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# FINAL REPORT

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To:  
Horticultural Development Council  
Bradbourne House  
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Tomato: Population growth  
of pests on speciality cultivars

March 2008

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**Commercial – In Confidence**

Project Title: Tomato: Population growth of pests on speciality cultivars

Project number: PC 272

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The results and conclusions in this report are based on information gathered from the scientific and horticultural literature, sampling in commercial crops, chemical analysis in a commercial laboratory and trials completed under controlled conditions in purpose grown experimental crops. The conditions under which the studies were carried out and the findings have been reported with detail and accuracy. However, because of the biological nature of the work it must be borne in mind that different circumstances and conditions could produce different results. Therefore, care must be taken with the interpretation of the results especially if they are used as the basis for commercial product recommendations.

### **Authentication**

I declare that this work was done under my supervision according to the procedures described herein and that this report represents a true and accurate record of the results obtained.

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## **GROWER SUMMARY**

### **HEADLINE**

Differences in susceptibility to leafminer damage were not found to be correlated to measured leaf nutrients. Results of biological studies and literature searches pave the way for investigations into other causal factors.

### **BACKGROUND AND EXPECTED DELIVERABLES**

UK tomato production is becoming increasingly dependent on speciality cultivars as the industry concentrates on the premium quality market. Many pest management strategies involving the release of biological control agents were developed on classic round tomato cultivars over a decade ago and have not been modified to allow for the different susceptibility of the speciality tomato cultivars. The quantity of these cultivars grown in the UK is likely to substantially increase over the next few years in response to retailer demand. It is therefore important that we gain an improved understanding of pest management in these crops.

Work in HDC funded project PC 240 in 2005/06 categorised over 30 cultivars of tomatoes in terms of their susceptibility to common pests. Some speciality cultivars in the cherry, baby cherry and cocktail groups had particularly high rankings to these species. In addition, there is now evidence that some of these cultivars are susceptible to insects that are not commonly considered to be important pests of tomatoes. For example, there have been several serious infestations of aphids and thrips in crops of cv Piccolo in the UK. This in turn could increase the risk of attack by viruses such as PVY and TSWV.

It has been assumed by many agronomists and IPM practitioners that Brix value (*i.e.* total dissolved solids) of fruit provided a guide to the nutritional value to insects of tomato plants. Preliminary studies indicated that while there did appear to be a loose correlation between Brix value of fruit and the population growth of pests, particularly tomato leafminer, there were inconsistent seasonal variations and other important anomalies.

The TGA Technical Committee felt it was important to understand the reasons for the increased susceptibility to pests of the speciality cultivars as a first step in modifying and improving the IPM programmes. In the first instance, this required an improved knowledge of the nutritional value (*i.e.* to insects) of the leaves of these cultivars. This study focused on primary metabolites (*i.e.* lipids, proteins and carbohydrates / sugar) and related factors.

Other factors, such as leaf morphology (principally trichomes on lower leaf surfaces, petioles and stems) are also known to affect pest establishment. Tomato leafminers (*Liriomyza bryoniae*) were chosen as the initial model species to explore interactions with leaf nutrients because the adults forage on the upper surface of the leaf and the larvae are within the leaf, both of which greatly reduced the possibility of any significant interactions with trichomes.

### **SUMMARY OF COMPLETED WORK**

The project initially investigated the hypothesis that differences in leaf nutrients were the underlying cause for differing susceptibility to pests among speciality tomato cultivars. Depending on the outcome of these studies, other factors such leaf morphology, secondary metabolites, semiochemicals and environmental conditions could be investigated at a later stage.

### **Literature search**

The project included an extensive literature search into factors that may influence pest establishment on plants. This initially revealed over 250 papers relating to insect nutritional requirements, relevant aspects of insect behaviour, factors influencing host plant selection, host plant quality and plant nutrition (including nitrogen, proteins, carbohydrates, sterols). There was very little published literature that was directly relevant to pests on the cultivars of speciality tomato grown in the UK. Furthermore, it was rarely possible to generalise about plant / herbivore interactions because most of the associated species have exerted evolutionary pressures on one another and have thus developed specialised relationships. As a consequence, many of the studies reported in the literature focus upon a single plant / herbivore interaction and it is not unusual to find conflicting information about different pairings. The results of the search are summarised as a comprehensive review in the main body of the report.

### **Practical investigation of nutrient status of leaves**

Five speciality tomato cultivars were selected for the practical studies with the aim of covering a wide range of tomato types and perceived susceptibility to leafminers. The following cultivars, which are listed in increasing order of leafminer susceptibility, were included in all the plant nutrition and insect performance experiments: Santa (Baby plum), Dometica (Classic), Conchita (Cherry), Piccolo (Baby cherry) and Capri (Cocktail).

The key factors relating to leafminer population growth on the selected cultivars were measured under controlled conditions in an experimental glasshouse where the pests could be released onto the plants without putting any commercial crops at risk. However, it was important to determine whether the nutritional status of tomato leaves grown under these conditions were comparable to commercial crops. Therefore, leaf samples were taken for analysis from both situations.

Winter (January / February) and spring (April / May) are key times for leafminer invasion and population growth respectively. Samples of foliage were therefore taken from the selected cultivars at both times of the year and immediately transported to Campden & Chorleywood Food Research Association (CCFRA) in chilled boxes. Each replicate sample was individually analysed at CCFRA for the following components: energy (k joules), protein, total carbohydrate, fat, moisture, ash (*i.e.* non-combustible minerals), total sugars, fructose, glucose and sucrose.

Overall, the measurement of nutrients revealed few significant differences within any of the data sets. Furthermore, where differences did exist, there were no consistent trends between cultivars and no apparent correlation with the susceptibility to leafminers that had been established in the previous project.

However, there was a seasonal effect, with apparent differences in the nutrient content of the leaves taken from the experimental crops in February and May.

Overall, protein content decreased by 13%, while carbohydrate, fat, sugars and minerals all increased substantially. The largest percentage increases were in fat (+58%) and sugars (+66%). The energy value stayed approximately the same although it must have come from different nutrients (*i.e.* more from carbohydrate, fat and sugars and less from protein).

### **Practical investigation of leafminer performance**

This experiment was first done in February and then repeated in May thus coinciding with leaf sampling and analysis. Tomato plants were grown in an experimental glasshouse and each trial began when the plants were approximately 1.5m in height. In each replicate, five mated adult female leafminers were confined for 48 hours in perforated cages positioned over the second fully expanded leaf on each plant. The insects were allowed to feed and lay eggs for 48 hours and were then removed. The numbers of feeding punctures were recorded after 48 hours, numbers of leafminer larvae recorded after 14 days and numbers of leafminer pupae recorded after 22 days.

There was no consistent correlation between leaf nutrient content and the key factors in leafminer population growth within any of the data sets. Overall, the numbers of feeding punctures recorded were similar in the two experiments but differed greatly between cultivars. With cv Dometica, the numbers of feeding marks were 2.3x greater in February than in May, while with cv Piccolo, the opposite was true and there were 1.6x more feeding marks in May than in February.

As with leafminer feeding activity, there was no consistent correlation between the nutrient content of leaves and the production of pupae within any of the individual data sets. However, unlike feeding activity, there was a marked difference in the overall number of pupae produced in the two experiments; *i.e.* overall there were almost 6x as many pupae in February than in May.

The ratio of feeding marks to pupae, which presumably gives some indication of the suitability of the host plant, was considerably lower in February than May in all cultivars, indicating that the pest was generally operating more efficiently in the earlier part of the season. The seasonal difference was greatest with the two cultivars that had previously been allocated the highest grades in terms of susceptibility to attack by leafminer (*i.e.* cv Piccolo and Capri). The experiment did not record the numbers of eggs laid because this would have been too destructive. As a consequence, the excessive leafminer feeding relative to pupal formation in May might have been due to fewer eggs being laid than in February or due to increased mortality of immature stages.

Cultivar Piccolo always caused leafminers to make more feeding punctures per pupa than cv Dometica, which implies that cv Piccolo is less palatable or produces more deterrents, even though, in commerce, it is regarded as more susceptible.

It is interesting to note that a high ratio of feeding punctures to mines has commonly been observed in commercial crops of cvs Piccolo and Capri between April and June. This has usually occurred with the last flush of adult leafminers before the population has been controlled by the parasitoids, *Diglyphus isaea*. The relatively small number of mines produced from these punctures has usually been attributed to "stinging out" by the parasitoid rather than excessive leafminer feeding relative to oviposition.

