 1. The cumulative growth of leaves and leaf senescence following artificial defoliation 54 days after transplanting. ○ , control; □ , 50% defoliation; △ , 100% defoliation. Experiment 6. 2.

The model parameters are presented in Appendix 8.1 and the model, including a compensation factor outlined below, in Appendix 8.2.

The leaf area output of the initial model is presented in Figure 8.2a for 0, 50 and 100% defoliation on day 54, the time of defoliation in the original experiment. The relationship between defoliation at stages throughout crop growth and yield output for the model is presented in Figure 8.2b. It can be seen that while the model adequately describes plant growth and sprout production in the absence of defoliation, plant growth following defoliation at early stages is not adequately represented. It appears that this is due to the omission of a compensatory factor from the model operating over the early stages of growth. Compensation is the result of an increase in the leaf area growth rate (LAGR) following defoliation. The compensation factor is calculated on the basis that the LAGR is increased until such time that the leaf area of the defoliated plant is again equal to that of the control plant after which the compensation factor returns to zero. The time taken for this to occur seems to be a maximum of six weeks for the 100% defoliated plants and proportionately less according to the degree of defoliation such that the compensation factor $COMPF = 0.053 \times \text{defoliation} / \text{leaf area}$ on previous day. It is also assumed that compensatory ability is at a maximum in the early stages of growth and

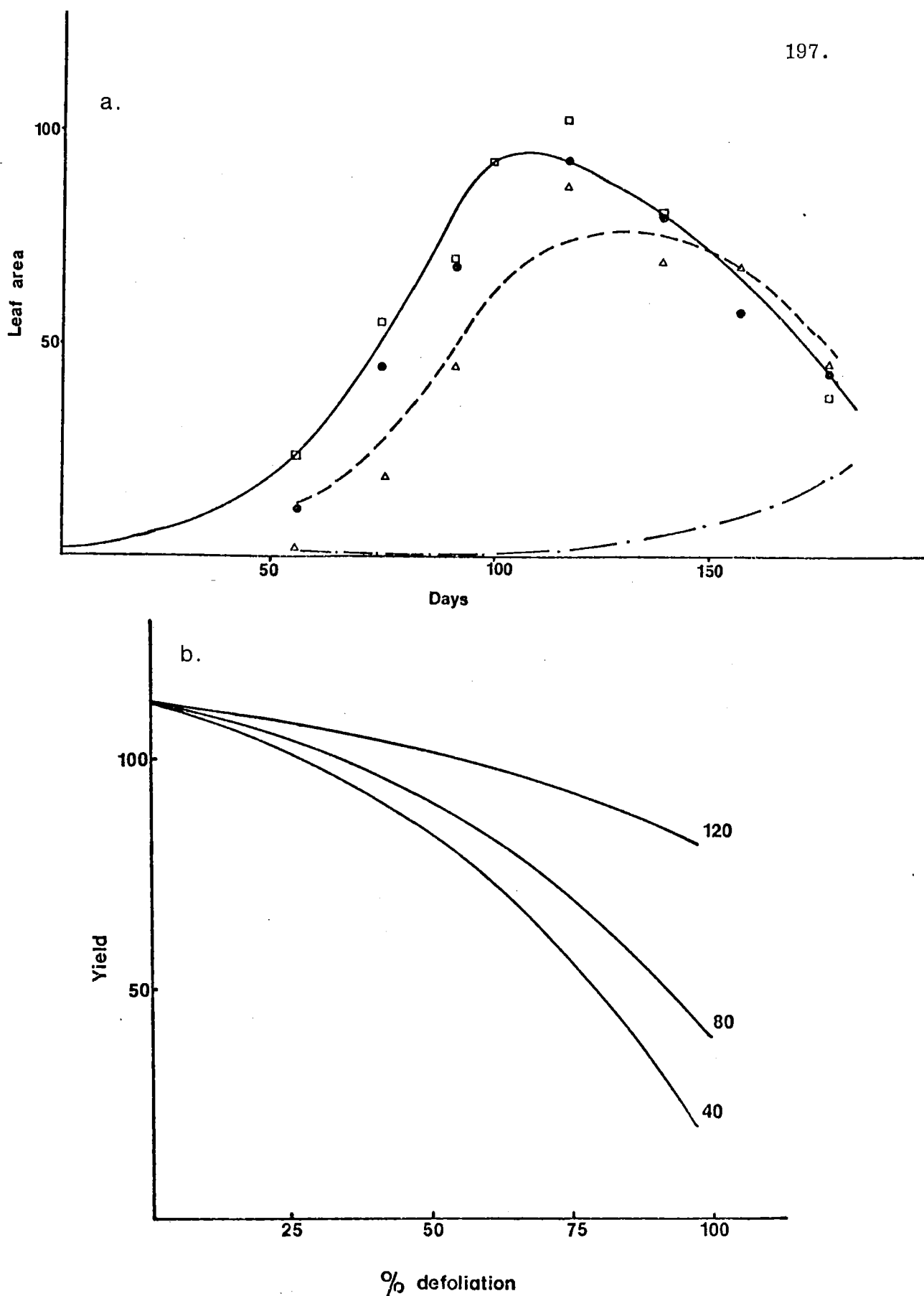


Fig. 8.2. (a) Leaf growth following defoliation, Experiment 6.2. □, control; ●, 50% defoliation; Δ, 100% defoliation. Model output without compensation (—), control; (---), 50% defoliation, (-;-), 100% defoliation. (b) Effects of defoliation at days 40, 80 and 120 on the model without defoliation.

then declines proportionately from day 50 to day 100. There is no indication of compensation in the later growth stages.

To account for differences in absolute leaf area due to defoliation, senescence is introduced into the model as a proportionate loss of leaf area from day 98 onwards.

b. Model output

The effects of introducing defoliation into the model at various stages through the crop's growth are shown in Figure 8.3. The results show the expected response with a high ability to compensate for defoliation in early stages of growth followed by a mid-growth stage of greatest susceptibility with limited compensation and a late stage where there is no compensation but yield losses are low due to much of the yield being already formed.

A more detailed comparison between model output and the independently obtained results of defoliations on days 43, 82 and 121 from Experiment 6.3 shows a close relationship between model output and empirically obtained results (Fig. 8.4).

The model thus presented has dealt with the proportion of the plant defoliated, i.e. damage from the plant point of view. It must be remembered, however, that the plant varies greatly in leaf area throughout its

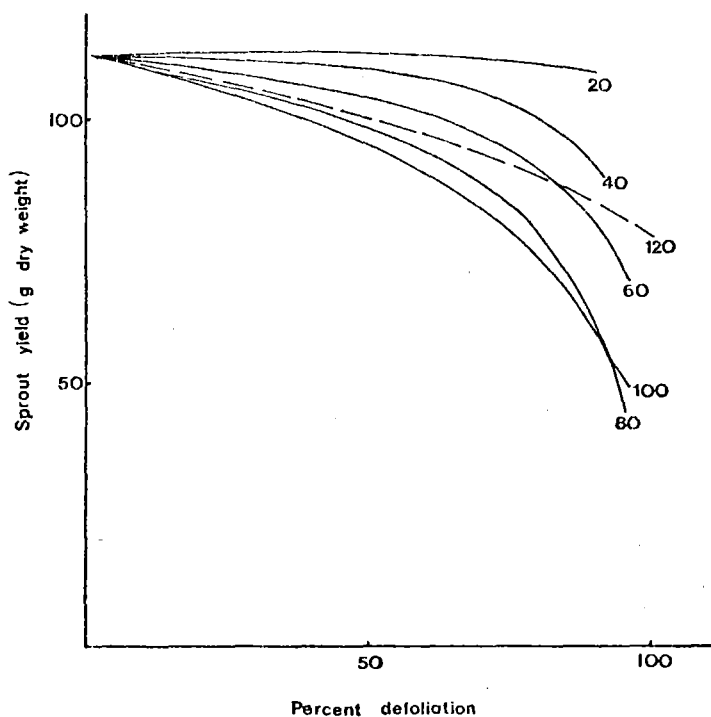


Fig. 8.3. Model output of the relationship between yield and defoliation at five stages between days 20 and 120 throughout the plant's growth.

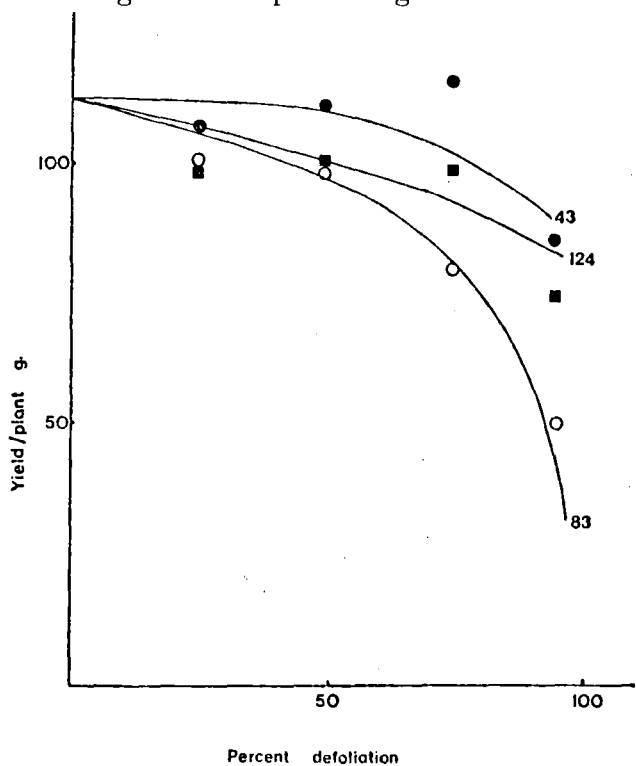


Fig. 8.4. Model validation by comparison of model output and actual yields following defoliations on days 43 (●), 83 (○) and 124 (■) from transplanting.

growth and of greater importance to the grower will be the relationship between absolute levels of damage and yield loss and how this relationship varies as the crop matures. Thus, Figure 8.5 shows the relationship between time of defoliation and the amount of leaf area removal necessary for yield losses ranging from 5-30%. It is clear that the plant is most sensitive to absolute defoliation in the early growth stages and that its tolerance to defoliation increases with age. The relationship between yield and pest populations will be examined further in Section 8.3.

2. The Effect of Insecticides in Reducing Foliage Losses Due to White Butterfly Feeding

Insecticides are usually evaluated on the basis of their efficacy in the short term with less attention given to their effects over the whole season. However, it is this reduction of pest population over the whole season and the consequent reduction in feeding and crop damage that is the principle^{a/} concern of the grower. Thus, in this section, the effects of a single insecticide spray applied at different times throughout the season will be evaluated from a graphical model in terms of its ability to reduce the number of 'larval days' and to reduce the amount of feeding on Brussels sprout plants.

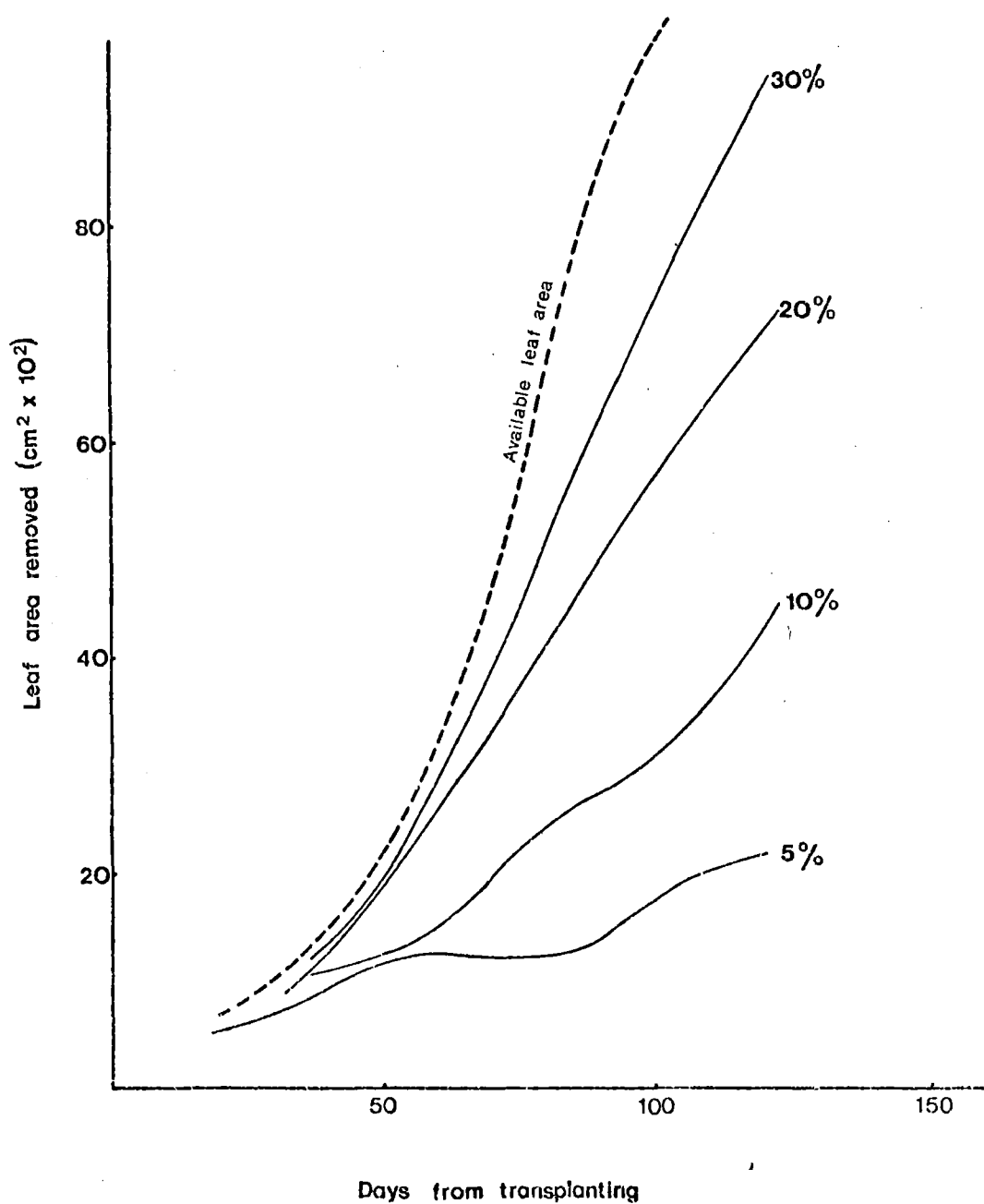


Fig. 8.5. Leaf area removal necessary for losses of yield ranging from 5 - 30% through the growing season of Brussels sprouts.

a. Methods

The graphical model used in this section is based on the seasonal population distribution for white butterfly larvae recorded in 1979 and adjusted for missing larvae (Section 4.3a). To assess the effects of insecticides in reducing this population and its feeding, the following information and assumptions are necessary.