### **Provisional conclusions**

The results from the practical studies indicate that leafminer performance is not primarily influenced by leaf nutrients in these cultivars. However, the original hypothesis has not yet been rejected. There is sufficient published evidence to show that leaf nutrients can influence the behaviour, development and survival of insects in many varied ways and it is possible that a subtle mechanism exists but has not yet been detected. It is also possible that more sophisticated analytical tests may be required to detect differences in leaf nutrients. Nonetheless, the project has also begun to look at other possible factors that could influence the performance of pests on these cultivars and thus pave the way for a wider range of studies in the future.

A second literature review has been completed and is incorporated in the main body of the report. In total, more than 400 references have been consulted in the course of this project but no obvious explanation for the differing pest susceptibility of speciality tomato cultivars has yet emerged. The results of the second literature search suggest that there are numerous other factors that could make cultivars such as Piccolo and Capri more susceptible to damage by leafminers. These factors might also account for many fewer pupae being produced in May than February on all the speciality cultivars tested here and for the adult leafminers having to make more leaf punctures per pupa produced.

The most obvious factors that might account for the seasonal differences in behaviour would be effects of 'season' on biochemical and physical characteristics of plant leaves. In this context, 'season' could mean increases in light quantity per day, daylength and / or temperature. Such changes could alter leaf size, affect light penetration into the leaf canopy producing micro-environments that were more or less suitable to leafminers, and increase leaf thickness making leaves tougher and less digestible.

Even more likely, perhaps, might be effects of season on the biochemical composition of leaves. Trichomes and their exudates are unlikely to be factors as tomato leafminer injects its eggs into the upper leaf surface and the trichomes are mainly on the lower leaf surface. Differences between cultivars could be due to differences in the lipid composition of their cuticles, or in the production of secondary metabolites, such as phenols, alkylating agents, terpenes, or other volatiles. It is also noteworthy that in the commercial production of tomato, average concentrations of CO<sub>2</sub> would be higher in February than May which might increase the carbon supply to leaves resulting in a reduction in leaf nutrient concentrations and an increase in herbivore food intake in summer. However, in general, herbivorous insects simply increase their consumption rates to compensate for lower quality leaves.

In the absence of data it is tempting to invoke differences in semiochemicals as these are involved in inducing plant defences, in attracting or repelling insects and in reducing the digestibility of leaf material. The results obtained in this project suggest that leafminers produce more pupae per feeding visit in February than in May and they always make twice as many feeding attempts on cv Piccolo than cv Dometica for a given number of larvae produced. The review of literature revealed that when leaf miners attack tomato plants, the plants increase peroxidase activity and produce four foliar proteins. The combined effect was to render the leaves unpalatable and the oxidised phenolics were toxic to the leaf miner. The proportions and mix of amino acids and proteases also act as deterrents to mining insects and those investigated appear to reduce the digestibility of leaf material. Oviposition stimulants, such as tyramine, could be different in different cultivars. Elicitors of defence responses, such as jasmonates, might be involved so that attack by a leafminer



induces the tomato's natural defences to operate at a higher level or even deters oviposition by the leaf miner. Of the non-volatiles produced by plants, the steroidal glycoalkaloid  $\alpha$ -tomatine has a toxic effect on insects and would be ingested by them from tomato tissues.

## **FINANCIAL BENEFITS TO GROWERS**

This study was a first step in gaining knowledge required to improve IPM programmes for speciality tomato crops. The TGA Technical Committee accepted that this project would not provide immediate financial benefits but would provide direction for subsequent studies that could eventually reduce the financial impact of pests in these crops.

## **ACTION POINTS FOR GROWERS**

There are no action points that commercial growers can implement at this stage. However, there is considerable information that will pave the way for further studies.

## **SCIENCE SECTION**

### **PART 1: GENERAL INTRODUCTION TO PROJECT**

#### **Background**

UK production is becoming increasingly dependent on speciality tomato cultivars as the industry concentrates on the premium quality market. Many pest management strategies involving the release of biological control agents were developed on classic round tomato cultivars over a decade ago and have not been modified to allow for the different susceptibility of the speciality tomato cultivars. The quantity of these cultivars grown in the UK is likely to substantially increase over the next few years in response to retailer demand. It is therefore important that we gain an improved understanding of pest management in these crops.

Work in HDC funded project PC 240 in 2005/06 categorised over 30 cultivars of tomatoes in terms of their susceptibility to common pests (Jacobson and Morley, 2007). Some speciality cultivars in the cherry, baby cherry and cocktail groups had particularly high rankings to these species. In addition, there is now evidence that some of these cultivars are susceptible to insects that are not commonly considered to be important pests of tomatoes. For example, in 2006 there were several serious infestations of aphids and thrips in crops of cv Piccolo in the UK. This in turn could increase the risk of attack by viruses such as PVY and TSWV.

It has been assumed by many agronomists and IPM practitioners that Brix value (*i.e.* total dissolved solids) of fruit provides a guide to the nutritional value to insects of the foliage of tomato plants. Prior to the start of this project, the Project Leaders had access to considerable information relating to the Brix value of fruit from a wide range of classic and speciality cultivars. While there did appear to be a loose correlation between Brix value of fruit and the population growth of pests, particularly tomato leafminer (*Liriomyza bryoniae*), there were inconsistent seasonal variations and other important anomalies.

The TGA Technical Committee felt it was important to understand the reasons for the increased susceptibility to pests of the speciality cultivars as a first step in modifying and improving the IPM programmes (TGA TC Minutes, 7 September 2006). In the first instance, this required an improved knowledge of the nutritional value (*i.e.* to insects) of the leaves of these cultivars and that was the basis of this project. This study focused on primary metabolites (lipids, proteins and carbohydrates / sugar) and related factors.

Other factors, such as leaf morphology (principally trichomes on lower leaf surfaces, petioles and stems) and secondary metabolites, are also known to affect pest establishment. Leafminers were chosen as the initial model species because the adults forage on the upper surface of the leaf and the larvae are within the leaf, both of which greatly reduced the possibility of significant interactions with trichomes. If necessary, secondary metabolites would be investigated at a later stage.

#### **Overall aim and objectives:**

The overall aim was to determine whether there was a correlation between the nutritional status of tomato leaves and pest development rate.

Specific objectives were:

1. To select key cultivars from the major tomato groups (ie classic, cherry, baby cherry, baby plum, cocktail)
2. To measure the nutritional status of leaves of the selected cultivars during winter (January / February) and spring (April / May).
3. To measure key factors relating to pest population growth on the selected cultivars, initially using tomato leafminer as a model species.
4. To correlate nutritional status of leaves and pest developmental rate.
5. To transfer new knowledge to tomato growers.
6. To provide direction for further studies.

In November 2007, the HDC agreed to fund an extension to the initial project to allow the results of literature searches to be prepared as two literature reviews which would form chapters in the Science Section of the Final Report.

## **PART 2: NUTRITIONAL FACTORS THAT MAY INFLUENCE PEST ESTABLISHMENT**

### **Some important aspects of the biology of the chosen herbivore model**

The main leafminer pest of the glasshouse tomato is *Liriomyza bryoniae* but such crops can also be infected by other leafminers, including *L. trifolii*, and *L. huidobrensis*. Leafminers have a relatively short life cycle and in the warm environment of a glasshouse can complete their life cycle in 21 to 28 days. The biology of the *Liriomyza* has been well researched (e.g. Spencer, 1973; Civelek, 1999; Parella *et al.*, 1985, Parella, 1987a). Adult females deposit eggs just below the epidermis on the upper surfaces of leaves (lower surfaces in the case of *L. huidobrensis*) and the larvae start to feed as soon as they hatch. They feed incessantly until they pupate outside of the leaf (Parrella, 1987a; Souza and Reis, 1999). The larvae complete their entire development within one leaf and so it is the ovipositing female that chooses the larval habitat and food.

The adults cause damage by puncturing the leaf surface to feed on the leaf tissue and to lay eggs but it is the larvae that cause greatest harm by tunnelling within the leaf tissue, feeding on the chloroplast-containing lower mesophyll (Weintraub and Horowitz, 1995).

### **Summary of insect nutritional requirements**

Reviews by Trager (1941, 1947) and work by Fraenkel (1959) established the basic food needs of insects as proteins, carbohydrates and sterols, minerals, and 'accessory food factors'. Experiments established that the B vitamins (thiamine, riboflavin, nicotinic acid, biotin) and folic acid were important factors in insect nutrition (Fraenkel, 1959); furthermore that the fat-soluble vitamins A, D, E, and K were not required for optimum insect growth (with the exception of some cockroaches, Fraenkel (1959); Fraenkel and Blewett (1943a, b)).

According to Chapman (1971), McNeil and Southwood (1978), Mattson (1980); Derridj *et al.* (1989), Bernays and Chapman (1984), insects require water, nitrogen for manufacturing proteins, nucleic acids, chitin, essential amino acids (including arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, valine), carbon for manufacturing carbohydrates and lipids, phosphorous for manufacturing nucleic acids and phospholipids. In general, insects require plenty of sodium (Na) but little potassium (K), while plants contain relatively little Na but plenty of K. They also require sources of energy which influence their developmental patterns (Alonso and Herrera, 2001). Amongst less general factors, the sterol, sitosterol, is important for insect chemoreception on tomato plants and ascorbic acid (Vitamin C) is required by some insects for xanthotoxin ingestion (Timmermann *et al.*, 1999).

Several reviews have detailed which nutrients may be supplied by host plants both for the adult insects' requirements and larval development (Johnson and Felton, 1999; Awmack and Leather, 2002). There is an extensive literature on aphid nutrition but less on Liriomyzids and it has been difficult to obtain a profile of their requirements. The majority of insect nutrition studies detail the individual function of each element but poorly explain the interface between the physical and chemical components in the diet. Many of the functional dietary components have been established through insect feeding studies where specific diets (oligodic, meridic and holidic) were designed for individual experiments

(<http://lhs.lps.org/staff/sputnam/Ent801/Ento801.htm>). Absorption and bioavailability have been reviewed elsewhere (Felton, 1996; Cohen, 2004 Chapters 4 and 5). With the exception of nitrogen and to a lesser degree carbon, information on individual nutritional components of plant tissues on leafminer nutritional requirements is limited (Faeth *et al.*, 1981; Faeth, 1985; 1987; 1990) although much research has investigated the dietary requirements of aphids.

### **Relevant aspects of insect behaviour**

Adult females act to maximise fitness of the population not only through offspring performance but through their own performance as well. Adult females should therefore preferentially inhabit host plants that will increase their own longevity and fecundity rather than those that improve offspring performance (Evans, 1976; Coll and Ridgeway, 1995; Jönsson, 1995; Nakashima and Hirose, 1999). Consequently, there are two apparently conflicting behavioural strategies - optimal oviposition (Jaenike, 1978) and optimal foraging. Optimisation of both strategies necessitates a trade-off between them. Various factors have been suggested to influence the adoption of either strategy, such as host plant defences, host plant chemistry, natural enemies, tritrophic interactions, density levels, whether the insect feeds in the adult stage, the extent to which larval food resource depends on oviposition site, the presence of alternative adult food resources, and the motivational and physiological state of the adult (Bernays and Graham, 1988; Thompson, 1988; Thompson and Pellmyr, 1991; Thompson and Dahlman, 1998; Sih, 1993a, 1993b; Scheirs and de Bruyn, 2002; Scheirs *et al.*, 2004). Conflicts could result, *eg.* when the nutritional needs of ovipositing females and their offspring are not the same (Evans, 1976).

### **Factors Influencing Host Plant Selection**

As Renwick (1989) summarised, “the selection of a suitable site for oviposition by phytophagous insects is critical for the successful development of their offspring”. The behavioural events leading to oviposition are mediated to a large extent by chemical cues associated with potential host plants. Orientation and landing are primarily guided by volatile constituents of a plant, whereas assessment of a leaf surface depends on contact stimuli. Abiotic and biotic environmental factors often influence the production or release of behaviour-modifying chemicals by a plant, and therefore affect oviposition preferences. Plant chemistry may be involved in associative learning, but may also lead to mistakes. Thus a clear correlation between oviposition preference and offspring success does not always exist.

Host finding and acceptance for oviposition by phytophagous insects is mediated to a large extent by chemicals associated with the plants they encounter. Variations in these chemical cues, caused by one or more biotic or abiotic factors, can profoundly affect the responses of an insect either positively or negatively. Individuals may vary in response to a chemical stimulus and such variation is probably the result of there being different thresholds for perception but learning, behaviour (Hawkes and Coaker, 1979) prior exposure (pre-imaginal) and variety are also involved (Facknath and Wright, 2007). Although the correlation between oviposition preference and offspring performance is not perfect, the majority of insects can depend on plant chemistry to select the most suitable site for development and survival of their progeny (Renwick, 1983).

Host plant suitability is based on quantitative factors such as the size and position of leaves, leaf morphology, thickness and cellular structure (Mooney and Gulmon, 1982), mechanical barriers on or within the leaf, and nutrient levels, as well as qualitative ones such as leaf cuticular composition (Jackson *et al.*, 1986; 1991) or

microstructure, specific allelochemicals, and phenological changes (Renwick, 1989). There is increasing evidence that these factors vary substantially within and among plants, and that such variations have a significant influence on the performance of insects feeding on them (Kimmerer and Potter, 1987; Suomela and Nilson, 1994; Fisher *et al.*, 2000; Facknath and Lalljee, 2005).

The total process of host selection is complex and most likely depends on combined inputs from chemical as well as physical stimuli and chemical signals influenced by abiotic and biotic factors (Renwick, 1983, Facknath, 2002; Facknath and Lalljee, 2005). Insect behaviour must also be considered, together with the level and intensity of herbivore attack, whether secondary predators are involved and the influence of tritrophic eating patterns (Awmack and Leather, 2002). Unfortunately, research has tended to focus on individual factors and elements and links between them are rarely made.

There is a considerable literature on site selection by herbivorous insects and this confirms that selection relates to leaf nutrient quality and plant characteristics that are especially important to the performance of offspring that feed exclusively on plant material during the first nymphal stages (Messina, 1982; Parker and Root, 1991; Hawthorne *et al.*, 1992; Hawthorne, 1998; 1999). Newly hatched larvae of many insects are relatively immobile, and depend on the behaviour of their mother to find the best source of food for their successful growth and development. However, female adult nutrition, fecundity and survival are also important factors which determine host plant selection (Evans, 1976) and involve a series of tradeoffs (Mayhew, 1997, 2001; Jauset *et al.*, 1998; Facknath and Lalljee, 2005; Johnson *et al.*, 2006; Müller and Arand, 2007; Groenteman *et al.*, 2006).

Almost all of these factors affect the host-plant preference of *Liriomyza* species and thus the impact of the *Liriomyza* as a pest of tomato. These include the nutrient content of the leaf, the presence of secondary metabolites, plant volatiles and non-volatile compounds, biochemical and enzymic defence mechanisms, leaf age and morphology, insect behaviour and performance as well as environmental factors such as fertiliser regimens and field conditions. In the case of cultivated tomatoes, the controlled environment of the glasshouse should limit the impact of environmental factors. In essence, female leafminers appear to base their decision to oviposit or decline on three main factors: (i) host plant suitability, (ii) presence or absence of other phytophagous organisms, and (iii) natural enemies (Faeth *et al.*, 1981; Faeth, 1985; 1987: 1990).

### **Host plant “quality”.**

Host plant “quality” is a key determinant of the fecundity of herbivorous insects. Scheirs *et al.* (2004) concluded that hosts optimal for insect adult nutrition were also optimal for offspring performance but not vice versa. Components of host plant quality (such as the plant’s content of carbon, nitrogen, and defensive metabolites) directly affect the potential and achieved herbivore fecundity. The nutritional ecology of insects, the behavioural fitness component and food utilization by insects have been reviewed by Slansky and Rodriguez (1987) together with the impact of individual nutritional components of plant tissues on insect performance (Albert and Bauce, 1994; Albert and Prisella, 1985). Recent reviews on host plant quality and herbivorous insects’ fecundity provide a good overview of the issues (Renwick, 1983; Cronin *et al.*, 2001; Awmack and Leather, 2002; Cronin, 2006).