- Relationship between feeding, instar and temperature (Chapter 5).
- Effect of pesticide; assume 90% reduction in population.
- Development of pest population. Thermal constants for development were given for larval stages in Chapter 5 and for eggs and pupae from Ashby (1972) and are combined in Figure 8.6; assume the population one generation from the application of the spray equals that of the unsprayed crop.
- Assume that the relationships between known data points are linear.

b. Results

The population curve corrected for larvae missed by direct counting is presented in Figure 8.7 together with the feeding rate curve of the population. It can be seen that peak feeding occurs at a later date than the peak population due to the increase in food consumption

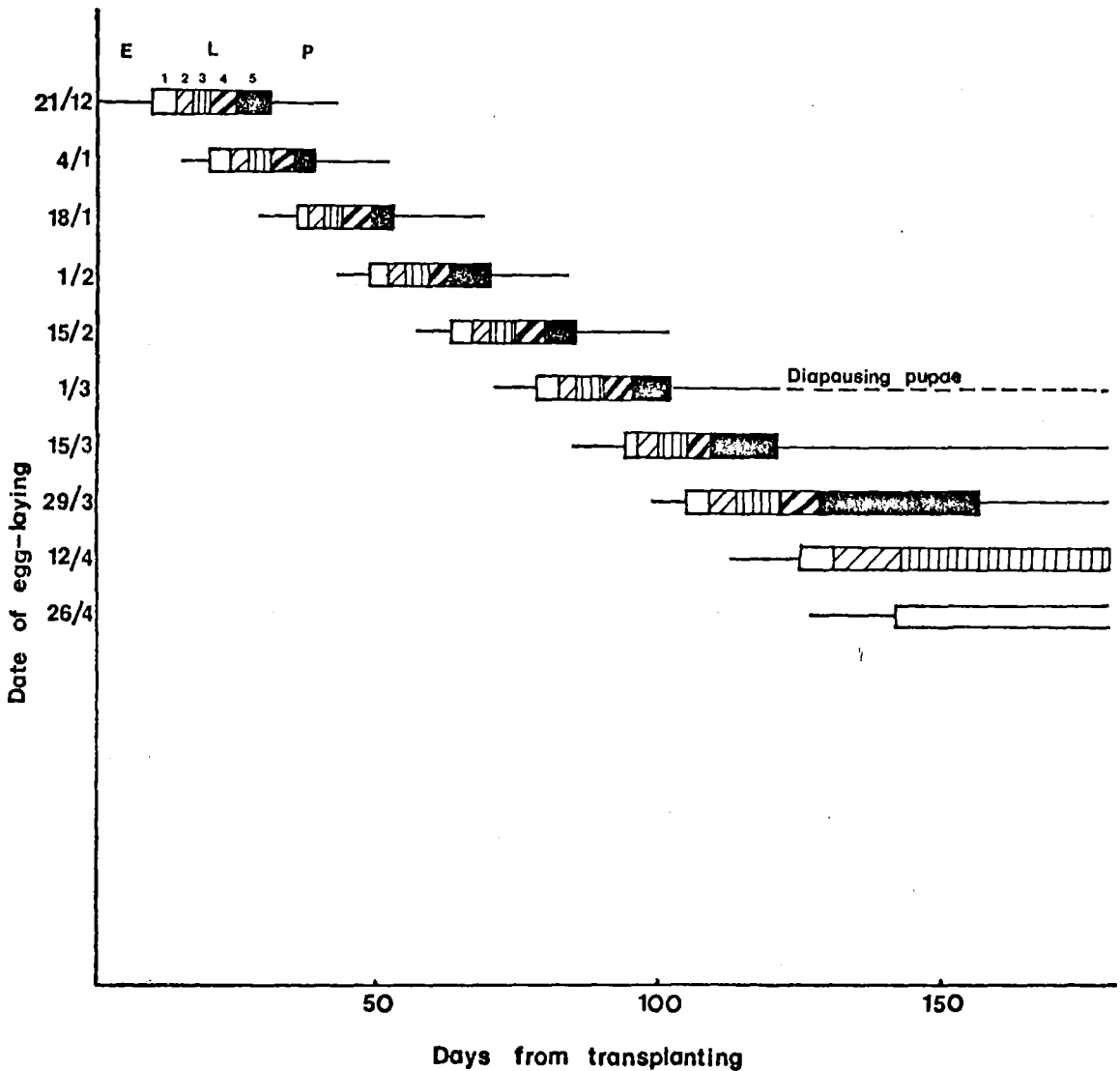


Fig. 8.6. Seasonal changes in the duration of the immature stages of white butterfly throughout the growth of a Brussels sprout crop in Canterbury. (E), egg; (L), larva; (P), pupa. Calculations based on thermal constants and heat accumulation ($>9.1^{\circ}\text{C}$) over 10 year average temperatures in Canterbury.

of the later larval instars. The effects, according to the graphical model, of insecticide sprays on larval populations at early, mid and late growth stages, are shown in Figure 8.8.

Early and late sprays have little effect but the mid season spray causes a reduction of approximately 60% in the number of larval days. The reduction in feeding was similarly examined and the results are shown in Figure 8.9 indicating again the greatest reductions in feeding following the mid-season spraying. The percentage reduction in larval days and feeding according to spray time is shown in Figure 8.10. The greatest reduction in the number of larval days, 59%, occurs following a spray in week 10, while the greatest reduction in feeding, 84%, follows a spray in week 12.

3. The Pest-Yield Interaction

White butterfly feeds through a large part of the Brussels sprout growing season and therefore the cumulative effects of the feeding of a population of this insect warrant further investigation. White butterfly populations showed a regular seasonal pattern in each of the three years of the study and thus the following daily feeding curve may be estimated from the data in Figure 8.7.

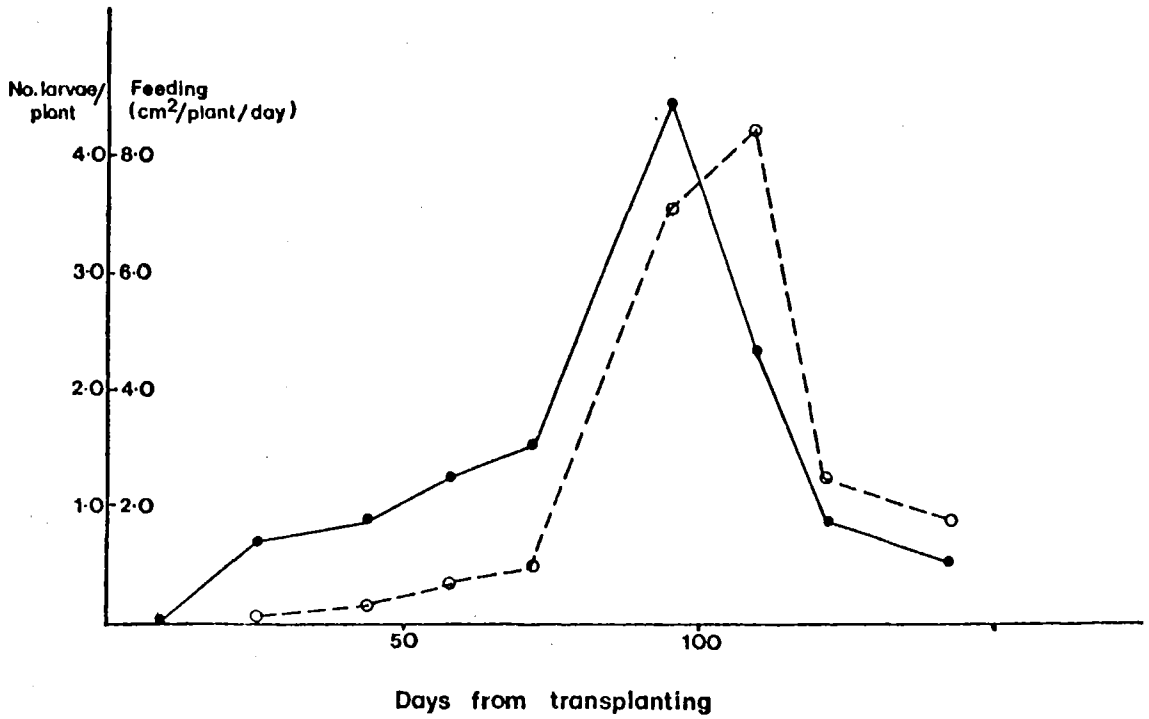


Fig. 8.7. Seasonal distribution of larval population (—) and feeding (---) of white butterfly on Brussels sprouts. Population data taken from an unsprayed crop, 1979.

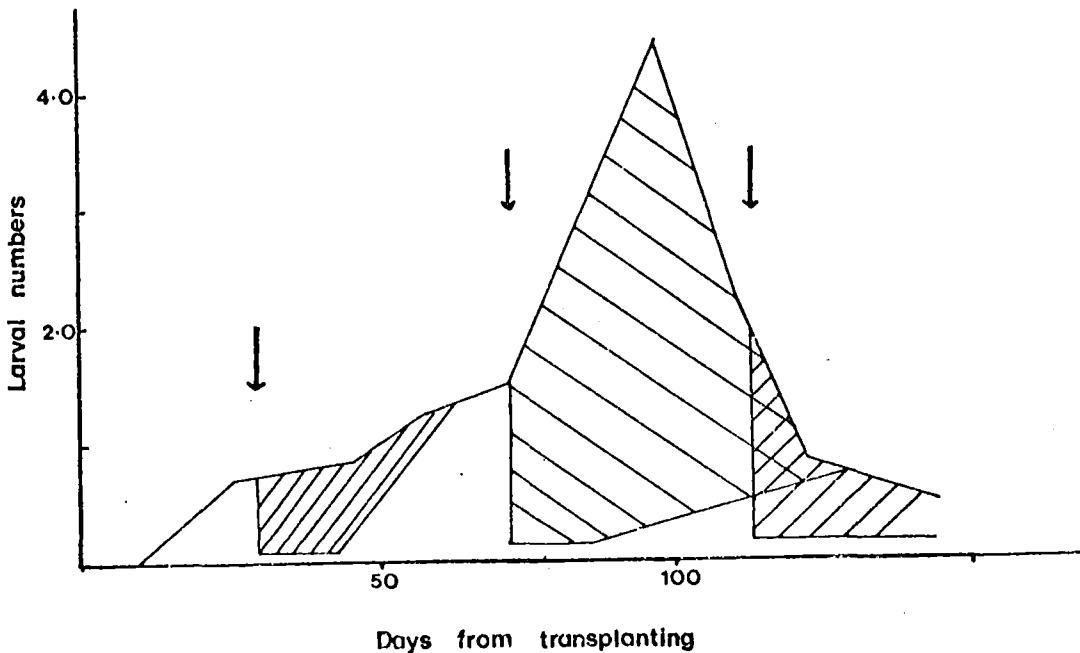


Fig. 8.8. White butterfly population on Brussels sprouts showing the estimated reduction in larval-days that would follow early (▨), mid (▩) and late (▧) applications of insecticide (↓).

of the later larval instars. The effects, according to the graphical model, of insecticide sprays on larval populations at early, mid and late growth stages, are shown in Figure 8.8.

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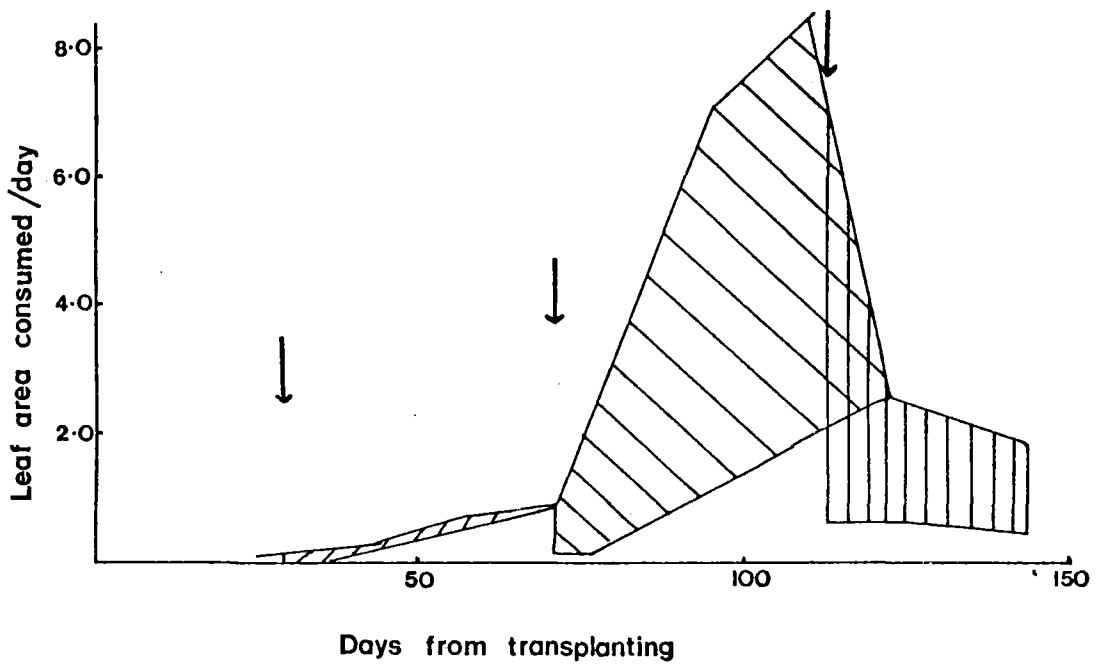


Fig. 8.9. Daily leaf area consumption by white butterfly on Brussels sprouts showing the estimated reduction in foliage loss following early (▨), mid (▩) and late (▧) applications of insecticide.

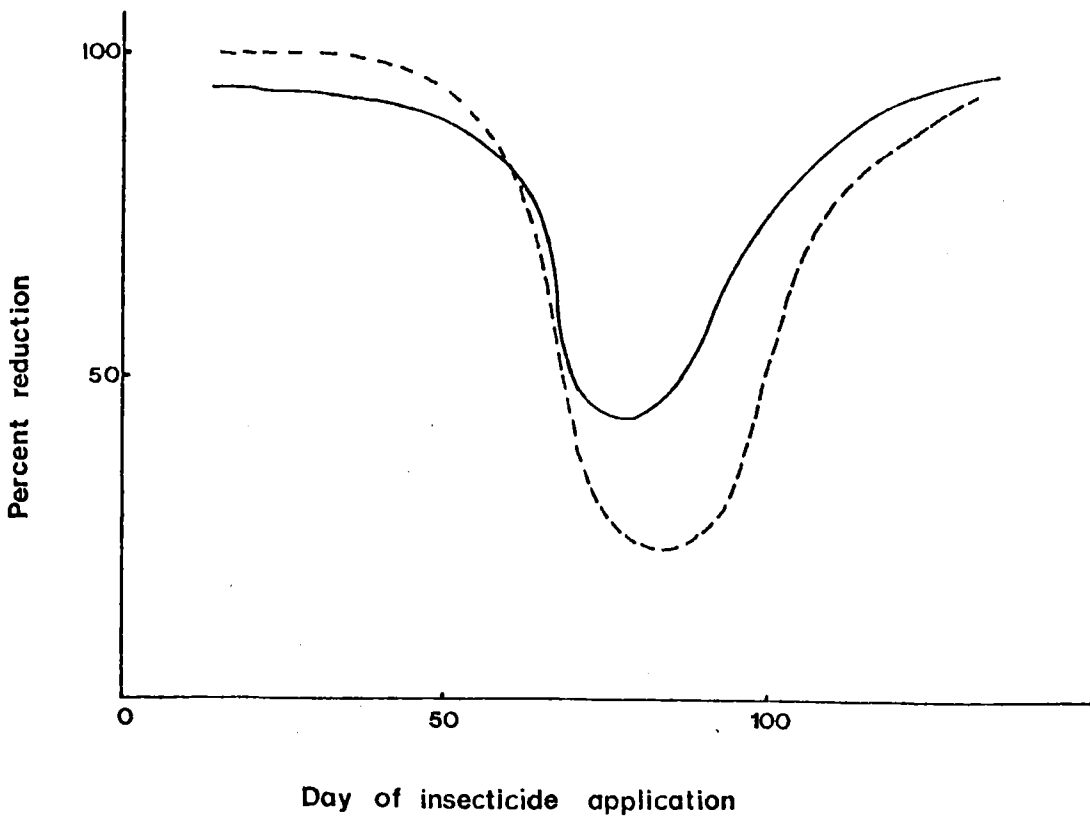


Fig. 8.10. Estimated percentage reduction in the number of larval days (—) or leaf area consumed (---) according to

$$\text{LAR}^1 = -0.7238 + 0.0000194J^3 - 0.000000131J^4 \dots$$

.. (a), (P < 0.05)

¹LAR, Leaf area removed (cm²);
J, days from transplanting.

The results of adding this feeding curve to the model and five and ten times this amount of defoliation are shown in Figure 8.11 and the relationship between population size and yield loss in Figure 8.12. The impact of a "normal" population is small resulting in only a 1.1% yield loss but increasing population size leads to an exponential increase in the yield loss.