The nutritional physiology of herbivorous insects and their utilisation of food, have been reviewed (Patel and Schuster, 1983; Slansky and Rodriguez, 1987; Cohen, 2004) as have the basic principles of nutritional ecology (Waldbauer 1968; Scriber and Slansky, 1981; Slansky and Scriber, 1982, 1985; Awmack and Leather, 2002). The nutritive quality of plant tissues plays an important role in insect-plant interactions (Feeny, 1976; Mattson, 1980; Strong *et al.*, 1984; Price, 1991) and host plant quality also affects insect reproductive strategies, such as egg size and quality, the allocation of resources to eggs, and the choice of oviposition sites and the outcome (Coley *et al.*, 2006). Recent reviews on host plant quality and the fecundity of herbivorous insects provide a good overview of the interdependence of the factors (Cronin *et al.*, 2001; Awmack and Leather, 2002; Cronin, 2006). The subject of host plant quality and plant fitness has been well reviewed (e.g. Leather, 1988, 1990, 2003; Awmack and Leather, 2002; Scheirs *et al.*, 2003; Scheirs and De Bruyn, 2002, 2004).

Van Emden (1966) initially suggested that plant nutrition had direct effects on insect (aphid) performance, supported by subsequent work on the impacts of low plant quality and nutritional differences on insect and larval growth (Cornelissen and Stiling, 2006). Low host plant quality can affect insect performance directly, by reducing growth rate, fecundity, and survival (Slansky, 1993; Haggstrom and Larsson, 1995a, b; Cornelissen and Stiling, 2006), as a plant defence (Augner, 1995), or indirectly by affecting the risk of mortality caused by natural enemies (Feeny, 1976; Price *et al.*, 1980; Clancy and Price, 1987). A plant may lower its nutritive quality for herbivores, by using secondary compounds, morphological characters and / or having a lowered nutrient content. However, the amount of compensatory feeding performed by the herbivores, or by prolonging their feeding periods, may render the defence useless. The extent of damage to the hostplant is also dependent on the herbivores' mobility in relation to the spatial structure of the plant. The impact of low nutritive quality as a plant defence has been reviewed by Augner (1995).

## **Plant Nutrition**

The nutrients available within the host plant are a reflection of the availability of nutrients in the root environment and the physiological responses of the plant to nutrient concentration. In general, there is considerable variation in nutrient concentrations within plant tissues of different individuals, species, and ecosystems (Chapin, 1980; Aerts and Chapin, 2000; Alonso and Herrera, 2003; Alyokhin *et al.*, 2005).

The impact of insect herbivores is usually greatest while leaves are actively growing (Alonso and Herrera, 2000) and so changes in nutrient content during leaf growth are likely to be very important. Host selection may be related not only to variation in mean concentration of particular nutrients (Bergström and Danell, 1986; Athey and Connor, 1989; McNaughton, 1983; 2001), but also to the relative proportions of different nutrients (Clancy *et al.*, 1988; Cates, 1996; Phelan *et al.*, 1996). Even so, many studies indicate that herbivores adapt to low nutrient concentrations, notably low N.

Chemical fertilisers are used in conventional greenhouse production to ensure the production of high quality crops and while they provide essential nutrients for plant growth they also elevate the nutritional quality and attractiveness of plants to phytophagous insects (van Emden, 1966; Minkenbergh and Fredrix, 1989). The application of fertilisers also has a direct effect on the levels of phenolics in plants, a

factor affecting host selection by phytophagous insects (McNeill and Southwood, 1978; Mattson, 1980).

## Nitrogen

In general, plants contain 0.03-7.0% nitrogen, whereas insects require 7-14%. Nitrogen (N) is a main component of proteins, amino acids and nucleic acids. These are required by phytophagous insects and are commonly the limiting nutrients for optimal growth (Bernays and Chapman, 1984).

There is much evidence to indicate the preference of insects for nitrogen-rich plants (eg. Van Emden and Bashford, 1969; Mattson, 1980; Valladares and Lawton, 1991; Kyto *et al.*, 1996; Bowdish and Stiling, 1998; Jauset *et al.*, 1998; Barros and Zucoloto, 1999; Bi, *et al.*, 2001). Indeed, nitrogen (N) is frequently a limiting resource for insects (Mattson, 1980) and leaf N content is generally accepted as an indicator of food quality (Scriber and Slansky, 1981). Several studies have shown that populations of *Frankliniella occidentalis* (western flower thrips) respond positively to increased fertilisation in field-grown tomatoes (Brodbeck *et al.*, 2001; Stavisky *et al.*, 2002). The concentration of nitrogenous fertilisers is directly linked to the N content of host plants and this influences population abundance, distribution and control in *Liriomyza trifolii* (Minkenberg and Fredrix, 1989) and *Frankliniella occidentalis* on chrysanthemum (Minkenberg and Fredrix, 1989; Chau and Heinz, 2006).

The effect of soil-applied fertiliser on insect-host plant relationship is well documented as is the effect of nitrogen availability on the expression of chemical defences in tomatoes (Broadway and Duffey, 1986; 1988; Barbour *et al.*, 1991; Stout *et al.*, 1994; 1998a, b, c; Broadway, 1996). The impact of N fertilisation and increasing rates of NPK fertiliser application during cultivation of tomato on feeding site selection and oviposition by *Liriomyza* species increased colonisation and herbivory (Gregory *et al.*, 1986; Wilkens *et al.*, 1996; Jauset *et al.*, 1998; Pickett, 1992; Pickett and Glinwood, 2007; Facknath, 2002; Facknath and Lalljee, 2005; Facknath and Wright, 2007). Leaf N affects the performance of adult insects (Scriber and Slansky 1981; Strong *et al.* 1984) though increased N levels do not always improve juvenile performance (Scriber, 1984).

In experiments with wild tomato plants, increasing the rate at which NPK fertilizer was applied reduced the plants' trichome-based resistance to pests of tomato (tobacco hornworm and a Colorado beetle) by lowering both the density of type VI glandular trichomes and the amount of 2-tridecanone contained in their tips (Barbour *et al.*, 1991). This confirms work in South America on the Lepidopteran tomato leafminer, *Tuta absoluta*, on *Lycopersicon hirsutum* f. *glabrum* compared to *L. esculentum* in terms of levels of types of trichomes present, and tridecan-2-one and undecan-2-one (Lin *et al.*, 1987; Leite *et al.*, 2001).

Female leafminers determine what food their offspring will eat because the larvae feed only in the leaf in which they hatch. Distribution patterns of eggs within plants are equal to those of feeding punctures and females tend to feed on similar plants and areas of plants as do their offspring (Minkenberg, 1988). *Liriomyza trifolii* females prefer plants with a high N content over plants with a low N content, if they have previously been exposed to high N plants, and there is a direct link between plant N content and adult performance (Minkenberg and Fredrix, 1989). Pre-imaginal experiences have also been reported where the quality of foliar N consumed by larvae impacts on the adult choice of host plant (Prudic *et al.*, 2005; Groenteman *et al.*, 2006; Videla *et al.*, 2006; Facknath and Wright, 2007).



The effect of N on the fitness of *L. trifolii* females has been confirmed by a consistent intrinsic rate of population increase, immature developmental time and survival of offspring on plants of different N content (Minkenberg and Ottenheim, 1990). Nitrogen use efficiencies are informative about insect performance because levels of plant nitrogen (an index of protein) are limiting to insect performance (Lindroth, 1993).

In most plants, N levels are higher in younger tissues than in older leaves and in general, N levels decline as the plant matures. Nitrogen is the most important nutrient for herbivorous insects (Scriber and Slansky, 1981; Coley *et al.*, 2006) followed by carbohydrates, lipids and sterols. Low N concentrations or low quality N in plant tissues are frequently used as a plant defence mechanism as the N content of host plants often limits the development and fecundity of herbivorous insects (McNeill and Southwood, 1978; Mattson, 1980; White, 1984; Denno and Roderick, 1990; Denno and Fagan, 2003; Prudic *et al.*, 2005).

Leaf N is a significant factor in the behaviour and population dynamics of *L. trifolii* (Minkenberg and Fredrix, 1989). *Liriomyza trifolii* prefers the uppermost leaves which have the highest N content. Leaf N content influences the preference, performance, selection, and oviposition behaviour of *L. trifolii* on tomato plants (Minkenberg and Ottenheim, 1990; Gonzales, 2003; and Groenteman *et al.*, 2006). Most mining occurs in leaves of a certain age and N content decreases with the age of the leaves (Raupp and Denno, 1983).

Pupal weights of *L. trifolii* larvae reared on leaves with various N levels increased significantly as leaf N increased, but *L. trifolii* fecundity was not significantly affected by N in the leaves upon which the females developed. *Liriomyza trifolii* is well adapted, however, because it has the ability to distinguish between plants with different leaf N contents; differences that will lead to increased fecundity, longevity and overall fitness (Minkenberg and Ottenheim, 1990).

Many frequently-used indicators of larval growth performance were shown to be positively correlated with leaf N content which supports the view that N is a limiting nutrient for larval growth. Furthermore, leaf N was more important than water content (Anderson *et al.*, 1995; 2001; Jönsson and Anderson, 1999). The percentage N levels in bean foliage were found to influence pupal weights. *Liriomyza trifolii* male larvae reared on leaves with various N levels had a 4.5% increase in developmental time over the ranges of nitrogen examined (2.76 - 6.27% leaf N). However, *L. trifolii* fecundity was not significantly affected by N in the leaves upon which the females developed. It appears that larval food acquisition of the female has less effect on fecundity than does adult food acquisition (Kaneshuro and Johnson, 1996). The relevance here is that the total progeny production of the natural enemy, *Chrysocharis oscinidis* (Ashmead), allowed to feed and oviposit on *L. trifolii* larva reared on leaves with differing N levels, may increase by as much as 40%. These changes in fecundity are highly significant and could greatly affect pest / parasitoid populations in both agroecosystems and mass rearing programs.

## Proteins

Proteins and amino acids make up between 1-40% of the dry weight of leaves. Most woody plants and grasses have a low percentage and the highest percentage is in herbaceous legumes (Bernays and Chapman, 1984). Free amino acids in plants make up only 5% of the total nutrient N. Increased protein quantity is frequently associated with enhanced herbivore survival, growth, and fecundity (McNeill and Southwood, 1978; Mattson, 1980; Ohgushi, 1991, 1992; Slansky, 1993; Nakamura

and Ohgushi, 2003). The variable nutritive quality of plant protein and its impact on insect herbivore responses have been reviewed (Felton, 1996). Most insects, except for true sap feeders (aphids, whiteflies and many leafhoppers), use whole proteins as their principal source of protein (polypeptides), which are broken down into their constituent amino acids and used for insect growth, enzymes and metabolic functions.

Protein quality has received comparatively little attention as a factor in the suitability of host plants for insects, although the nutritive quality and variation of host plant protein does affect insect herbivore behaviour and physiology (Felton, 1996). Plant protein quality is subject to considerable variation from genetic and environmental influences and may significantly impact herbivore performance. However, some phytochemicals, e.g. phenols (Kennedy, 2003), that are ingested with protein may negatively impact protein utilization (Berenbaum, 1980, 1983, 1995; Behemer *et al.*, 2002). The quality of the nitrogenous components (*i.e.* the proportion and concentration of specific amino acids) may also influence digestibility (Duffey and Bloem, 1986). The amino-acid requirements of insects have been well investigated but research into the specific dietary needs of Lyriomyzids is limited.

### **Carbohydrates**

Carbon-based compounds, such as carbohydrates and lipids, also have a major impact on the performance of herbivorous insects. In general, high concentrations of soluble carbohydrates in plant tissues have negative effects on insect herbivores because they dilute other nutrients and so require the herbivores to increase their consumption rates to compensate (Kause *et al.*, 1999).

Carbohydrates (polysaccharides, oligosaccharides and monosaccharides) are used by most insects as structural components and energy sources. Cellulose, a carbohydrate in plants cannot be used by insects but assist with gut motility. Phytophagous insects fail to thrive on diets of less than 50% carbohydrates (House, 1974). The majority of carbohydrates are water-soluble substances. Carbohydrates are important in defining growth at low food levels (Turunen, 1979; 1985). Starch palatability is an important issue that Bartlet *et al.* (1990) investigated.

Sugars are phagostimulants for most insects (Bartlet *et al.*, 1994). Where glucose, fructose and sucrose have been collected from the phylloplane (leaf surface) of maize, the sugar ratios on the phylloplane were quite different from those observed within the leaf (Fiala *et al.*, 1985; 1990). Fructose is reported to be important for herbivorous insects for host plant selection and oviposition sites. This role has been reviewed (Maher *et al.*, 2006; Derridj *et al.*, 1992). In greenhouse experiments, plant phenological stages were more important than the plant species in the insect oviposition preference, which were accentuated by the amounts of glucose and sucrose (Derridj *et al.*, 1989; Soldaat *et al.*, 1996).

Insects require energy for metabolic processes, growth, reproduction and movement. The main source of energy is usually from the host plant and in particular carbohydrates in the leaf (Lindroth 1993; Alonso and Herrera, 2001; Cohen, 2004). Energy also has an influence on developmental patterns in offspring.

### **Lipids, Fatty Acids and Sterols**

Phytosterols are lipids or fat-soluble organic compounds, such as ergosterol and cholesterol, present in the cell membranes of plants and in chloroplasts, particularly in mesophyll tissues and between the layers of epidermis. Lipids are important

structural components (Cohen, 2004). Sterols are important in the ripening of green tomatoes (Chow and Jen, 1978) and in addition some of these compounds are important for insect chemoreception on tomato plants. The nutritional relevance of phytosterols for insects has been reviewed (Slansky and Rodriguez, 1987; Bloem *et al.*, 1989; Bloem and Duffey, 1990). Earlier reviews described sterols, namely sitosterol, and their role in pest resistance but little recent research exists (Beck, 1965). In some cases, host plant sterols may have positive effects on herbivore performance by acting as phagostimulants (Bartlett *et al.*, 1990).

### **Nutrient Interactions**

Additional aspects to consider in studies of leaf nutrients are the possible ontogenetic changes in either the extent or pattern of nutrient integration taking place during leaf development. Changes in leaf nutrients during the leaf growing period may be ecologically relevant for at least two reasons: i) possible nutritional deficiencies affecting leaves at this early stage might have consequences for subsequent plant growth and reproduction (Pigliucci *et al.*, 1997) and ii) the impact of insect folivores is usually greatest during the leaf growth period, even in evergreen species (Alonso and Herrera, 2000). Patterns of nutrient variation in leaves would be particularly important if host and habitat selection, and / or herbivores' fitness, were related not only to variation in the mean concentration of particular nutrients (Bergström and Danell, 1986; Athey and Connor, 1989; McNaughton, 1983; 2001; Awmack and Leather, 2002) but also were responsive to the relative proportions of different nutrients in their food (Clancy *et al.*, 1988; Cates, 1996; Phelan *et al.*, 1996).

## PART 3: CHOICE OF TOMATO CULTIVARS

A wealth of practical experience is available among crop managers who have been growing the new speciality cultivars over the last few years. A study in HDC project PC 240 surveyed the opinions of 12 crop managers / supervisors and collated their replies (Jacobson and Morley, 2007). While it was acknowledged that this was a subjective approach to the subject, it did provide a good starting point for more focused studies.

Thirty one cultivars and four pest species were included in the study. Four tomato cultivars (eg Dometica), which were considered to be similar in their susceptibility to the classic round cultivars commonly grown in the mid-1990s, were used as standards. All other cultivars were compared to them and graded on the following 1 to 5 scale:

- Grade 1 - Much less susceptible than standards
- Grade 2 - Less susceptible than standards
- Grade 3 - Similar to standard cultivars
- Grade 4 - More susceptible than standards
- Grade 5 - Much more susceptible than standards

The following cultivars were selected for this study with the aim of covering a wide range of tomato types and perceived susceptibility to leafminers:

| <u>Cultivar</u> | <u>Tomato type</u> | <u>Susceptibility to leafminers</u> |
|-----------------|--------------------|-------------------------------------|
| Santa           | Baby plum          | Grade 2                             |
| Dometica        | Classic            | Grade 3                             |
| Conchita        | Cherry             | Grade 4                             |
| Piccolo         | Baby cherry        | Grade 5                             |
| Capri           | Cocktail           | Grade 5                             |

## **PART 4: NUTRITIONAL STATUS OF TOMATO LEAVES**

### **Introduction:**

The key factors relating to leafminer population growth on the selected cultivars were measured under controlled conditions in an experimental glasshouse where the pests could be released onto the plants without putting any commercial crops at risk (See Part 5 of this Report). However, it was important to determine whether the nutritional status of tomato leaves grown under these conditions were comparable to commercial crops. Therefore, leaf samples were taken for analysis from both situations.

Winter (January / February) and spring (April / May) are key times for leafminer invasion and population growth respectively. Samples of foliage were therefore taken from the selected cultivars at both times of the year.