The purpose of insecticide use is to reduce yield loss. The effects of early, mid and late insecticide applications on feeding were shown in Figure 8.7. The daily feeding curve (a) can similarly be modified by insecticide application and the model output can be compared with estimates of the feeding rates of field populations of white butterfly monitored in 1979 following early, mid and late applications of insecticide (Experiment 7.2). The model results show a similar pattern of feeding to that estimated from the field data indicating the validity of the assumptions upon which the model is based (Fig. 8.13). The relationship between the time of application of a single insecticide and yield loss is shown in Figure 8.14 indicating that yield loss by white butterfly will be minimized by application of

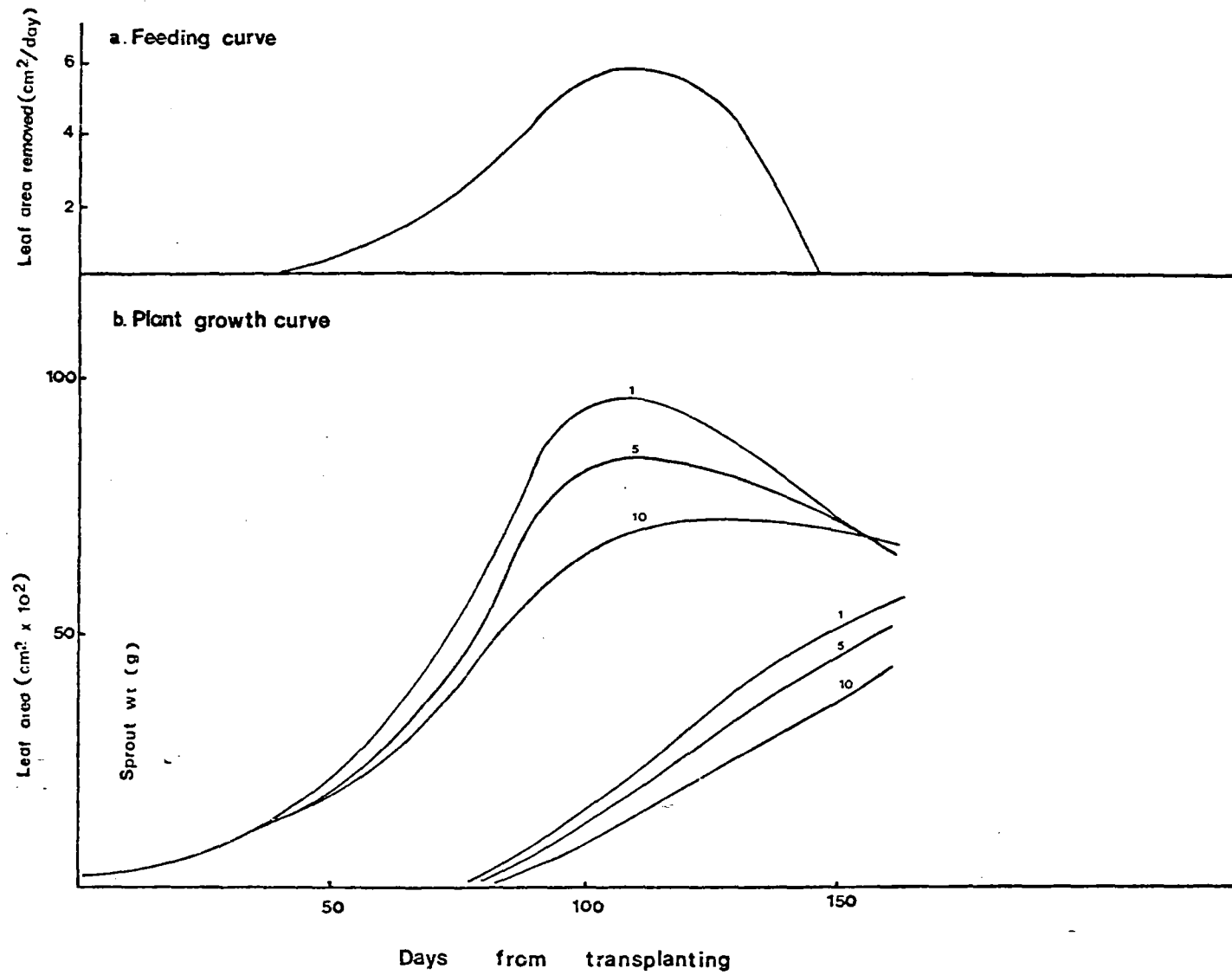


Fig. 8.11. The effects of feeding of a normal population of white butterfly and five and ten times that number on the growth of Brussels sprouts, as indicated by the model.

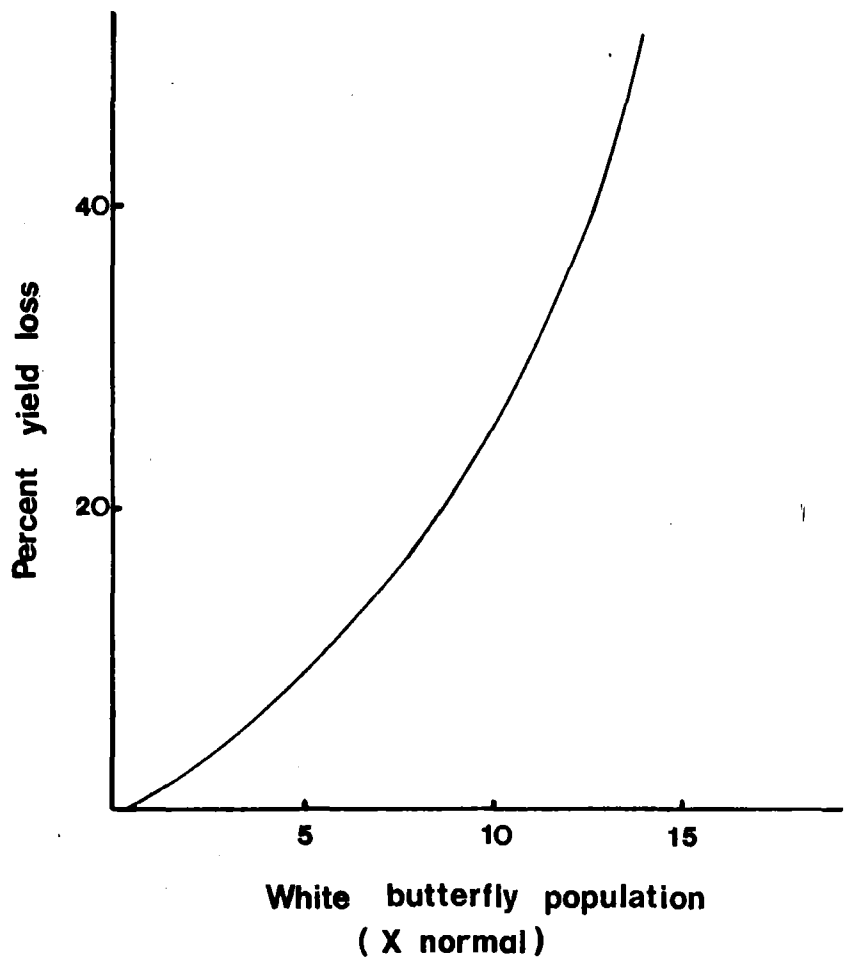


Fig. 8. 12. Model output showing the relationship between white butterfly population size and yield loss in Brussels sprouts.

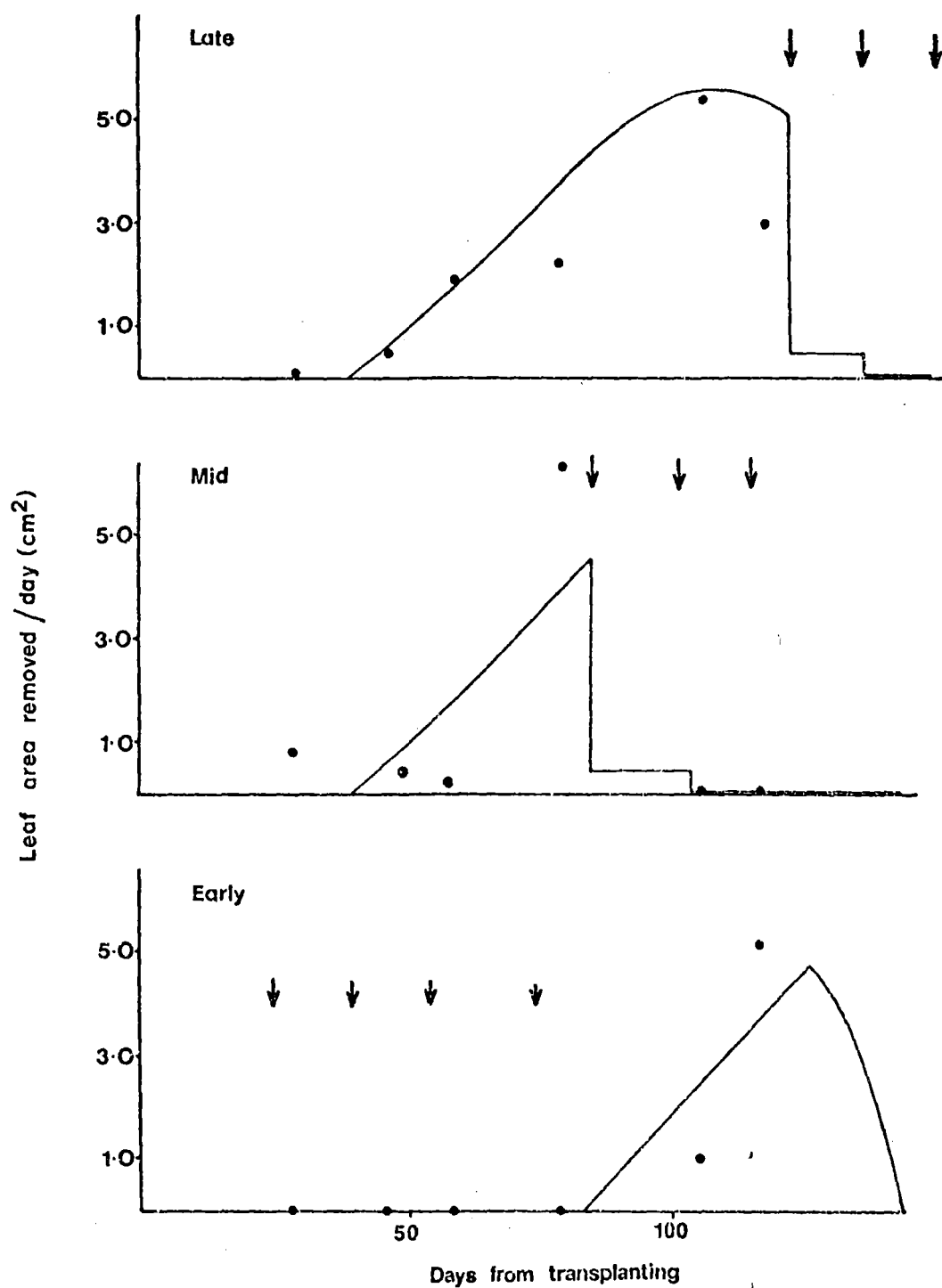


Fig. 8. 13. The effect of insecticide application on feeding of white butterfly as indicated by the model (---) or estimated from the field population (●). ↓, insecticide applications.

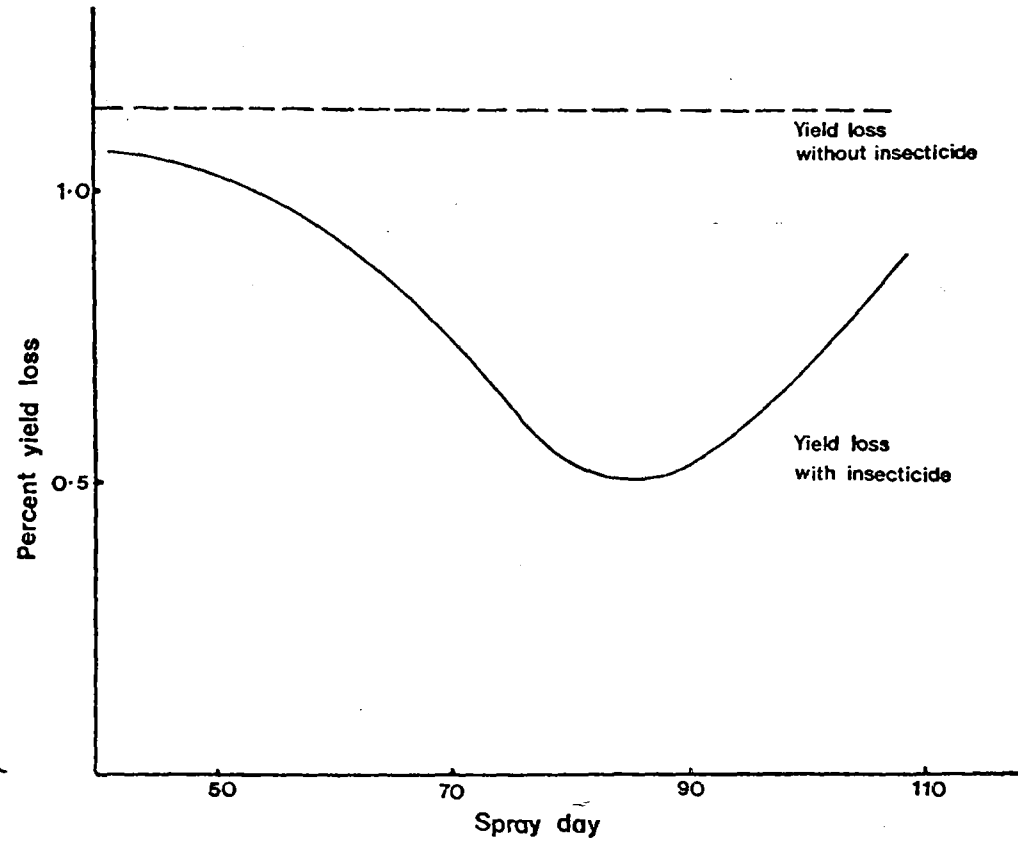


Fig. 8. 14. Model predictions of the effect of time of application of a single insecticide spray in reducing yield loss due to white butterfly feeding on Brussels sprouts.

insecticides in the 13th week from transplanting and that the potential yield loss can be reduced by 56% by a single insecticide application at this stage.

4. Discussion

The simple simulation model thus developed represents the Brussels sprout plant and seems to adequately describe the interaction between defoliation and yield and can, therefore, assist our understanding of the relationship between defoliating pests and yield in this crop. The model indicates that the plant is most susceptible to loss of leaf area in the mid-growth stage but when considered in absolute terms heavy defoliation in the early stages of growth can cause high yield loss. Such relationships can be determined by the use of static models but the pest/plant interaction becomes more complicated when the feeding of a population of insects over the whole season is considered.

For defoliation by white butterfly, static models such as could be represented by the regression lines in Figure 8.3, indicate that, on day 100, 37% defoliation or approximately 3700 cm^2 of leaf removal would be necessary to cause 10% yield loss. This would represent about 100 larvae per plant. The dynamic model, however, indicated that a population of five times the normal would cause this loss, i.e. only 22 larvae per plant at peak

populations. The effects of gradual defoliation, are, therefore, most insidious but no less important than sudden removal of large amounts of leaf area but cannot be represented by static models. It is interesting to note that in most cases where economic injury levels have been established or pest impact determined using static models it has generally been concluded that the pests under study have little effect on yield (e.g. Tamaki and Hagel, 1978).

While the development of models such as that described here aid the understanding of the system that is being modelled, the true benefit from such models will arise from their use in assisting pest managers to manipulate that system to minimize crop losses. Experiments can be carried out on such a model and may indicate the relative benefits of pest control measures at different times throughout the crop's growth and can even pinpoint the optimum time for the use of control measures. The criteria for initiating control actions may also receive attention as maximum reductions in numbers, feeding and yield loss may not be synchronous as in this case where the optimum time for spraying to maintain yields was later than that to provide the maximum reduction in insect numbers but about the same time as that for greatest reduction in total feeding. These differences would be greater where the critical period is more defined or occurs at a markedly different

time to peak populations. The dangers of using simple models such as this are that the mathematical requirements of the model may distort biological reality. It is often appropriate that stochastic elements are entered into pest/crop models to reflect chance events that occur in nature. In the case modelled here, however, the use of a deterministic model appears warranted due to both the uniformity of both Brussels sprout growth and white butterfly populations between years.

CHAPTER 9

A RATIONAL APPROACH TO PEST CONTROL IN
BRUSSELS SPROUTS PRODUCTION

Dunn and Coaker (1965) proposed the concept of rational control of pests in vegetable crops which was defined as use of the minimum amounts of insecticide in crop production by utilizing an understanding of both crop growth and insect ecology. It was proposed as an alternative to the then fashionable integrated control concept because natural enemies, which are essential to the integrated control concept, were not considered as providing adequate control of pests for the high quality standards demanded in vegetable production.

To meet these high standards many growers use insecticides on a schedule basis but it would appear, from this study as already reported, that insecticide use in Brussels sprouts can be reduced without loss in quantity or quality of yield, and that a theoretical rational control programme can be proposed, based on an understanding of the insect ecology, crop growth and damage relationships gained in the previous chapters.

1. Schedule Spraying - An Appraisal

Many commercial growers of Brussels sprouts apply chemicals for pest control on a schedule basis every two

weeks from transplanting. They do this in the belief that this programme is necessary to insure against pest attack. However, for schedule spraying to be rational it would imply that there is a constant, persistent threat from insects throughout the season. This, however, is not the case. The data presented in Chapter 4 indicated that, for all the pests, numbers varied throughout the year. Between years the seasonal distribution of white butterfly is regular but for diamondback moth and cabbage aphid the pattern was highly irregular with few colonies of the latter recorded in the third year. It is also evident that the plant response will vary with two major periods of susceptibility (Chapters 6 and 7). The first of these occurs in February when the plants are most susceptible to indirect damage and the second occurs later in the season when direct damage and contamination can occur. Thirdly, it is evident that the pests themselves will pose less of a threat as the season progresses and their development and feeding rates are lowered by declining autumn temperatures.

Therefore, in the face of varying attack and varying sensitivity, schedule spraying is an irrational form of control and leads to the use of greater amounts of pesticide than are necessary to ensure the production of high quality, damage free, sprouts.

2. Potential Improvements in Pest Control

a. Pre-emptive measures

There are a number of measures that the grower can take before sowing that may limit pest attack to the crop.

Sowing date

Adjustment of sowing date has been used in many crops as a means of avoiding pest attack. While there is little direct evidence from this study, some speculation may be made as to the effect of sowing date on damage. Potential attack on the crop is delineated by sowing and harvesting dates and also by intrinsic factors in the pest population such as diapause and temperature dependent feeding and development rates. Simulation of pest attack by white butterfly indicates that the potential attack would be greatest following sowing in September and would be decreased by each subsequent sowing due to a shorter potential time for pest development in the crop (Jackson, unpub.). Thus, January and February transplantings would result in low levels of damage. However, research indicates that yield of Brussels sprouts declines markedly with each transplant after December (P. Bull, pers. comm.). In this study, in 1978, yield following the second sowing and January transplanting was only 70% that of the first sowing. Thus delayed sowing, while potentially limiting damage, does not appear to be a feasible method of pest control while maintaining yields.

Varietal selection

Dunn and Kempton (1971, 1976) have shown considerable variation in response to pest attack among varieties of brassicas. The limited testing of varieties reported in Chapter 7 also indicated considerable differences in pest levels on the plants. The most noticeable of these was for the low numbers of aphid colonies on varieties Lunet and Rasmunda. Resistance to white butterfly and diamondback moth was less evident and all unsprayed sprout varieties displayed considerable levels of damage by diamondback moth at harvest. Thus it appears that rapid selection for resistance to cabbage aphid can be made from current commercial cultivars without loss in commercial yield but that the potential for resistance to other pests is less clear and requires further evaluation.

Spacing

While all experiments were carried out at single spacing some speculation can be made as to the effect of spacing on pest attack, particularly in regard to direct damage by diamondback moth. Experiments reported in Chapter 7 revealed a critical size threshold of 7 mm diameter below which sprouts are not, or cannot be, attacked by diamondback larvae. In the crop grown at 60 x 60 cm spacing, basal sprouts passed this threshold in late February. However, at high densities Verheij (1970) reported two major effects, delayed maturity and greater uniformity in the sprouts. Thus, increasing

density can decrease the period of susceptibility of the sprouts and, therefore, enable a reduction in insecticide usage. Hence the relationship between density, sprout growth and pest attack needs further evaluation in local conditions.

- b. Pest control measures at stages throughout crop growth

Establishment phase

This period is characterised by a high compensation potential in the plants. Artificial damage studies revealed that the plants could tolerate up to 75% defoliation without yield loss although cage studies indicated a lower threshold. However, in this period the plants showed greatest susceptibility to attack by cabbage aphid.

At this time diamondback moth and cabbage aphid pose the greatest threat as white butterfly are only present in low numbers. Due to the variability of attack by cabbage aphid and diamondback moth a threshold approach to control will be most appropriate. As this is a period of rapid plant growth the relationship between pest numbers and yield will be constantly changing. Thus initial thresholds can be more easily based on visual effects on the plant than pest numbers. For cabbage aphid it appears that only populations causing severe leaf curling and obvious stunting would cause yield loss and

consequently require control. The effects of diamondback moth populations are less clear although the results indicate that 50% defoliation of the young leaves in the crown of the plant would warrant control of the pest.

Mid season

Following establishment, the plant enters a period of stem elongation and rapid leaf growth. In both artificial defoliation and field studies this period was found to be the period of highest susceptibility to pest attack. While threshold measures are possible in this phase it was calculated in Chapter 8 that the optimum time for a spray to minimise white butterfly damage was in mid March. There would be little value in adopting a threshold approach for the control of this pest as, at least within this cropping system and location, it is extremely regular in its timing between seasons. Thus a single effective schedule spray would provide protection from both defoliating pests over this period.

Sprout growth

In Chapter 7 it was established that diamondback moth larvae only enter sprouts with a diameter greater than 7 mm. Thus once the sprouts have passed this size they will be susceptible to direct damage. Tolerance

levels for direct damage in sprouts are ill defined, thus the aim of the grower is to avoid this type of damage. Therefore the most appropriate pest control strategy is one of schedule sprays once sprout size has passed the 7 mm barrier. While there is no information available on the frequency of sprays within the schedule it seems likely that the present two weekly programme may be necessary throughout March and early April but this could be reduced to every 3-4 weeks in May and June due to lower levels of insect activity at this time. A visual threshold, based on aphid presence, could be used throughout the whole season with particular importance placed on late season contamination of the sprouts.

c. A rational approach to pest control in Brussels sprouts

It would appear, therefore, that a rational spray programme, with considerable reductions in the present spray loading is feasible for Brussels sprouts. The programme would combine pre-emptive measures such as selection of varieties, sowing date and spacing, with visual thresholds for the main pests in the early stages of growth. Once sprouts have passed the 7 mm size threshold, schedule spraying would commence with intervals between spraying widening into the autumn as the damage potential of diamondback moth was reduced by lower feeding rates and lower flight activity (Fig. 9.1).

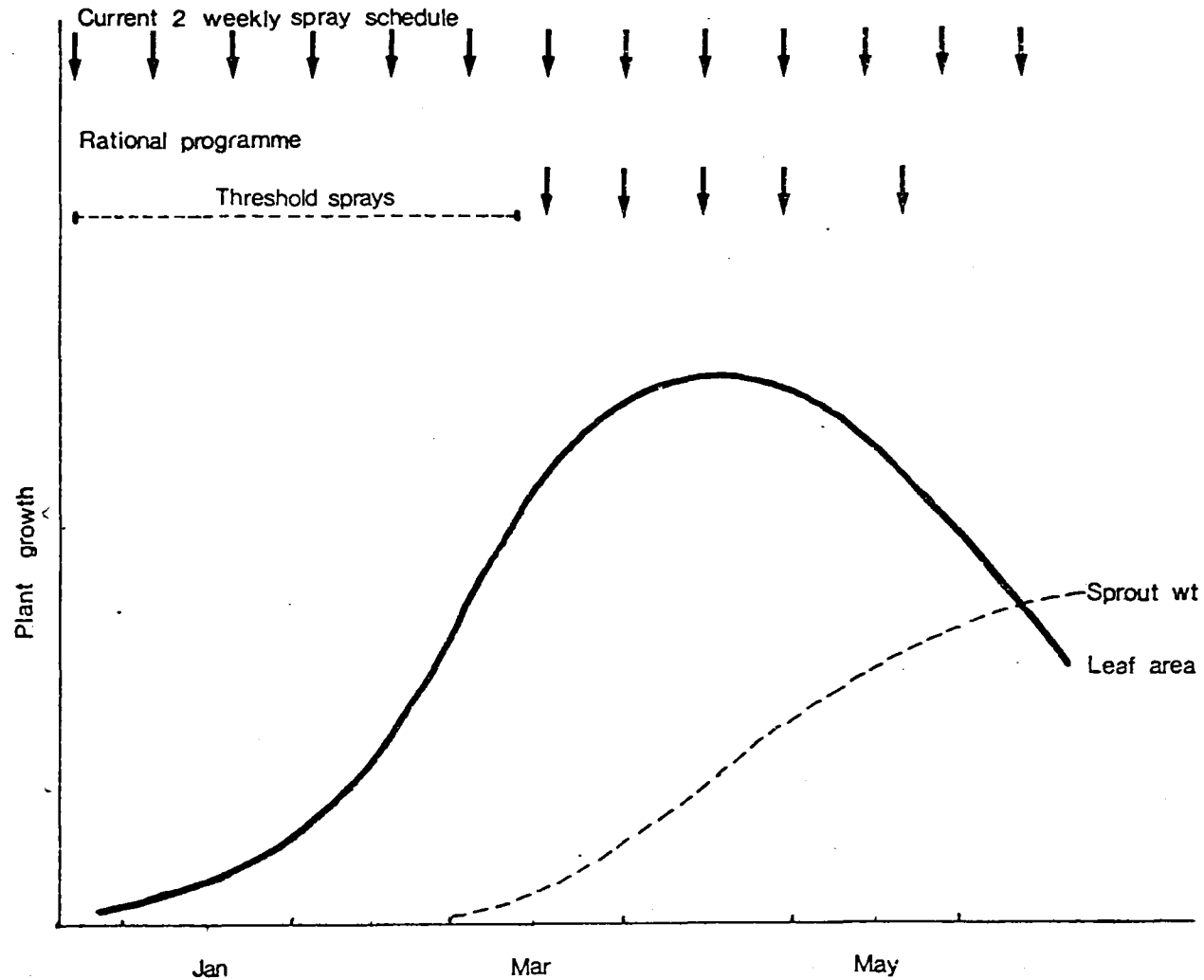


Fig. 9. 1. Comparison of current two-weekly spray schedule and rational spray programme incorporating threshold initiated sprays and schedule sprays over the critical phase of plant growth.

Thus it is possible that by adopting a rational spray programme based on an understanding of pest ecology and plant response, insecticide usage could be halved. Before being adopted by growers the proposed programme obviously needs testing as a package under field conditions with further definition of thresholds, and identification of the most effective materials and methods of application.

CHAPTER 10

CONCLUSIONS

1. The characteristics of attack by each of the major pest species of Brussels sprouts, white butterfly, diamondback moth and cabbage aphid, were markedly different. White butterfly was noted for its uniformity in population growth within each season. Each year larval numbers increased to a similar peak in late March. Diamondback moth larvae were present on the leaves throughout most of the season but the numbers fluctuated with no consistent pattern between years. Cabbage aphid populations showed the greatest variability with no consistency in the pattern between years and huge differences in the peak numbers recorded.

2. The distribution of the pests on the plant changed markedly through the season. White butterfly fed randomly over the young plant but in the latter part of the season were found primarily in the upper leaves. Diamondback moth larvae were located mainly in the crown of the young plant but after sprout formation the majority of the larvae were found in the young sprouts. Colonies of cabbage aphid were initially found over the whole plant but in the later stages were predominantly found on the lower leaves.

3. The rate of feeding of white butterfly larvae increased throughout its development such that the bulk

of feeding occurred in the final instar. The rate of feeding within each instar was dependent on temperature but this was not directly proportional to the development rate. At high temperatures larvae consumed less and the resultant pupae weighed less than those from within the lower range. Calculation of feeding and development thresholds indicated that feeding by white butterfly continued at low temperatures where development had ceased. Feeding by diamondback moth larvae followed a similar pattern with absolute consumption approximately 7% that of white butterfly.

4. Brussels sprout growth after transplanting followed an establishment phase, a period of stem elongation with rapid leaf growth and then a period of sprout growth in the autumn and winter months. The plants were able to compensate even for high levels of defoliation in the early stages of growth. Greatest yield losses followed mid season defoliation but some compensation still occurred. Following late defoliation, the relationship was linear but yield losses were low due to much of the yield being formed prior to defoliation.

5. Total yield may be reduced indirectly by feeding of each of the pests on the leaves. Yield losses due to white butterfly and diamondback moth feeding were greatest in the mid season while attack by cabbage aphid

early in the growth of the crop in 1979 had most effect on yield

6. Direct damage, by feeding on the sprouts, was caused by diamondback moth in contrast to white butterfly where even very high numbers of larvae had no effect on damage levels among the sprouts. Only sprouts over 7 mm in diameter were affected by diamondback moth showing that there is a critical point defined by sprout size, after which the crop is susceptible to diamondback moth attack. This period occurs after 15 weeks from transplanting.

7. The pattern of growth varied markedly between varieties. The use of late maturing varieties such as Rampart and Rasmunda may reduce the need for insecticide by delaying the onset of the critical period for direct damage to the sprouts. No firm conclusions could be reached regarding differential levels of feeding between the varieties but consistent differences in response to aphid attack were noted. The variety Lunet had consistently less cabbage aphid than the other varieties.

8. Examination of the relationship between defoliation by white butterfly and yield loss using a simulation model showed that the effect of feeding by a normal population of white butterfly was low, reducing yield by little more than 1%, but that increasing population size led to an

exponential increase in the yield loss. The optimum time for application of a single insecticide was the 13th week from transplanting which reduced the potential yield loss by 56%.

9. The present high use of insecticides for pest control in Brussels sprouts may be rationalised by changing from the current two weekly schedule to a flexible control strategy based on insect numbers and stage of plant growth. A rational spray programme would involve adoption of a threshold for insect control through the early stage of growth followed by scheduled sprays through the critical period.

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LIST OF REFERENCES

- Anon. (1887). The new turnip pest. (Diamond-back moth - *Plutella crucifarum*. N.Z. Country J. 11: 255-256.
- Anon. (1938). Insect pests in cabbages. N.Z. J1 Agric. 56: p 124.
- Anon. (1957). Aphid control in brassica crops in Canterbury. N.Z. J1 Agric. 94: p 11.
- Anon. (1961). Around the research stations.- Aphid resistant rape. N.Z. J1 Agric. 102: p 485.
- Anon. (1979). Fenvalerate. Suppl. to Guide to Ag. Chem., Ag. Chem. Board. Wellington.
- Anon. (1963). The home vegetable garden. N.Z. Dept. Agric. Bull. 342: 413 pp.
- Abraham, E.V. and Padmanaban, M.D. (1968). Bionomics and control of the diamondback moth *Plutella maculipennis* Curtis. Indian J. agric. Sci. 38: 513-519.
- Adkisson, P.L. (1973). The principles, strategies and tactics of pest control in cotton. In Insects - studies in population management. P.W Geier, L.R. Clark, D.J. Anderson and H.A. Nix (Eds) Ecol. Soc. Aust. (Memoirs 1): Canberra, p 274-283.
- Allan, H.H. (1961). Flora of New Zealand. Volume 1. Indigenous tracheophyta, psilopsida, lycopsida, filicopsida, gymnosperma and dicotyledons. Government Printer: Wellington, 1085 pp.
- Allison, J.C.S., Wilson, J.H. and Williams, J.H. Effect of partial defoliation during the vegetative phase on subsequent growth and grain yield of maize. Ann. appl. Biol. 81: 367-375.
- Ashby, J.W. (1972). A study of factors regulating populations of *Pieris rapae* (Linnaeus) in Canterbury, New Zealand. Ph.D. Thesis, Lincoln College, University of Canterbury, 456 pp.
- Aung, L.H. and Kelly, W.C. (1966). Influence of defoliation on vegetative, floral and fruit development in tomatoes (*Lycopersicon esculentum* Mill.) Proc. Amer. Soc. hort. Sc. 89: 563-569.
- Bailey, N.T.J. (1959). Statistical methods in biology. English Universities Press Ltd: London, 200 pp.
- Baker, R.S. and Wilcox, G.E. (1961). Effect of foliage damage and stand reduction on onion yield. Proc. Amer. Soc. hort. Sc. 78: 400-405.
- Bardner, R. (1974). *Leptohylemyia coarctata* (Fall.) - Integrated control and the use of economic thresholds. EPP0 Bull. 4: 329-334.