### **Methods:**

Leaf samples were collected, packed and transported according to instructions provided by Mr Richard Butler, Campden & Chorleywood Food Research Association (CCFRA). Only leaflets were to be processed at CCFRA but whole leaves including petioles were despatched because this helped to maintain their condition during transit. The whole leaves were removed from immediately above the second flowering truss, which is the position favoured for adult leafminers to feed and lay eggs. Each sample weighed approximately 180g, which had been shown in preliminary tests to yield the 150g of leaflets required by CCFRA. The samples were packed with cool blocks in insulated boxes and sent to CCFRA by overnight courier service.

The number of replicates per cultivar varied between trials. In February, the emphasis for leaf analysis was placed on the commercial crops as had been originally planned in the protocols agreed with the HDC. In this case, there were five replicate samples per cultivar and each was collected from a separate crop bay. A reduced number of replicates was taken from the experimental crop because this was simply to check whether the nutrient levels were comparable to the commercial crops. The approach was changed in May in response to the findings of the earlier trial. In May, more emphasis was placed on the leaf samples from the experimental crop in an attempt to obtain a closer correlation between the nutrient analysis and the leafminer performance.

Each replicate sample was individually analysed at CCFRA for the following components:

| <u>Test</u>            | <u>Test reference</u> |
|------------------------|-----------------------|
| Energy (k joules)      | TES-AC-335 UKAS       |
| Protein (Kjeldahl)     | TES-AC-087 UKAS       |
| Total carbohydrate     | TES-AC-335 UKAS       |
| Fat (Weibull-Stoldt)   | TES-AC-536 UKAS       |
| Moisture (Vac 70°C)    | TES-AC-097 UKAS       |
| Ash (@ 525°C)          | TES-AC-086 UKAS       |
| Total sugars (Enzymic) | TES-AC-444 UKAS       |
| Fructose (Enzymic)     | TES-AC-444 UKAS       |
| Glucose (Enzymic)      | TES-AC-444 UKAS       |
| Sucrose (Enzymic)      | TES-AC-444 UKAS       |

The total sugars were the sum of glucose, fructose and sucrose expressed as monosaccharides. Sugar and fat results were expressed to two decimal places and below limit of detection for information purposes.

The data were subjected to analysis of variance (or covariance) and comparisons of means were done using least significant difference at the 5% level.

Brix values (*i.e.* total dissolved solids) of fruit were measured at the same time as the leaf samples were collected from the commercial crops in February 2007. There were ten replicates from each cultivar.

## **Results:**

### ***February trial – Commercial crops***

The results of analyses of nutrients in leaf samples taken in commercial crops in February 2007 are shown in Table 1.

The mean moisture content was significantly different ( $P < 0.05$ ) in leaf samples from all cultivars except cvs Santa and Dometica, which were similar, and there was a reasonable correlation between moisture content and all other factors. This was taken into account by subjecting the remaining data to analysis of covariance.

In terms of energy potential, cv Piccolo (170.1 k joules) was significantly ( $P < 0.05$ ) less than cv Dometica (178.7 k joules), while all other cultivars were intermediate.

In terms of fat content, cv Piccolo and cv Santa were similar (0.465g/100g) but significantly less ( $P < 0.05$ ) than cvs Dometica, Conchita and Capri (0.54-0.69g/100g).

In terms of total sugar, cv Capri (0.39g/100g) was significantly ( $P < 0.05$ ) less than cv Conchita (0.67g/100g), while all other cultivars were intermediate.

In terms of fructose, cv Piccolo (0.15g/100g) was significantly ( $P < 0.05$ ) less than cv Conchita (0.29g/100g), while all other cultivars were intermediate.

In terms of ash (*i.e.* non-combustable minerals), cv Dometica (0.189g/100g) was significantly ( $P < 0.05$ ) less than cv Piccolo (2.11g/100g), while all other cultivars were intermediate.

No significant differences were found between cultivars with respect to protein, carbohydrate, glucose or sucrose.

**Table 1. Analyses of nutrients in all leaf samples taken in commercial crops in February 2007 (means of replicates)**

|                              | <b>Cultivar [pest susceptibility category]</b> |                     |                     |                    |                  | <b>df</b> | <b>sed</b> |
|------------------------------|--|---------------------|---------------------|--------------------|------------------|-----------|------------|
|                              | <b>Santa [2]</b>                               | <b>Dometica [3]</b> | <b>Conchita [4]</b> | <b>Piccolo [5]</b> | <b>Capri [5]</b> |           |            |
| <b>Moisture (%)</b>          | 87.82  | 87.44               | 89.72               | 88.94              | 88.12            | 30        | 0.23       |
| <b>Energy (kJ / 100g)</b>    | 171.1  | 178.7               | 173.3               | 170.1              | 176.0            | 29        | 2.46       |
| <b>Protein (g/100g)</b>      | 3.92   | 4.30                | 3.89                | 4.20               | 4.25             | 29        | 0.25       |
| <b>Carbohydrate (g/100g)</b> | 5.11   | 4.69                | 5.15                | 4.80               | 4.68             | 29        | 0.31       |
| <b>Fat (g/100g)</b>          | 0.46   | 0.69                | 0.54                | 0.47               | 0.67             | 29        | 0.09       |
| <b>Total sugars (g/100g)</b> | 0.05*  | 0.49                | 0.67                | 0.46               | 0.39             | 29        | 0.09       |
| <b>Glucose (g/100g)</b>      | 0.21   | 0.15                | 0.28                | 0.24               | 0.16             | 29        | 0.08       |
| <b>Fructose (g/100g)</b>     | 0.22   | 0.25                | 0.29                | 0.15               | 0.21             | 29        | 0.04       |
| <b>Sucrose (g/100g)</b>      | 0.04   | 0.05                | 0.18                | 0.19               | 0.02             | 29        | 0.10       |
| <b>Ash (g/100g)</b>          | 2.06   | 1.89                | 1.98                | 2.11               | 2.04             | 29        | 0.08       |

\* Anomalous result raised with CCRFA but not resolved

### ***Correlation to Brix values in February trial***

The mean Brix values for each cultivar measured on samples from commercial crops in February 2007 are shown in Table 2. It can be concluded that there was no consistent correlation between the pest category previously allocated to each cultivar and the total dissolved solids expressed as Brix values.

**Table 2. Mean Brix values of fruit of each cultivar in February 2007**

|                      | <b>Cultivar</b> |                 |                 |                |              |
|----------------------|-----------------|-----------------|-----------------|----------------|--------------|
|                      | <b>Santa</b>    | <b>Dometica</b> | <b>Conchita</b> | <b>Piccolo</b> | <b>Capri</b> |
| <b>Pest Category</b> | 2               | 3               | 4               | 5              | 5            |
| <b>Brix Value</b>    | 8.26%           | 4.74%           | 7.46%           | 8.48%          | 5.02%        |

### ***February trial – Experimental crops***

The mean results of analyses of nutrients in leaf samples taken in both commercial and experimental crops in February 2007 are shown in Table 3. There was very little correlation between the two sets of data in terms of either the size of the measurements or the rankings of the individual cultivars. As a consequence, it was decided that in May more emphasis should be placed on the leaf samples from the experimental crop in an attempt to obtain a closer correlation between the nutrient analysis and leafminer performance.

**Table 3. Comparison of analyses of nutrients in leaf samples taken in commercial and experimental crops in February 2007**