- Bardner, R. and Fletcher, K.E. (1974). Insect infestations and their effects on growth and yield of field crops. Bull. ent. Res. 64: 141-160.
- Barrer, P.R. (1957). Pest control and pasture management. N.Z. J1 Agric. 95: p 463.
- Berntsen, R. (1975). Growing techniques for Brussels sprouts. Acta Agric. Scand. 25: 25-29.
- Berridge, J. (1914). The cabbage moth or caterpillar: a method of prevention. N.Z. J1 Agric. 8: 371-372.
- Bullen, F.T. (1970). Benefit/cost analysis of various degrees of crop protection. Proc. ecol. Soc. Aust. 5: 63-75.
- Biever, K.D., Hostetter, D.L., and Boldt, P.E. (1972). Reliability of climate studies utilizing *Pieris rapae* (L.). Environ. Ent. 1: 440-443.
- Blau, P.A., Feeny, P., Contardo, L. and Robson, D.S. (1978). Allylglucosinolate and herbivorous caterpillars: a contrast in toxicity and tolerance. Science 200: 1296-1298.
- Boldt, P.E., Biever, K.D. and Ignoffo, C.M. (1975). Lepidopteran pests of soybeans: consumption of soybean foliage and pods and development time. J. econ. Ent. 68: 480-482.
- van den Bosch, R. (1978). The pesticide conspiracy. Doubleday: New York, 226 pp.
- Bowling, C.C. (1978). Simulated insect damage to rice: effects of leaf removal. J. econ. Ent. 71: 377-378.
- Bracken, G.K. and Bucher, G.E. (1977). An estimate of the relation between density of bertha armyworm and yield loss on rapeseed, based on artificial infestations. J. econ. Ent. 70: 701-705.
- Brandenburg, W. (1980). Outdoor vegetable growing with the Canterbury Growers' Society. (Rev. ed.) Cant. Gr. Soc.: Christchurch, 304 pp.
- Brett, C.H. and Sullivan, M.J. (1974). The use of resistant varieties and other cultural practices for control of insects on crucifers in North Carolina. N. C. Agric. Exp. Sta. Bul. No. 449. 31 pp.
- Brown, E.S. and Odiyo, P. (1968). The rate of feeding of the African armyworm *Spodoptera exempta* (Walk.) and its significance for control operations. E. Afr. agric. For. J. 33: 245-256.
- Brown, E.S. and Mohamed, A.K.A. (1972). The relation between simulated armyworm damage and crop-loss in maize and sorghum. E. Afr. agric. For. J. 37: 237-257.

- Brown, K.J. (1965). Response of three strains of cotton to flower removal. Cotton Grow. Rev. 42: 279-286.
- Brown, K.J. (1973). Effect of selective defoliation on development of cotton bolls. Cotton Grow. Rev. 50: 106-114.
- Bullen, F.T. (1966). Locusts and grasshoppers as pests of pastures - a preliminary economic approach. J. appl. Ecol. 3: 147-168.
- Buranday, R.P. and Raros, R.S. (1975). Effects of cabbage-tomato intercropping on the incidence and oviposition of the diamondback moth, *Plutella xylostella* (L.) Philipp. Ent. 2: 369-374.
- Burbutis, B.P. and Kelsey, L.P. (1970). Pest status of the green cloverworm on lima beans in Delaware. J. econ. Ent. 63: 1956-1958.
- Burt, P.E., Bardner, R. and Etheridge, P. (1965). Factors influencing effects of soil applied systemic insecticides. Ann. appl. Biol. 56: 411-418.
- C.I.E. (1952,1977). Distribution maps of pests. Series A (agricultural). Commonwealth Inst. Ent: London.
- Capinera, J.L. (1978). Consumption of sugarbeet foliage by the saltmarsh caterpillar. J. econ. Ent. 71: 661-663.
- Capinera, J.L. (1978). Consumption of sugar beet foliage by the palestriped flea beetle. J. econ. Ent. 71: 301-303.
- Capinera, J.L. and Roltsch, W.J. (1980). Response of wheat seedlings to actual and simulated migratory grasshopper defoliation. J. econ. Ent. 73: 258-261.
- Carlson, G.A. (1971). Economic aspects of crop loss control at the farm level. In Crop Loss Assessment Methods. FAO manual on the evaluation and prevention of losses by pests, diseases and weeds. FAO/Commonwealth agric. Bureaux. p 2.3.1 - 6.
- Carruth, L.A. and Moore, L. (1973). Cotton scouting and pesticide use in eastern Arizona. J. econ. Ent. 66: 187-190.
- Chalfant, R.B., Denton, W.H., Schuster, D.J. and Workman, R.B. (1979). Management of cabbage caterpillars in Florida and Georgia by using visual damage thresholds. J. econ. Ent. 72: 411-413.
- Chamberlain, H. de O. (1957). Pasture management and pest control. N.Z. J1 Agric. 95: p 559.
- Chiang, H.C. (1978). Insects and their environment. In Fundamentals of ecology. R.E.Pfadt (Ed.) Macmillan publishing Co.: New York.
- Chiarappa, L. (1971). Crop loss assessment methods. FAO manual on the evaluation and prevention of losses by pests, diseases and weeds. FAO/Commonwealth agric. Bureaux.

- Chen, C. and Chen, C. (1978). The population levels of *Nilaparvata lugens* (Stal) in relation to the yield loss of rice. Plant Prot. Bull. (Taiwan). 20: 197-209.
- Chen, C. and Su, W. (1978). Influence of temperature on the development and feeding amount of diamondback moth larvae on cauliflower. Plant Prot. Bull. (Taiwan). 20: 224-231.
- Chua, T.H. and Lim, B.H. (1977). Effect of interplant distance on the distribution pattern of diamondback moth, *Plutella xylostella* (L.) among host plants. Mal. Appl. Biol. 6: 19-23.
- Church, B.M. (1971). The place of sample survey in crop loss assessment. In Crop loss assessment methods. FAO manual on the prevention of losses by pests, diseases and weeds.
- FAO Commonwealth agric. Bureaux. 2.2/1-12.
- Church, B.M. and Strickland, A.H. (1954). Sampling cabbage aphid populations on Brussels sprouts. Plant Path. 3: 76-80.
- Coaker, T.H. (1965). Further experiments on the effect of beetle predators on the numbers of the cabbage root fly, *Erioschia brassicae* (Bouche), attacking brassica crops. Ann. appl. Biol. 56: 7-20.
- Coaker, T.H. (1970). Plant tolerance to cabbage root fly damage. Rep. natn. Veg. Res. Stn. for 1969, p 87.
- Coaker, T.H. (1976). Crop pest problems resulting from chemical control. In Origins of pest, parasite, disease and weed problems. 18th Symp. Brit. Ecol. Soc., J.M. Cherrett and G.R. Sagar (Eds). Blackwell Sci. Pub.: Oxford, p 313-328.
- Cock, J.H. (1978). A physiological basis of yield loss in cassava due to pests. Proc. Cassava Protection Workshop. CIAT: Cali, Columbia 7-12 Nov. 1977. p 9-16.
- Conway, G.R. (1973). Experience in insect pest modelling: A review of models, uses and future directions. In Insects - studies in population management. P.W Geier, L.R. Clark, D.J. Anderson and H.A. Nix (Eds.) Ecol. Soc. Aust. (Memoirs 1): Canberra, p 103-130.
- Conway, G.R. (1976). Man versus pests. In Theoretical ecology. R.M. May (Ed.). Blackwell: London, p 257-281.
- Conway, G.R., Norton, G.A., Small, N.J. and King, A.B.S. (1976). A systems approach to the control of the sugar cane froghopper. In Study of agricultural systems. G.E. Dalton (Ed.). Applied Science: London, p 193-229.
- Cottier, W. (1935). Aphides affecting cultivated plants (5). Aphides of the bean, turnip, strawberry, pumpkin and primrose. N.Z. Jl Agric. 51: 92-97.

- Cottier, W. (1936). The use of insecticides in the control of the white butterfly. Progress report. N.Z. Jl Agric. 52: 24-29.
- Cottier, W. (1939). Work on insecticides against the cabbage white butterfly, *Pieris rapae* L. N.Z. Jl Sci. Technol. (A) 21: 23-45.
- Cottier, W. (1956). Insect pests. In Plant protection in New Zealand. J.D. Atkinson et al (Eds.). Government Printer: Wellington, p 209-481.
- Cottier, W. and Jacks, H. (1945a). Relative efficiencies of nicotine sulphate and certain arsenates for the control of diamond-back moth (*Plutella maculipennis* Curt.) N.Z. Jl Sci. Technol. (A) 27:37-39.
- Cottier, W. and Jacks, J. (1945b). The effects of rotenone bearing dusts on the diamond-back moth (*Plutella maculipennis* Curt.). N.Z. Jl Sci. Technol. (A) 27: 37-39.
- Cranshaw, W.E. and Radcliffe, E.B. (1980). Effect of defoliation on yield of potatoes. J. econ. Ent. 73: 131-134.
- Cutler, B.L. and Harris, M.K. (1979). Foliage consumption and damage by the walnut caterpillar on pecan in Texas. J. econ. Ent. 72: 315-318.
- Danthanarayana, W. (1975). Factors determining variation in fecundity of the light brown apple moth, *Epiphyas postvittana* (Walker)(Tortricidae). Aust. J. Zool. 23: 439-451.
- Davidson, R.L. and Roberts, R.J. (1969). Scarab damage to grass and clover as influenced by depth of feeding. Bull. ent. Res. 58: 559-565.
- Dempster, J.P. (1967). The control of *Pieris rapae* with DDT. I. The natural mortality of the young stages of *Pieris*. J. appl. Ecol. 4: 485-500.
- Dempster, J.P. (1968). The control of *Pieris rapae* with DDT. II. Survival of the young stages of *Pieris* after spraying. J. appl. Ecol. 5: 451-462.
- Denenberg, V.H. (1976). Statistics and experimental design for behavioral and biological researchers. John Wiley and Sons: New York, 344 pp.
- Detling, J.K., Dyer, M.I. and Winn, D.T. (1979). Effect of simulated grasshopper grazing on CO₂ exchange rates of western wheat leaves. J. econ. Ent. 72: 403-406.
- Dhillon, S.S. (1974). Effect of deficiency in nutrition on the life span of *Athalia proxima* (Klug) . Indian Jour. Ent. 36: 190-193.
- Dina, S.O. (1976). Effect of insect application at different growth phases on insect damage and yield of cowpea. J. econ. Ent. 69: 186-188.

- Dugdale, J.S. (1971). Lepidoptera, excluding non-crambine Pyralidae. In Entomology of the Aucklands and other Islands south of New Zealand. Pacific Insects Monograph 27: 55-172.
- Dugdale, J.S. (1973). The genus *Plutella* (Hyponomeutidae) in New Zealand and the family position of *Circoxena* (Lepidoptera). N.Z. Jl Sc. 16: 1009-1023.
- Dunn, J.A. and Coaker, T.H. (1965). Rational control of vegetable crop pests. Ann. appl. Biol. 56: 340-345.
- Dunn, J.A. and Kempton, D.P.H. (1971). Differences in susceptibility to attack by *Brevicoryne brassicae* (L.) on brussels sprouts. Ann. appl. Biol. 68: 121-134.
- Dunning, R.A. and Winder, G.H. (1972). Some effects, especially on yield, of artificially defoliating sugar beet. Ann. appl. Biol. 70: 89-98.
- Dyer, M.I. and Bokhari, U.G. (1976). Plant-animal interactions: studies of the effects of grasshopper grazing on blue grama grass. Ecology 57: 762-772.
- van Emden, H.F. and Way, M.J. (1972). Host plants in the population dynamics of insects. In Insect/Plant relationships. H.F. van Emden (Ed.) Blackwell Sci. Pub.: Oxford, p 181-199.
- Empson, D.W. (1952). Survey of cabbage aphid populations on Brussels sprouts. Plant Path. 1: 35-38.
- Farrington, J.F. (1977). Economic thresholds of insect pest infestation in peasant agriculture: a question of applicability. PANS 23: 143-148.
- Feeny, P. (1975). Biochemical evolution between plants and their insect herbivores, p 3-19. In Coevolution of animals and plants. L.E. Gilbert and P.H. Raven (Eds). Univ. Texas Press: Austin, 246 pp.
- Ferguson, A.M. (1978). Vegetable weevil control in cabbages. Proc. 31st N.Z. Weed and Pest Control Conf., p 108-112.
- Ferro, D.N.(Ed.) (1976). New Zealand insect pests. Lincoln University College of Agriculture: Canterbury, New Zealand, 311 pp.
- Ferro, D.N., Chapman, R.B. and Penman, D.R. (1979). Observations on insect microclimate and insect pest management. Environ. Ent. 8: 1000-1003.
- Fisher, N.M. (1974a). The effect of plant density, date of apical bud removal and leaf removal on growth and yield of single-harvest Brussels sprouts (*Brassica oleracea* var. *gemmifera* D.C.). II. Variation in bud size. J. agric. Sci., Camb. 83: 489-496.

- Fisher, N.M. (1974b). The effect of plant density, date of apical bud removal and leaf removal on growth and yield of single-harvest Brussels sprouts (*Brassica oleracea* var. *gemmifera* D.C.). III. Components of marketable yield. J. agric. Sci., Camb. 83: 497-503.
- Fisher, N.M. and Milbourn, G.M. (1974). The effect of plant density, date of apical bud removal and leaf removal on the growth and yield of Brussels sprouts (*Brassica oleracea* var. *gemmifera* D.C.). I. Whole plant and axillary bud growth. J. agric. Sci., Camb. 83: 479-487.
- French, R.A. and Douglas, J.A. (1967). Control of insect pests of establishing brassicas. Proc. 20th N.Z. Weed and Pest Control Conf., p 179-184.
- French, S.A.W. and Humphries, E.C. (1977). The effect of partial defoliation on yield of sugar beet. Ann. appl. Biol. 87: 201-212.
- Fry, K.E., Kittock, D.L. and Henneberry, T.J. (1978). Effect of number of pink bollworm larvae on yield of Pima and upland cotton. J. econ. Ent. 71: 499-502.
- Gage, S.H. and Mukerji, M.K. (1978). Crop losses associated with grasshoppers in relation to economics of crop production. J. econ. Ent. 71: 487-498.
- Gates Clarke, J.F. (1971). The Lepidoptera of Rapa Island. Smithsonian Contributions to Zoology 56: 282 pp.
- Geier, P.W. and Clark, L.R. (1961). An ecological approach to pest control. Proc. 8th Tech. Meet. Int. Union for Conserv. of Nature and Natural Res., 1960, Warsaw, p 10-18.
- Geier, P.W. and Springett, B.P. (1974). The context of pest control. Agric. Environm. 1: 373-383.
- Getzin, L.W. (1978). Effect of cabbage maggot damage on yield and quality of hybrid cabbage seed. J. econ. Ent. 71: 528-530.
- Given, B.B. (1944). The relative food consumption of diamond-back moth and white butterfly larvae. N.Z. Jl Sci. Technol. 26: 195-197.
- Goldson, S.L. and Penman, D.R. (1979). Effect of time of sowing on Argentine stem weevil (*Hyperodes bonariensis* Kuschel) damage in autumn-sown Tama ryegrass. N.Z. Jl Agric. Res. 22: 367-371.
- Goodman, A. (1956). The effects of leaf, bud and fruit pruning upon X1730A cotton at Tokar, Sudan. Emp. Cotton Grow. Rev. 33: 24-34.
- Goodman, A. (1968). Physiological analysis of the effects of different soils on sugar beet crops in different years. J. appl. Ecol. 5: 339-357.