|                       | Commercial and (experimental) crops of:<br>[pest susceptibility category] |                          |                          |                          |                          |
|-----------------------|---|--------------------------|--------------------------|--------------------------|--------------------------|
|                       | Santa<br>[2]  | Dometica<br>[3]          | Conchita<br>[4]          | Piccolo<br>[5]           | Capri<br>[5]             |
| Moisture (%)          | 87.82<br><b>(88.15)</b>   | 87.44<br><b>(86.35)</b>  | 89.72<br><b>(87.30)</b>  | 88.94<br><b>(87.20)</b>  | 88.12<br><b>(87.10)</b>  |
| Energy (kJ / 100g)    | 171.1<br><b>(177.50)</b>  | 178.7<br><b>(211.00)</b> | 173.3<br><b>(193.50)</b> | 170.1<br><b>(195.00)</b> | 176.0<br><b>(199.50)</b> |
| Protein (g/100g)      | 3.92<br><b>(4.05)</b>   | 4.30<br><b>(4.60)</b>    | 3.89<br><b>(4.10)</b>    | 4.20<br><b>(4.55)</b>    | 4.25<br><b>(4.60)</b>    |
| Carbohydrate (g/100g) | 5.11<br><b>(5.15)</b>   | 4.69<br><b>(6.30)</b>    | 5.15<br><b>(5.90)</b>    | 4.80<br><b>(5.45)</b>    | 4.68<br><b>(5.60)</b>    |
| Fat (g/100g)          | 0.46<br><b>(0.29)</b>   | 0.69<br><b>(0.33)</b>    | 0.54<br><b>(0.29)</b>    | 0.47<br><b>(0.33)</b>    | 0.67<br><b>(0.35)</b>    |
| Total sugars (g/100g) | 0.05 *<br><b>(0.30)</b>   | 0.49<br><b>(0.44)</b>    | 0.67<br><b>(0.33)</b>    | 0.46<br><b>(0.49)</b>    | 0.39<br><b>(0.39)</b>    |
| Glucose (g/100g)      | 0.21<br><b>(0.12)</b>   | 0.15<br><b>(0.20)</b>    | 0.28<br><b>(0.09)*</b>   | 0.24<br><b>(0.24)</b>    | 0.16<br><b>(0.19)</b>    |
| Fructose (g/100g)     | 0.22<br><b>(0.16)</b>   | 0.25<br><b>(0.20)</b>    | 0.29<br><b>(0.21)</b>    | 0.15<br><b>(0.23)</b>    | 0.21<br><b>(0.19)</b>    |
| Sucrose (g/100g)      | 0.04<br><b>(0.03)</b>   | 0.05<br><b>(0.05)</b>    | 0.18<br><b>(0.03)</b>    | 0.19<br><b>(0.02)</b>    | 0.02<br><b>(0.02)</b>    |
| Ash (g/100g)          | 2.06<br><b>(2.08)</b>   | 1.89<br><b>(2.07)</b>    | 1.98<br><b>(2.01)</b>    | 2.11<br><b>(2.09)</b>    | 2.04<br><b>(1.98)</b>    |

\* Anomalous result raised with CCRFA but not resolved

#### **May trial – Experimental crops**

The results of analyses of nutrients in all leaf samples taken in experimental crops in May 2007 are shown in Table 4.

There were very few statistical differences in this data set. In terms of glucose, cv Capri (0.22g/100g) was significantly ( $P < 0.05$ ) less than cv Santa (0.33g/100g), while all other cultivars were intermediate. In terms of ash, cv Santa (2.36g/100g) was significantly ( $P < 0.05$ ) less than cvs Dometica, Conchita and Capri (2.67-2.73g/100g), while cv Piccolo was intermediate.

**Table 4. Analyses of nutrients in all leaf samples taken in experimental plots in May 2007**

|  | Cultivar [pest category] |         |          |        |       | df | sed |
|--|--------------------------|---------|----------|--------|-------|----|-----|
|  | Santa                    | Dometic | Conchita | Piccol | Capri |    |     |



|                       | [2]    | a<br>[3] | [4]    | o<br>[5] | [5]    |   |       |
|-----------------------|--------|----------|--------|----------|--------|---|-------|
| Moisture (%)          | 86.72  | 86.00    | 86.70  | 86.08    | 86.12  | 5 | 0.58  |
| Energy (kJ / 100g)    | 195.50 | 203.50   | 192.00 | 203.00   | 199.80 | 5 | 10.02 |
| Protein (g/100g)      | 3.70   | 3.90     | 3.65   | 3.75     | 4.00   | 5 | 0.17  |
| Carbohydrate (g/100g) | 6.70   | 6.77     | 6.55   | 7.15     | 6.75   | 5 | 0.37  |
| Fat (g/100g)          | 0.50   | 0.59     | 0.44   | 0.48     | 0.45   | 5 | 0.09  |
| Total sugars (g/100g) | 0.78   | 0.56     | 0.59   | 0.70     | 0.64   | 5 | 0.14  |
| Glucose (g/100g)      | 0.33   | 0.23     | 0.23   | 0.27     | 0.22   | 5 | 0.36  |
| Fructose (g/100g)     | 0.40   | 0.33     | 0.32   | 0.42     | 0.36   | 5 | 0.09  |
| Sucrose (g/100g)      | 0.06   | 0.02     | 0.04   | 0.02     | 0.07   | 5 | 0.04  |
| Ash (g/100g)          | 2.36   | 2.73     | 2.67   | 2.55     | 2.67   | 5 | 0.09  |

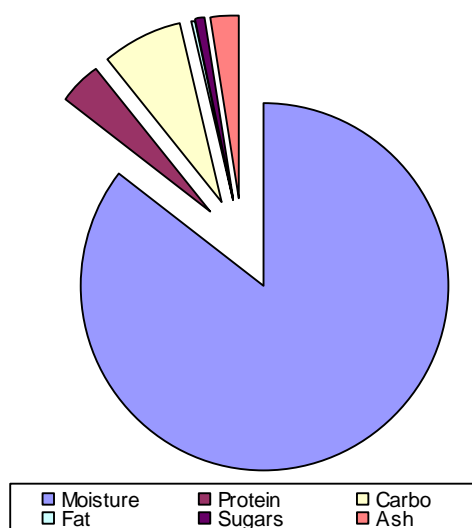
### Conclusions:

A typical breakdown in the nutrient content of tomato leaves positioned immediately above the second flowering truss is shown in Figure 1.

Overall, measurement of nutrients in such leaves revealed few significant differences within any of the data sets. Furthermore, where differences did exist, there were no consistent trends between cultivars and no apparent correlation with the susceptibility to leafminers that had been established in a previous project (PC 240 – Jacobson and Morley, 2007).

However, there were apparent differences in the nutrient content of the leaves taken from the experimental crops in February and May although these could not be compared statistically due to the limited replication in the first data set. The means of both data sets are shown in Table 5 with the percentage change between February and May. Overall, it can be seen that protein content decreases by 13%, while carbohydrate, fat, sugars and ash (minerals) all increase substantially. The largest percentage increases are in fat (+58%) and sugars (+66%). The energy value stayed approximately the same although it must have come from different nutrients (*i.e.* more from carbohydrate, fat and sugars and less from protein). The possible implications of these observations are discussed in Part 6 of this report.

**Figure 1. Typical breakdown in nutrients (expressed in g per 100g leaflet) in a tomato leaf positioned just above the second truss.**



**Table 5. Comparison of nutrients in all leaf samples taken in experimental plots in May and (February) 2007**

|                              | Cultivar [pest category]  |                           |                           |                          |                           | % change in means from February to May |
|------------------------------|---------------------------|---------------------------|---------------------------|--------------------------|---------------------------|--|
|                              | Santa                     | Dometi<br>ca              | Conchita                  | Piccol<br>o              | Capri                     |  |
| <b>Moisture (%)</b>          | 86.72<br><b>(88.15)</b>   | 86.00<br><b>(86.35)</b>   | 86.70<br><b>(87.30)</b>   | 86.08<br><b>(87.20)</b>  | 86.12<br><b>(87.10)</b>   | - 1%                                   |
| <b>Energy (kJ / 100g)</b>    | 195.50<br><b>(177.50)</b> | 203.50<br><b>(211.00)</b> | 192.00<br><b>(193.50)</b> | 203.00<br><b>(195.0)</b> | 199.80<br><b>(199.50)</b> | + <1%                                  |
| <b>Protein (g/100g)</b>      | 3.70<br><b>(4.05)</b>     | 3.90<br><b>(4.60)</b>     | 3.65<br><b>(4.10)</b>     | 3.75<br><b>(4.55)</b>    | 4.00<br><b>(4.60)</b>     | - 13%                                  |
| <b>Carbohydrate (g/100g)</b> | 6.70<br><b>(5.15)</b>     | 6.77<br><b>(6.30)</b>     | 6.55<br><b>(5.90)</b>     | 7.15<br><b>(5.45)</b>    | 6.75<br><b>(5.60)</b>     | + 19%                                  |
| <b>Fat (g/100g)</b>          | 0.50<br><b>(0.29)</b>     | 0.59<br><b>(0.33)</b>     | 0.44<br><b>(0.29)</b>     | 0.48<br><b>(0.33)</b>    | 0.45<br><b>(0.35)</b>     | + 58%                                  |
| <b>Total sugars (g/100g)</b> | 0.78<br><b>(0.30)</b>     | 0.56<br><b>(0.44)</b>     | 0.59<br><b>(0.33)</b>     | 0.70<br><b>(0.49)</b>    | 0.64<br><b>(0.39)</b>     | + 66%                                  |
| <b>Glucose (g/100g)</b>      | 0.33<br><b>(0.12)</b>     | 0.23<br><b>(0.20)</b>     | 0.23<br><b>(0.09)*</b>    | 0.27<br><b>(0.24)</b>    | 0.22<br><b>(0.19)</b>     | + 36%                                  |
| <b>Fructose (g/100g)</b>     | 0.40<br><b>(0.16)</b>     | 0.33<br><b>(0.20)</b>     | 0.32<br><b>(0.21)</b>     | 0.42<br><b>(0.23)</b>    | 0.36<br><b>(0.19)</b>     | + 85%                                  |
| <b>Sucrose (g/100g)</b>      | 0.06<br><b>(0.03)</b>     | 0.02<br><b>(0.05)</b>     | 0.04<br><b>(0.03)</b>     | 0.02<br><b>(0.02)</b>    | 0.07<br><b>(0.02)</b>     | + 33%                                  |
| <b>Ash (g/100g)</b>          | 2.36<br><b>(2.08)</b>     | 2.73<br><b>(2.07)</b>     | 2.67<br><b>(2.01)</b>     | 2.55<br><b>(2.09)</b>    | 2.67<br><b>(1.98)</b>     | + 26%                                  |