- Goodwin, S. (1979). Changes in numbers in the parasitoid complex associated with the diamondback moth *Plutella xylostella* (L.) (Lepidoptera) in Victoria. Aust. J. Zool. 27: 981-989.
- Greene, G.L. (1972). Economic damage threshold and spray intervals for cabbage looper control on cabbage. J. Econ. Entomol. 65: 205-208.
- Greene, G.L. and Minnick, D.R. (1967). Snap bean yields following simulated insect defoliation. Proc. Fla. State Hort. Soc. 80: 132-134.
- Gunning, B.A. (1963). Seasonal notes - aphid control in brassica crops. N.Z. Jl Ag. 107. p 553.
- Gupta, das.D.K. (1968). The effect of decapitation on growth of the sugar beet storage root. In Root growth. W.T. Wittington(Ed). Proc. 15th Easter School in Ag. Sc., University of Nottingham. Butterworths: London, p 247 -255.
- Gutierrez, A.P., Falcon, L.A., Loew, W., Leipzig, P.A. and van den Bosch, R. (1975). An analysis of cotton production in California: A model for Acala cotton and the effects of defoliators on its yields. Environ. Ent. 4: 125-136.
- Gutierrez, A.P., Leigh, T.F., Wang, Y. and Cave, R. (1977). An analysis of cotton production in California: *Lygus hesperus* (Heteroptera: Miridae) injury - an evaluation. Can. Ent. 109: 1375-1386.
- Gutierrez, A.P. and Wang, Y. (1979). An optimization model for *Lygus hesperus* (Heteroptera: Miridae) damage in cotton: the economic threshold revisited. Can. Ent. 111: 41-54.
- Hafez, M. (1961). Seasonal fluctuations of population density of the cabbage aphid *Brevicoryne brassicae* (L.) in the Netherlands, and the role of its parasite *Aphidius* (*Diaeretiella*) *rapae* (Curtis). Tijdschr. Plziekt. 67: 445-548.
- Hagel, G.T. (1978). *Lygus* spp.: Damage to beans by reducing yields, seed pitting, and control by varietal resistance and chemical sprays. J. econ. Ent. 71: 613-615.
- Hall, F.R. and Feree, D.C. (1975). Influence of two spotted spider mite populations on photosynthesis of apple leaves. J. econ. Ent. 68: 517-520.
- Hall, F.R. and Feree, D.C. (1976). Effects of insect injury simulation on photosynthesis of apple leaves. J. econ. Ent. 69: 245-248.
- Hamilton, J.T. (1979). Seasonal abundance of *Pieris rapae* (L.), *Plutella xylostella* (L.) and their diseases and parasites. Gen. appl. Ent. 11: 59-66.
- Hanaway, J.J. (1969). Defoliation effects on different corn (*Zea mays*, L.) hybrids as influenced by plant population and stage of development. Agron. Jour. 61: 534-538.

- Harcourt, D.G. (1957). Biology of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera : Plutellidae), in eastern Ontario. II. Life history, behaviour, and host relationships. Can. Ent. 89: 554-564.
- Harcourt, D.G. (1960). Distribution of the immature stages of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae), on cabbage. Can. Ent. 92: 517-521.
- Harcourt, D.G. (1961a). Spatial pattern of the imported cabbageworm, *Pieris rapae* (L.) (Lepidoptera: Pieridae), on cultivated cruciferae. Can. Ent. 93: 945-952.
- Harcourt, D.G. (1961b). Design of a sampling plan for studies on the population dynamics of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae). Can. Ent. 93: 820-831.
- Harcourt, D.G. (1962). Design of a sampling plan for studies on the the population dynamics of the imported cabbageworm, *Pieris rapae* (L.) (Lepidoptera: Pieridae). Can. Ent. 94: 894-859.
849
- Harcourt, D.G. (1963). Major mortality factors in the population dynamics of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae). Mem. ent. Soc. Can. 32: 55-66.
- Harcourt, D.G. (1966). Major factors in survival of the immature stages of *P. rapae* (L.). Can. Ent. 98: 653-662.
- Harcourt, D.G. (1970). Crop life tables as a pest management tool. Can. Ent. 102: 950-955.
- Harcourt, D.G., Banks, R.H. and Cass, L.M. (1955). Abundance and relative importance of caterpillars attacking cabbage in Eastern Ontario. Can. Ent. 87: 400-405.
- Hardy, J.E. (1938). *Plutella maculipennis* Curt.; its natural and biological control in England. Bull. ent. Res. 29: 343-372.
- Hare, J.E. (1980). Impact of defoliation by the colorado potato beetle on potato yields. J. econ. Ent. 73: 369-373.
- Harris, P. (1972). Insects in the population dynamics of plants. In Insect plant relations. van Emden (Ed.). Blackwell Sci. Pub.: Oxford, p 201-209.
- Harris, P. (1974). A possible explanation of plant yield increases following insect damage. Agro-ecosystems 1: 219-225.
- Harrison, J.A.C. and Isaac, I. (1968). Leaf area development in King Edward potato plants inoculated with *Verticillium albo-atrum* and *V. dahliae*. Ann. appl. Biol. 61: 217-230.
- Harvey, I.C., Somerfield, K.G. and Headley, J. (1979). A survey of pests and diseases of Brussels sprouts grown for processing in Canterbury, 1978/79. Internal report of Plant Health Diagnostic Station, MAF,

Lincoln.

- Haskell, P.T. (1977). Integrated pest control in small farmer crop protection in developing countries. Outlook in Agriculture 9: 121-126.
- Headley, J.C. (1972). Defining the economic threshold. In Pest control strategies for the future. National Academy of Science: Washington, DC. p 100-108.
- Headley, J.C. (1975). The economics of pest management. In Introduction to insect pest management. R.L. Metcalf and W.H. Luckman (Eds) Wiley: New York. pp. 75-79.
- Hella, A.N. and Stoa, T.E. (1964). Simulated hail injury to wheat and flax. Res. Rep. 12, N. Dakota agric. Exp. Stn., 31pp.
- Helson, G.A.H. (1970). Insecticides for farmlands. N.Z. Jl Ag. 123: 26.
- Helson, G.A.H. (1973). Cabbage white butterfly. N.Z. Jl Ag. 126: 45.
- Helson, G.A.H. (1974). Insect pests. Min. of Agric. and Fish., New Zealand. Bull. 413.
- Heslop-Harrison, J. (1969). Development, differentiation, and yield. In Physiological aspects of crop yield. J.D. Eastin et al (Eds) Amer. Soc. Agron.: Madison, Wisconsin, p 291-321.
- Hilgendorf, F.W. (1901). Life-history of *Plutella cruciferarum*, Zeller. Trans. Proc. N.Z. Inst. 33: 145-146.
- Hilgendorf, F.W. (1924). Farmers foes in New Zealand and how to cope with them. Whitcombe and Tombs Ltd., 82 pp.
- Howell, J.F. (1978). Spotted cutworm: simulated damage to apples. J. econ. Ent. 71: 437-439.
- Hughes, R.D. (1963). Population dynamics of the cabbage aphid *Brevicoryne brassicae* (L.). J. Anim. Ecol. 32: 393-424.
- Hughes, R.D. and Gilbert, N.E. (1968). A model of an aphid population. - A general statement. J. anim. Ecol. 37: 553-563.
- Hull, R. (1963). The influence of disease on yield of sugar beet. Ann. appl. Biol. 51: 516-517.
- Hull, R. (1968). The spray warning scheme for control of sugar beet yellows in England. Summary of results between 1959-66. Pl. Path. 17: 1-10.
- Humphries, E.C. (1967). The dependence of photosynthesis on carbohydrate sinks: current concepts. Proc. 1st Int. Symp. on Tropical Root Crops. University of the West Indies.

- Hussey, N.W. (1970). Some economic considerations in the future development of biological control. In Tech. Economics of Crop Prot. and Pest Control. S.C.I. Monograph. No. 36, p 109-118.
- Hussey, N.W. and Parr, W. J. (1963). The effect of glasshouse red spider mite (*Tetranychus urticae* Koch) on the yield of cucumbers. J. hort. Sci. 38: 255-263.
- Ivey, W.E. (1888). School of agriculture, Lincoln. Abstract from the report of the Director, for 1887. N.Z. Country J. 12: 314-320.
- Jackson, T.A. (1980). The effect of defoliation on yield of radish. Ann. appl. Biol. 94: 415-419.
- James, W.C. (1974). Assessment of plant diseases and loss. Ann. Rev. Phytopath. 12: 27-48.
- James, W.C., Shih, C.S., Hodgson, W.A. and Callbeck, L.C. (1972). The quantitative relationship between late blight of potato and loss in tuber yield. Phytopath. 62: 92-96.
- Jones, F.W.G., Dunning, R.A. and Humphries, K.P. (1955). The effects of defoliation and loss of stand on yield of sugar beet. Ann. appl. Biol. 43: 63-70.
- Jones, F.W.G. and Jones, M.G. (1974). Pests of field crops. 2nd edn, Edward Arnold: London, 488 pp.
- Jones, L.H. (1972). The effects of topping and plant population on dry matter synthesis and distribution in Brussels sprouts. Ann. appl. Biol. 70: 77-87.
- Jones, F.G.W., Dunning, R.A. and Humphries, K.P. (1955). The effects of defoliation and loss of stand upon yield of sugar beet. Ann. appl. Biol. 43: 63-70.
- Joy, K.W. (1964). Translocation in sugar beet: 1. Assimilation of 14CO_2 and distribution of materials from the leaves. J. exp. Bot. 15: 485-494.
- Judenko, E. (1969). An experiment to assess losses caused by frit-fly (*Oscinella frit* L.) shoot attack and the application of phorate in a crop of sweet corn (*Zea mays* L.). PANS 15: 47-53.
- Judenko, E. (1972). The assessment of economic losses in yield of annual crops caused by pests and the problem of the economic threshold. PANS 18: 186-190.
- Judenko, E. (1973). Analytical method for assessing yield losses caused by pests on cereal crops with and without pesticides. Tropical Pest Bulletin 2. Centre for overseas Pest Research: London, 31 pp.
- Kain, W.M. (1975). Population dynamics and pest assessment studies of grass grub, (*Costelytra zelandica* (White), Melolonthinae) in the North Island of New Zealand. PhD Thesis, Lincoln College, 297 pp.

- Kelsey, J.M. (1957). Viruses and sprays for the control of *Pieris rapae*. N.Z. Jl Sci. Technol. (A) 38: 644-646.
- Kelsey, J.M. (1958). Control of *Pieris rapae* by granulosis virus. N.Z. Jl Ag. 1: 778-782.
- Kennedy, G.G. and Oatman, E.R. (1976). *Bacillus thuringiensis* and Pirimor: selective insecticides for use in pest management on broccoli. J. econ. Ent. 69: 767-772.
- Kennelly, A.G. (1961). Cabbage growing. N.Z. Jl Ag. 102: 237-49.
- Kincade, R.T., Laster, M.L. and Brazzel, J.R. (1970). Effect on cotton yield of various levels of simulated *Heliothis* damage to squares and bolls. J. econ. Ent. 63: 613-615.
- King, J.E. (1977). Surveys of diseases of winter wheat in England and Wales, 1967-70. Pl. Path. 26: 8-20.
- Knipling, E.F. (1979). The basic principles of insect population suppression and management. U.S. Dept. Agric. Handbook No. 502, 659 pp.
- Kobayashi, S. and Takano, H. (1978). Survival rate and dispersal of the adults of *Pieris rapae crucivora* BOISDUVAL. Jap. J. appl. Ent. Zool. 22: 250-254.
- Kogan, M. (1976). Evaluation of economic injury levels for soybean insect pests. World Soybean Research L.D. Hill (Ed.). Interstate: Illinois, p 515-533.
- Kronenberg, H.G. (1972). Sprout uniformity in growing brussels sprouts. Neth. J. agric. Sci. 20: 73-75.
- Kronenberg, H.G. (1975). Influence of temperature and light on the growth of young brussels sprout plants. Neth. J. agric. Sci. 23: 83-88.
- Kronenberg, H.G. (1975). A crop geography of brussels sprouts. Neth. J. agric. Sci. 23: 291-298.
- Latheef, M.A. and Irwin, R.D. (1979). Factors affecting oviposition of *Pieris rapae* on cabbage. Environ. Ent. 8: 606-609.
- Lamb, K.P. and Lowe, A.E. (1967). Studies on the ecology of the cabbage aphid (*Brevicoryne brassicae* (L.)) on brassica field crops in Canterbury, New Zealand. II. Population study, 1959-60. N.Z. Jl agric. Res. 10: 87-108.
- Lawson, H.M. (1979). Feral pigeon damage to field beans. Ann. appl. Biol. 92: 153-157.
- LeClerc, E.L. (1971). Field experiments for the assessment of crop losses In Crop loss assessment methods. FAO manual on the evaluation and prevention of losses by pests, diseases and weeds. FAO - Commonwealth agric. Bureaux, p 2.1/1 - 2.1/16.

- Lilley, C.E. and Harper, A.M. (1962). Effects of defoliation and reduction of stand on yield of sugar beet in southern Alberta. J. Am. Soc. Sugar Beet Technol. 12: 192-199.
- Lowe, A.D. (1956). Control of brassica seed crop aphids. N.Z. Jl Ag. 93: 256.
- Lowe, A.D. (1966). Aphids trapped at three sites in Canterbury, New Zealand, over four years, with flight patterns for nine main species. N.Z. Jl agric. Res. 9: 771-807.
- Lowe, A.D. (1975). Problems of pest assessment: field crops. N.Z. Entomol. 6: 14-16.
- Luckman, W.H. and Metcalf, R.L. (1975). The pest management concept. In Introduction to insect pest management. R.L. Metcalf and W.H. Luckman (Eds). New York: Wiley. p 3-35.
- Lynch, R.E., Robinson, J.F. and Berry, E.C. (1980). European corn borer: Yield losses and damage resulting from a simulated natural infestation. J. econ. Ent. 73: 141-144.
- McConnell, P. (1911). Aphis and diamondback moth - the effects of spraying. N.Z. Jl Ag. 3: 9-10.
- McEwen, J. (1972). Effects of defoliating different zones on the plant in field beans (*Vicia Faba* L.). J. agric. Sci., Camb. 78: 487-490.
- McLaren, G.F. (1975). The population dynamics of the cabbage aphid, *Brevicoryne brassicae* (L.), in Central Otago, New Zealand. PhD thesis Lincoln College, 291 pp.
- McNaughton, S. J. (1979). Grazing as an optimization process; grass-ungulate relationships in the Serengeti. Amer. Nat. 113: 691-703.
- Menke, W.W. (1974). Identification of viable biological strategies for pest management by simulation studies. IEEE Trans. on Syst. Man, and Cyb. SMC-4: 379-386.
- Metcalf, H.N. (1954). Effect of leaf and terminal bud removal on yield of Brussels sprouts. Proc. Amer. Soc. hort. Sci. 64: 322-326.
- Metcalf, R.L. (1980). Changing role of insecticides in crop protection. Ann. Rev. Entomol. 25: 219-56
- Meyrick, E. (1891). New species of Lepidoptera. Trans. Proc. N.Z. Inst. 23: 97-101.
- Milthorpe, F.L. (1969). Some physiological principles determining the yield of root crops. Proc. Int. Symp. Trop. Root Crops, Trinidad, vol. 1, 2: 1-19.

- Miner, F.D. (1947). Life history of the diamondback moth. J. econ. Ent. 40: 581-583.
- Moore, L.B. and Irwin, J.B. (1978). The Oxford book of New Zealand plants. Oxford University Press: Wellington, 234 pp.
- Moss, J.E. (1933). The natural control of the cabbage caterpillars, *Pieris* spp. J. Anim. Ecol. 2: 210-231.
- Mueller, A. J. and Engroff, B.W. (1980). Effects of infestation levels of *Heliothis zea* on Soybean. J. econ. Ent. 73: 271-275.
- Muggeridge, J. (1930). The diamond-back moth. Its occurrence and control in New Zealand. N.Z. Jl Agric. 41: 253-264.
- Muggeridge, J. (1931). *Pieris rapae*: a recently introduced cabbage pest. N.Z. Jl Agric. 42: 428-432.
- Muggeridge, J. (1932). Spread of *Pieris rapae* butterfly and progress of parasite work. N.Z. Jl Agric. 45: 132-135.
- Muggeridge, J. (1933). The white butterfly (*Pieris rapae*) and its parasites. A record of recent control work. N.Z. Jl Agric. 47: 135-142.
- Muggeridge, J. (1935a). Progress in control of the white butterfly by *Pteromalus puparum*. N.Z. Jl Agric. 50: 175-176.
- Muggeridge, J. (1935b). The white butterfly menace. Efficient control by the pupal parasite, *Pteromalus puparum*. N.Z. Jl Agric. 51: p109.
- Muggeridge, J. (1939). Parasitic control of pests. Experiments with white butterfly and diamond-back moth. N.Z. Jl Agric. 58: 305-307.
- Muggeridge, J. (1942). The white butterfly (*Pieris rapae* L.). I. Its establishment, spread and control in New Zealand. N.Z. Jl Sci. Technol. (A). 24: 107-129.
- Muggeridge, J. (1943). The white butterfly (*Pieris rapae* L.). II and III. Introduction of parasites, method and technique. N.Z. Jl Sci. Technol. (A) 25: 1-30.
- Muggeridge, J. and Given, B.B. (1941). The white butterfly and the diamond-back moth. N.Z. Jl Agric. 63: 371-377.
- Mukerji, M.K., Pickford, R. and Randell, R.L. (1976). A quantitative evaluation of grasshopper (Orthoptera: Acrididae) damage and its effect on spring wheat. Can. Ent. 108: 255-270.
- Mumford, J.D. (1977). Farmer attitudes towards the control of aphids on sugar beet. Proc. 1977 Brit. Crop Prot. Conf., Brighton: England, p 263-270.

- Mumford, J.D. (1981). A study of sugar beet growers' pest control decisions. Ann. appl. Biol. 97: 243-252.
- Mumford, J.D. (1981). Pest control decision making: sugar beet in England. J. agric. Econ. 32: 31-41.
- N.A.S. (1969). Principles of plant and animal pest control. National Academy of Sciences: Washington D.C., 508 pp.
- Newsom, L.D. (1973). Outbreaks of secondary pests and resurgence of treated populations. Proc. FAO Conference. Ecol. in relation to Plant Pest Control. Rome. p 79-92.
- Nieuwhof, M. (1969). Cole crops. Leonard Hill: London, 353 pp.
- Norton, G.A. (1976a). Pest control decision making: an overview. Ann. appl. Biol. 84: 444-447.
- Norton, G.A. (1976b). Analysis of decision making in crop protection. Agro-ecosystems. 3: 27-44.
- Norton, G.A. and Evans, D.E. (1974). The economics of controlling froghopper (*Aeneolamia varia saccharina* (Dist.)) on sugar cane in Trinidad. Bull. ent. Res. 63: 619-627.
- Norton, G.A. Background to agricultural pest management modelling. In Pest management. Institute for applied systems analysis, Proc. 4. G.A. Norton and Holling (Eds.), p 161-176. Pergamon: Oxford, 394 pp.
- Ogunlana, M.O. and Pedigo, L.P. (1974). Economic injury levels of the Potato Leafhopper on Soybeans in Iowa. J. econ. Ent. 67: 29-31.
- Ordish, G. and Toft, H. (1964). The relation of insect infestation to the growth and yield of plants and crops. XII Cong. Ent. p 603-605.
- Owen, D.F. and Wiegert, R.G. (1976). Do consumers maximize plant fitness?. Oikos 27: 488-492.
- Parker, F.D. (1970). Seasonal mortality and survival of *Pieris rapae* (Lepidoptera: Pieridae) in Missouri and the effect of introducing an egg parasite, *Trichogramma evanescens*. Ann. Ent. Soc. Amer. 63: 985-994.
- Parker, F.D. and Pinnell, R.E. (1973). Effect on food consumption of the imported cabbage worm when parasitised by two species of *Apanteles*. Environ. Ent. 2: 216-219.
- Parr, W. J. and Hussey, N.W. (1962). Response of the cucumber plant to different levels of artificial leaf damage to simulate the effects of red spider mite. Rep. Glasshouse Crops Res. Inst. 1961. p 95-99.
- Peairs, L.M. (1927). Some phases of the relation of temperature to the development of insects. W.V.A. Agr'l experiment Station Bulletin. 208: 1-62.

- Pedigo, L.P., Hammond, R.B. and Poston, F.L. (1977). Effects of green cloverworm larval intensity on consumption of soybean leaf tissue. J. econ. Ent. 70: 159-162.
- Pickford, R. and Mukerji M.K. (1974). Assessment of loss of yield in wheat caused by the migratory grasshopper *Melanopus sanguinipes* (Orthoptera: Acrididae). Can. Ent. 106: 1219-1226.
- Pimentel, D. (1961). The influence of plant spatial patterns on insect populations. Ann. entomol. Soc. Amer. 54: 61-69.
- Pimentel, D., Krummel, J., Gallahan, D., Hough, J., Merrill, A., Schreiner, I., Vittum, P., Koziol, F., Back, E., Yen, D., Fiance, S. (1978). Benefits and costs in pesticide use in U.S. food production. BioScience 28: 772-784.
- Pinstrup-Andersen, P., Londono, N.de, and Infante, M. (1976). A suggested procedure for estimating yield and production losses in crops. PANS 22: 359-365.
- Poston, F.L. and Pedigo, L.P. (1976). Simulation of painted lady and green cloverworm damage to soybeans. J. econ. Ent. 69: 423-426.
- Poston, F.L., Pedigo, L.P., Pearce, R.B. and Hammond, R.B. (1976). Effects of artificial and insect defoliation on soybean net photosynthesis. J. econ. Ent. 69: 423-426.
- Poston, F.L., Pedigo, L.P. and Hammond, R.B. (1978). A leaf-consumption model for the painted lady on soybeans. J. Kansas Entomol. Soc. 51: 191-197.
- Prasad, S.K. (1961). Quantitative estimation of damage to cabbage by cabbage worm, *Pieris rapae* (Linn.). Indian J. Entomol. 23: 54-61.
- Prasad, S.K. (1963). Quantitative estimation of damage to crucifers caused by cabbage worm, cabbage looper, diamondback moth and cabbage aphid. Indian J. Entomol. 25: 242-259.
- Radcliffe, E.B. and Chapman, R.K. (1965). Seasonal shifts in the relative resistance to insect attack of eight commercial cabbage varieties. Ann. ent. Soc. Am. 58: 892-897.
- Radcliffe, E.B. and Chapman, R.K. (1966). Varietal resistance to insect attack in various cruciferous crops. J. econ. Ent. 59: 120-125.
- Rahman, M. (1969). Effect of different foods on the development of *Pieris* L. larvae. Pakistan J. Zool. 1: 35-40.
- Rahman, M. (1970). Effects of parasitism on food consumption of *Pieris rapae* larvae. J. econ. Ent. 63: 820-821.
- Raman, K.V., Singh, S.R. and van Emden, H.F. (1978). Yield losses in Cowpea following leafhopper damage. J. econ. Ent. 71: 936-938.

- Reynolds, H.T., Adkisson, P.L. and Smith, R.F. (1975). Cotton insect pest management. In Introduction to insect pest management. R.L. Metcalfe and W.H. Luckman (Eds). Wiley: New York, p 379-444.
- Rhoades, H.L. (1971). Pathogenicity and control of a Florida population of the sugar beet nematode *Heterodera schachtii* on cabbage. Proc. Florida State Hort. Soc. **84**: 139-142.
- Richards, O.W. (1940). The biology of the small white butterfly (*Pieris rapae*) with special reference to the factors controlling its abundance. J. Anim. Ecol. **9**: 243-288.
- Ridler, R.D. (1975). The control of diamond backed moth and cabbage aphid white butterfly larvae with phenthoate. Proc. 28th N.Z. Weed and Pest Control Conference. p 230-233.
- Robertson, P.L. (1939). Diamondback moth investigations in New Zealand. N.Z. Jl Sci. Technol. (A) **20**: 330-340.
- Rogers, C.E. (1976). Economic injury level for *Contarinia texana* on Guar. J. econ. Ent. **69**: 693-696.
- Root, R.B. and Selsey, J.J. (1969). Biotic factors involved in crucifer aphid outbreaks following insecticide application. J. econ. Ent. **62**: 223-233
- Ru, N. and Workman, R.B. (1979). Seasonal abundance and parasites of the imported cabbageworm, diamondback moth and cabbage webworm in northeast Florida. Fla. Ent. **62**: 68-69.
- Ruesink, W.G. (1975). Analysis and modelling in pest management. In Introduction to insect pest management. R.L. Metcalf and W.H. Luckman (Eds) Wiley: New York, p 353-376.
- Salter, P.J. (1959). The effect of different irrigation treatments on the growth and yield of early summer cauliflowers. J. hort. Sci. **34**: 23-31.
- Sharpe, C.J. and MacDiarmid, B.N. (1976). Control of brassica aphid and blue-green lucerne aphid with chlorpyrifos. Proc. 29th N.Z. Weed and Pest Control Conf. p 189-202.
- Shaw, M.W. (1959). The diamondback moth. Trans. Royal Highland Ag. Soc. of Scot. **6**: 56-80.
- Slansky, F.Jr. and Feeny, P. (1977). Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated foodplants. Ecol. mono. **47**: 209-228.
- Slosser, J.E., Phillips, J.R. and Herzog, G.A. (1978). Bollworm damage and population development in relation to the phenology of the cotton plant. Environ. Ent. **7**: 144-148.

- Southwood, T.R.E. (1966). Ecological methods. Chapman and Hall: London, 391pp.
- Southwood, T.R.E. and Norton, G.A. (1973). Economic aspects of pest management strategies and decisions. In Insects - studies in population management. P.W. Geier, L.B. Clark, D.J. Anderson and H.A. Nix (Eds). Ecol. Soc. Aust. Memoirs 1): Canberra. p 168-184
- Shoemaker, C.A. (1973). Optimization of agricultural pest management I: Biological and mathematical background. Math. Biosci. 16: 143-175.
- Shoemaker, C.A. (1976). Management models for integrated pest control - mathematical structure and solution. In Modeling for pest management: Concepts, techniques and applications. R.L. Tummalla, D.L. Haynes and B.A. Croft (Eds). East Lansing: Mich. State Univ., p 32-39.
- Smith, J.G. (1976). The influence of crop background on aphids and other phytophagous insects on Brussels sprouts. Ann. appl. Biol. 83: 1-13. Smith, R.F. (1967). Principles of measurement of crop losses caused by insects. FAO Symposium on Crop Losses. Rome, October 2-6. p 205-224.
- Smith, C.L. and Smilowitz, Z. (1976). Growth and development of *Pieris rapae* larvae parasitized by *Apanteles glomeratus*. Entomologia exp. appl. 19: 189-195.
- Soine, O.C. (1967). The effect of simulated hail damage on sugar beet. J. Amer. Soc. Sug. Beet Technol. 14: 424-432.
- Steel, G.D. and Torrie, J.H. (1960). Principles and procedures of statistics. McGraw-Hill: New York, 481 pp.
- Stepanova, L.A. (1962). Ecology of crucifer pests. Entomol. Rev. URSS. 41: 451-460.
- Stern, V.M. (1973). Economic thresholds. Ann. Rev. Ent. 18: 259-280.
- Stern, V.M., Smith, R.F., van den Bosch, R. and Hagen, K.S. (1959). The integrated control concept. Hilgardia 29: 81-101.
- Stone, J.D. and Pedigo, L.P. (1972). Development and economic-injury level of the green cloverworm on soybeans in Iowa. J. econ. Ent. 67: 197-201.
- Stoy, V. (1969). Interrelationships among photosynthesis, respiration and movement of carbon in developing crops. In Physiological aspects of crop yield. J.D. Eastin et al (Eds). Amer. Soc. Agron.: Madison, Wisconsin,
- Strickland, A.H. (1954). Assessment of cabbage aphid damage in commercial Brussels sprout crops. Pl. Path. 3: 107-117.

- Strickland, A.H. (1957). Cabbage aphid assessment and damage in England and Wales, 1946-55. Pl. Path. 6: 1-9.
- Strickland, A.H. and Bardner, R. (1967). A review of current methods applicable to measuring crop losses due to insects. FAO Symposium on Crop Losses. Rome, October 2-6. p 289-309.
- Sudderuddin, K.I. (1978). Insecticide resistance in *Plutella xylostella* collected from the Cameron Highlands. Plant Prot. Bull. FAO. 26: 53-57.
- Sun, C., Chi, H. and Feng, H. (1978). Diamondback moth resistance to diazinon and methomyl in Taiwan. J. econ. Ent. 71: 551-554.
- Sylvén, E. (1968). Threshold values in the economics of insect pest control in agriculture. PANS 14: 356-366.
- Tamaki, G. and Hagel, G.T. (1978). Evaluation and projection of *Lygus* damage to sugarbeet seedlings. J. econ. Ent. 71: 265-268.
- Tamaki, G. and Butt, B.A. (1977). Biology of the false celery leaf-tier and damage to sugarbeets. Environ. Ent. 6: 35-38.
- Tamaki, G. and Butt, B.A. (1978). Impact of *Perillus bioculatus* on the colorado potato beetle and plant damage. U.S.D.A., Technical Bulletin 1581, 11pp.
- Tammes, P.M.L. (1961). Studies in yield losses II: Injury as a limiting factor of yield. Tijdschr. Plziekt. 67: 257-263.
- Taylor, W.H. (1922). The garden: The cabbage moth *Plutella crucifera*. N.Z. Jl Agric. 24: 116.
- Taylor, G.G. (1948). Experiments for control of white-butterfly (*Pieris rapae* L.) and diamond-back moth (*Plutella maculipennis* Curt.) on cabbages. N.Z. Jl Sci. Technol. (A) 29: 265-272.
- Taylor, W.E. (1972). Effects of artificial defoliation (simulating pest damage) on varieties of upland rice. Expl. Agric. 8: 79-83.
- Taylor, W.E. and Bardner, R. (1968a). Leaf injury and food consumption by larvae of *Phaedon cochleariae* (Coleoptera: Chrysomellidae) and *Plutella maculipennis* (Lepidoptera: Plutellidae) feeding on turnip and radish. Entomologia exp. appl. 11: 177-184.
- Taylor, W.E. and Bardner, R. (1968b). Effects of feeding by larvae of *Phaedon cochleariae* (F.) and *Plutella maculipennis* (Curt.) on the yield of radish and turnip plants. Ann. appl. Biol. 62: 249-254.
- Thomas, G.D., Ignoffo, C.M., Biever, K.D., and Smith, D.B. (1974). Influence of defoliation and depodding on yield of soybeans. J. econ. Ent. 67: 683-689.

- Thomas, G.D., Ignoffo, C.M., Smith, D.B. and Morgan, C.E. (1978). Effects of single and sequential defoliations on yield and quality of soybeans. J. econ. Ent. 71: 871-874.
- Thompson, (1976). Crucifer crops. In Evolution of crop plants. N.W. Simmonds (Ed.). Longmans: London, 339 pp.
- Thorne, G.N. (1971). Physiological factors limiting the yield of arable crops. In Potential crop production. P.F. Waring and J.P. Cooper (Eds) Heinemann: London, p 143-158.
- Thorsteinson, (1960). Host selection in phytophagous insects. Ann. Rev. Ent. 5: 193-218.
- Thrower, S.L. (1962). Translocation of labelled assimilates in the soybean: II. The pattern of translocation in intact and defoliated plants. Aust. J. Biol. Sci. 15: 629-649.
- Todd, D.H. (1958). Incidence and parasitism of insect pests of cruciferous crops in Hawke's Bay, Wairarapa, Manawatu, Rangitikei and Taranaki, 1956-1957. N.Z. Jl agric. Res. 1: 847-858.
- Todd, D.H. (1960). Virus disease effectively controls white butterfly. N.Z. Jl Agric. 100: 83-85.
- Toms, A.M. (1967). Crop protection economics. World Crops. 19: 7-8.
- Toms, A.M. (1976). Crop protection economics - today and tomorrow. World Crops. 28: 113-115.
- Trought, T.E.T. (1975). A comparison of chemicals for the control of Nysiuson brassicas. Proc. 28th N.Z. Weed and Pest Control Conf., p 226-229.
- Travers, W.T.L. (1884). Acclimatisation in Canterbury. N.Z. Country J. 8: 496-500.
- Tummala, R.L. (1976). Concept of on-line pest management. In Modeling for pest management; concepts techniques and applications. R.L. Tummala, D.L. Haynes and B.A. Croft (Eds). Mich. State Univ.: East Lansing, p 28-31.
- Turnipseed, S.G. (1972). Response of soybeans to foliage losses in South Carolina. J. econ. Ent. 65: 224-228.
- Umeya, K. and Yamada, H. (1973). Threshold temperature and thermal constants for development of the diamond-back moth, *Plutella xylostella* L., with reference to their local differences. Jap. J. appl. Ent. Zool. 17: 19-24.
- Valentine, E.W. (1975). Diamondback moth (*Plutella xylostella* Linnaeus) life cycle. DSIR Information Series, No. 105 /16, 3pp.

- Verheij, E.W.M. (1970). Spacing experiments with Brussels sprouts grown for single-pick harvests. Neth. J. agric. Sci. 18: 89-104.
- Waldbaur, G.P. (1968). The consumption and utilization of food by insects. Adv. Insect Physiol. 5: 229-288.
- Walker, P.T. (1977). Crop losses: some relationships between yield and infestation. Med. Fac. Landbouww. Rijksuniv. Gent. 42: 919-926.
- Waters, W.E. and Ewing, B. (1976). Development and role of predictive modeling in pest management systems-insects. In Modeling for Pest Management Concepts, Techniques and Applications. R.L. Tummala, D.L. Haynes and B.A. Croft (Eds). Mich. State Univ.: East Lansing, p 19-27.
- Watson, D.J. (1971). Size, structure, and activity of the productive system of crops. In Potential crop production - a case study. P.F. Waring and J.P. Cooper (Eds). London: Heinemann, p 76-88..
- Watt, K.E.F. (1963). Mathematical population models for five agricultural crop pests. Mem. ent. Soc. Can. 32: 83-91.
- Way, M.J. (1973). Objectives, methods, and scope of integrated control. In Insects - studies in population management. P.W. Geier, L.R. Clark, D.J. Anderson and H.A. Nix. (Eds) Ecol. Soc. Aust. (Memoirs 1): Canberra, p 137-152.
- Webster, A.B. (1960). Brussels sprout trial at Levin. N.Z. Jl Agric. 100: 71-72.
- West, E.S. (1930). Occurrence of *Pieris (Ganoris) rapae* L. in New Zealand. Ent. mon. Mag. 66: 224-225.
- Wheatley, G.A. (1971). The role of pest control in modern vegetable production. World Rev. Pest Control. 10: 81-93.
- Wigglesworth, V.B. (1972). Principles of insect physiology. 7th ed. Chapman and Hall: London, 827 pp.
- Williams, J.M. (1974). The effect of artificial rat damage on coconut yields in Fiji. PANS 20: 275-282.
- Wilson, A.G.L., Hughes, R.D. and Gilbert, N. (1972). The response of cotton to pest attack. Bull. ent. Res. 61: 405-414.
- Wilson, M.C., Treece, R.E., Shade, R.E., Day, K.M. and Stivers, R.K. (1969). Impact of cereal leaf beetle larvae on yields of oats. J. econ. Ent. 62: 699-702.
- Wood, B.J. (1977). The economics of crop protection in oil palms. PANS. 23: 235-267.
- Wyman, J.A. and Oatman, E.R. (1977). Yield responses in broccoli plantings sprayed with *Bacillus thuringiensis* at various lepidopterous larval density treatment levels. J. econ. Ent. 70: 821-824.

- Yasseen, M. (1974). Biology, seasonal incidence and parasites of *Plutella xylostella* (L.) in Trinidad and the introduction of exotic parasites into the Lesser Antilles. In Crop protection in the Caribbean. C.W.D. Braithwaite, R.H. Phelps and F.D. Bennett (Eds).
- Zar, J.H. (1974). Biostatistical analysis. Prentice - Hall: Englewood Cliffs, N.J., 620 pp.

Appendix 6.i Results summary for intermediate harvests, Experiment 6.1. Mean values for leaf number, leaf area, sprout weight and total weight. S.E., standard errors for comparison of treatment means within each sowing time.

Harvest	Sowing time	Defoliation time	Leaf number	Leaf area ($\text{cm}^2 \times 10^2$)	Sprout weight (g)	Total weight (g)
II	1	0	52.4	79.9	3.6	114.4
		I	51.5	72.5	2.4	102.1
	2	0	60.2	76.2	11.5	150.3
		I	58.4	70.2	8.3	139.4
	SE		0.93	7.43	1.92	9.63
III	1	0	63.9	100.1	39.1	246.3
		I	62.6	98.4	39.5	238.7
		II	58.7	65.4	13.6	145.4
	2	0	72.0	102.7	41.7	214.2
		I	72.3	107.2	40.9	212.8
		II	73.8	79.3	32.9	171.7
	SE		1.68	6.94	5.49	11.94
IV	1	0	70.3	85.5	75.3	254.7
		I	73.5	92.3	80.9	275.7
		II	74.3	87.2	71.0	257.5
		III	72.5	63.6	78.9	247.3
	2	0	59.4	83.4	62.7	198.1
		I	56.8	80.6	76.5	225.3
		II	55.2	65.2	60.2	177.3
		III	58.9	53.8	60.3	170.1
	SE		3.24	6.18	7.18	12.89

Appendix 6.ii Results summary for sequential samplings of Brussels sprouts, 1978/79. Experiment 6.3. Mean values for leaf numbers, leaf/area, sprout weight and total plant weight. S.E., standard error.

Harvest date	Defoliation level	Leaf no.	Leaf area (cm ² x10 ²)	Sprout weight (g)	Total weight (g)
6 Mar	0	54.4	55.7	3.1	74.7
	50	55.8	44.9	3.0	67.2
	100	21.8	19.2	0.9	33.3
	SE	2.04	5.83	0.9	9.82
23 Mar	0	65.4	70.7	14.2	108.4
	50	71.8	78.6	11.6	122.9
	100	36.2	45.2	2.4	58.3
	SE	2.76	5.58	1.85	7.98
18 Apr	0	74.2	104.2	52.9	213.8
	50	79.8	93.8	43.5	189.5
	100	61.2	87.9	25.0	148.4
	SE	2.71	6.51	4.51	14.35
10 May	0	66.0	81.4	71.2	200.8
	50	62.2	80.5	68.4	199.8
	100	52.6	69.9	53.8	168.7
	SE	2.60	7.47	7.26	18.49
28 May	0	55.2	66.4	137.0	275.6
	50	47.0	57.9	119.8	253.6
	100	41.0	68.6	88.1	218.3
	SE	3.68	7.49	10.14	23.72
18 June	0	29.6	38.6	111.4	198.5
	50	29.8	44.2	117.2	215.5
	100	25.2	36.0	91.1	174.7
	SE	1.87	6.08	14.02	19.61

Appendix 6.iii Results summary for final harvest,
Experiment 6.1. Mean results for leaf
number, leaf area, sprout weight and
total plant weight.

	Defoliation time	Level of defoliation			
		Control	25	50	75
Leaf number					
Sowing 1		43.7			
	I		40.5	40.0	45.3
	II		40.8	44.0	39.5
	III		40.7	38.8	39.0
	IV		35.2	37.5	33.3
Sowing 2		35.2			
	I		31.2	35.3	31.7
	II		31.5	34.2	29.5
	III		32.3	33.3	21.7
	IV		37.2	35.7	19.3

S.E.1 = 2.29;

S.E.2 = 2.31

Leaf area ($\text{cm}^2 \times 10^2$)					
Sowing 1		33.8			
	I		34.2	37.1	27.6
	II		29.7	31.8	23.4
	III		25.6	27.3	18.5
	IV		30.1	21.5	9.5
Sowing 2		31.7			
	I		34.2	37.1	27.6
	II		29.7	31.8	23.3
	III		25.6	27.3	18.5
	IV		30.0	21.5	9.5

S.E.1 = 31.12;

S.E.2 = 3.15.

Appendix 6.iii continued:

	Defoliation time	Level of defoliation			
		Control	25	50	75
Sprout wt (g)					
Sowing 1		124.1			
	I		118.3	119.8	114.2
	II		123.8	108.2	105.4
	III		120.0	100.5	105.4
	IV		140.0	123.0	105.4
Sowing 2		87.3			
	I		102.7	97.2	76.7
	II		80.0	70.6	74.2
	III		83.6	80.8	82.6
	IV		95.1	88.8	76.7
S.E.1 = 5.34; S.E.2 = 5.37.					
Total wt (g)					
Sowing 1		253.0			
	I		233.6	251.1	239.9
	II		261.3	223.4	202.2
	III		251.6	216.2	201.0
	IV		265.4	244.2	215.3
Sowing 2		180.6			
	I		209.4	197.2	155.3
	II		168.8	158.0	152.8
	III		170.6	169.2	163.0
	IV		194.9	186.1	142.4
S.E.1 = 11.61; S.E. 2 = 11.66.					

S.E.1 - Standard error for comparison of common control means with treatment means within each time of sowing.

S.E.2 - Standard error for comparison of treatment means within each sowing time.

Appendix 6.iv Mean sprout yield (g dry wt) following defoliation (Experiment 6.3), and summary of F tests from trend analysis for the relationship between yield and defoliation at each time of defoliation.

Time of defoliation	Level of defoliation				
	0	25	50	75	100
1 Feb	116.3	105.8	110.2	116.6	85.9
13 Mar	105.0	99.8	98.3	79.0	49.9
23 Apr	114.2	99.3	100.6	98.9	77.1

F-tests for trends

	1 Feb	13 Mar	23 Apr
Linear	5.71*	39.16**	12.70**
Quadratic	2.40 ns	7.02*	0.46 ns
Cubic	6.17*	0.42 ns	0.68 ns

* - $P < 0.05$

** - $P < 0.01$

ns - not significant at the 5% level

APPENDIX 8.i

Model parameters

1. Initial leaf area

245 cm² (measured leaf area of transplants).

2. Leaf area growth

Smooth curve drawn through data points from Brussels sprouts harvested in Experiment 6.3.

Logistic function fitted.

Asymptote assumed to be 155 cm² x 10².

Leaf area growth curve $LAGR = 155 / (1 + e^{4.18 - 0.047J})$ *

Regression accounts for > 99% of variation.

3. Senescence; calculated daily as a proportion of the total leaf area and accumulated daily after day 98.

For undefoliated plants

$$\text{Senesced leaf area} = 0.92J - 89.73$$

% of leaf area senesced/day

$$\begin{aligned} \% \text{ SEN} &= 0.0000266J^3 - 0.01044J^2 \\ &+ 1.344785J - 55.25 \quad (P < 0.01) \end{aligned}$$

Absolute defoliation/day

$$\text{SEN}(J) = \% \text{ SEN} \times \text{LA} \text{ACT} / 100$$

Cumulative senescence

$$\text{SENE} \text{SC}(J) = \text{SEN}(J) + \text{SENE} \text{SC}(J-1)$$

4. Yield g = (0.016 x leaf area duration) - 21.654.

5. Compensation factor COMPF

to day 50, COMPF = 0.053 x defoliation/leaf area

days 50-100, COMPF = COMPF x (1 - ((Day-50)/50))

past day 100, COMPF = 0.

* J = days from transplanting.

```

C*****
C*
C*   S P R O U T   D E F O L I A T I O N   M O D E L
C*
C*****

      DIMENSION LA(200),LL(30),SENESEC(200),LAACT(200),DAY(6)
      REAL LAG,LAIN,LAD,LA,LL,LAACT,LAC

      DATA LL/  ** DEFOLIATION PARAMETERS (SIX GROUPS OF FIVE) **/
      DATA DAY/ **   DAY OF DEFOLIATION (SIX PARAMETERS)   **/

C***  DO 30 LOOP CONTRCLS DAY OF DEFOLIATION
      DO 30 K=1,6

C***  DO 20 LOOP CONTRCLS PERCENTAGE DEFOLIATION
      DO 20 IJ=1,5

          SENESEC(1)=0.0
          LAD=0.0
          LA(1)=2.45
          YIELD=0.0
          LAACT(1)=2.56
          LAGR=0.048

          WRITE(6,50)

C***  DO 10 LOOP CONTRCLS LENGTH OF RUN IN DAYS
      DO 10 J=2,200

          DEFOL=0.0
          C CALCULATE LEAF AREA OF CONTROL PLANT (LAC)
          LAC=155/(EXP(4.18-0.047*J)+1)

          C TEST TO SEE IF DEFOLIATION OCCURS (DEFOL)
          IF(J.EQ.DAY(K))DEFOL=LL((K-1)*5+IJ)

          C CALCULATE INCREMENTAL LEAF GROWTH FOR DAY (LAIN)
          LAIN=LAGR*(LA(J-1)-DEFOL)*((155-(LA(J-1)-DEFOL))/155)

          C FIND LEAF AREA ON DAY J (LA)
          LA(J)=LA(J-1)+LAIN-DEFOL
          IF(LA(J).LT.1.0)LA(J)=1.0

          C DOES SENESCENCE OCCUR? IF SO, CALCULATE. (SENESEC)
          IF(J.GT.98)SENESEC(J)=SENESEC(J-1)+((0.0000266*(J-1)**3)-
          *(.01044*(J-1)**2)+(1.344785*(J-1))-55.25)*LAACT(J-1)/100

          C ACTUAL LEAF AREA. (LAACT)
          LAACT(J)=LA(J)-SENESEC(J)

          C CUMULATIVE LEAF AREA OR LEAF AREA DURATION. (LAD)
          LAD=LAD+LAACT(J)

          C CALCULATE YIELD
          YIELD=(0.016*LAD)-21.654

          C CALCULATE COMPENSATION FACTOR (COMPF) FOR SUCCEEDING DAYS
          C AFTER DEFOLIATION.

          COMPF=0.053*(DEFOL/LAACT(J-1))
          IF(LA(J).GE.LAC)LAGR=0.048
          IF(J.GT.50)COMPF=COMPF*(1.-(FLOAT(J-50)/50.))
          IF(J.GT.100)COMPF=0.0
          IF(LA(J).GE.LAC.AND.DEFOL.GT.0.0)LAGR=LAGR+COMPF

          C WRITE RESULTS EVERY TEN DAYS
          IF(MOD(J,10).EQ.0)WRITE(6,100)J,SENESEC(J),DEFOL,LAIN,
          *LAACT(J),LAD,YIELD,LAGR,COMPF,LAC

      10 CONTINUE
      20 CONTINUE
      30 CONTINUE

50  FORMAT('1',10X,'D E F O L I A T I O N   M O D E L'///
          *2X,'TIME(DAYS)',13X,'SENESCENCE',2X,'DEFOLIATION',2X,
          *'LA INCREMENT',2X,'DAILY LA',2X,'CUMULATIVE LA',4X,'YIELD',
          *5X,'LAGR',7X,'COMPF',5X,'LAC')
100  FORMAT('0',4X,I3,18X,4(F8.2,4X),F8.2,2X,F10.3,3(2X,F8.3))
      END

```