\* Anomalous result raised with CCRFA but not resolved - excluded from mean

## **PART 5: POPULATION GROWTH OF LEAFMINERS**

### **Objective:**

To measure the key factors relating to leafminer population growth on five cultivars of speciality tomatoes.

### **Materials and methods:**

#### ***Leaf miner cultures***

Pupae of *Liriomyza bryoniae* (tomato leafminer) were supplied from commercial tomato crops on the Isle of Wight and were maintained on tomato plants (cv Carousel) at STC Research Foundation. The cultures were synchronised approaching each experiment to ensure that adequate numbers of known age individuals were available.

#### ***Timetable of events***

The trial was run twice; in February and May 2007:

##### February 2007

- 11 December - Plants sown
- 31 January - Plants transferred to production house
- 21 February - Adult leafminers released
- 26 February - Leaves sampled for analysis
- 15 February - Leafminer pupae counted

##### May 2007

- 19 February - Plants sown
- 2 April - Plants transferred to production house
- 8 May - Adult leafminers released
- 17 May - Leaves sampled for analysis
- 1 June - Leafminer pupae counted

#### ***Crop management***

Five speciality tomato cultivars (cvs Santa, Dometica, Conchita, Piccolo and Capri) were included in each experiment. The plants were propagated at STCRF and then transferred to a small production glasshouse. Each cultivar was replicated in two plots with four plants per plot.

The temperature regime varied between experiments. In the first trial, it was held at minimum 19°C with venting at 21°C. The same temperature settings were used for the second trial until 19 April when it was changed to a more commercial growing regime; *i.e.* minimum temperatures of 18 °C from one hour before sunrise to 10.00hrs; 20 °C between 10.00 and 15.00hrs; 18 °C from 15.00hrs to one hour before sunset; 14 °C pre-night (one hour before sunset to four hours after sunset); 16-17 °C during the dark period.

#### ***Insect infestation***

The trials began when the plants reached approximately 1.5m in height. Five mated adult female leafminers (3-5 days old) from synchronised cultures were confined for 48 hours in perforated cages positioned over the second fully expanded leaf on each plant. The insects were allowed to feed and lay eggs for 48 hours and were then removed.

### **Assesments**

The following assessments were completed:

- The numbers of feeding punctures were recorded after 48 hours.
- The numbers of viable eggs (based on the numbers of first and second instars) were recorded after 14 days.
- Larval mortality (based on the number developing into pupae) was recorded after 22 days in experiment 1 and 24 days in experiment 2.

### **Statistical Analysis**

Analysis was done using ANOVA on square root transformed data, and comparisons of means were done using least significant difference at the 5% level.

### **Results:**

#### **February 2007**

The mean and square root transformed numbers of feeding punctures, larvae and pupae of *L. bryionae* on the five cultivars of speciality tomatoes in February 2007 are shown in Table 6.

Feeding activity was significantly greater ( $P < 0.05$ ) on cv Dometica than cvs Conchita, Capri and Piccolo, while cv Santa was intermediate. At the extremes, the number of feeding marks on cv Dometica was approximately 1.8x greater than cv Piccolo.

There were significantly more ( $P < 0.05$ ) first and second instar larvae in the leaves of cvs Dometica, Santa and Capri than cv Piccolo, while cv Conchita was intermediate. The numbers of pupae recorded were generally greater than the numbers of first and second instar larvae. At first sight this may appear difficult to explain because the pupal assessment was included as a means of measuring larval mortality. In fact, this situation arose because the larval assessment was done in situ where it was difficult to detect individual larvae amongst the sometimes dense and interconnected network of mines. By comparison, individual pupae were very distinct and easily found on the excised leaflets. We must therefore discount the larval assessment and use pupal numbers as a single record of the number of individuals that successfully completed their development in the tomato leaf.

There were approximately 2.5x more ( $P < 0.05$ ) pupae on the leaves of cv Dometica than cv Piccolo. The other cultivars were intermediate with cv Conchita statistically similar to cv Piccolo, and cvs Capri, and Santa statistically similar to cv Dometica.

**Table 6. The mean (square root transformed) numbers of feeding punctures, larvae and pupae of *Liriomyza bryionae* on five different cultivars of speciality tomatoes in February 2007**

| Cultivar | Feeding punctures | First and second | Pupae |
|----------|-------------------|------------------|-------|
|----------|-------------------|------------------|-------|

|             |       |         | instar larvae |        |      |        |
|-------------|-------|---------|---------------|--------|------|--------|
| Piccolo     | 149.1 | (11.29) | 32.4          | (5.46) | 36.3 | (5.74) |
| Santa       | 202.3 | (14.05) | 67.6          | (8.02) | 65.1 | (7.87) |
| Dometica    | 269.0 | (16.31) | 81.4          | (8.98) | 92.0 | (9.51) |
| Conchita    | 152.1 | (11.89) | 52.5          | (7.08) | 56.6 | (7.37) |
| Capri       | 158.6 | (12.18) | 58.5          | (7.47) | 69.0 | (8.14) |
| LSD(P<0.05) |       | (3.44)  |               | (1.65) |      | (1.75) |

### May 2007

The mean and square root transformed numbers of feeding punctures, larvae and pupae of *L. bryionae* on the five cultivars of speciality tomatoes in May 2007 are shown in Table 7.

There were approximately 2x more (P<0.05) feeding marks on the leaves of cv Piccolo than on cv Dometica. The other cultivars were all intermediate with cvs Conchita and Capri statistically similar to cv Piccolo, and cvs Capri and Santa statistically similar to cv Dometica.

Overall, the numbers of feeding punctures recorded were similar in the two experiments. However, there were generally fewer first and second instar larvae recorded in the second experiment than in the first. This suggested that either fewer eggs had been laid or fewer had successfully hatched. As in the first experiment, fewer larvae were recorded than pupae and so we have focused on the pupae for reasons given above.

Despite having high numbers of feeding punctures, the subsequent development of larvae to pupae was the lowest on Piccolo, although this was not significantly different (P<0.05) to the other cultivars.

**Table 7. The mean (square root transformed) numbers of feeding punctures, larvae and pupae of *Liriomyza bryionae* on five different cultivars of speciality tomatoes in May 2007**

| Variety     | Feeding punctures |         | First and second instar larvae |        | Pupae |        |
|-------------|-------------------|---------|--------------------------------|--------|-------|--------|
| Piccolo     | 232.6             | (14.78) | 6.9                            | (2.48) | 8.8   | (2.66) |
| Santa       | 126.5             | (10.72) | 7.4                            | (2.60) | 9.1   | (2.79) |
| Dometica    | 117.1             | (10.03) | 8.8                            | (2.90) | 10.9  | (3.12) |
| Conchita    | 233.3             | (15.21) | 11.0                           | (3.27) | 15.5  | (3.75) |
| Capri       | 201.4             | (13.66) | 7.25                           | (2.58) | 9.4   | (2.77) |
| LSD(P<0.05) |                   | (3.71)  |                                | (0.78) |       | (1.31) |

### Discussion and conclusions:

Overall, these two experiments have probably raised more questions than they have answered in terms of leafminer population growth on speciality tomatoes. For instance:

- In February, there were more feeding marks on cv Dometica than cvs Conchita, Capri and Piccolo, with 1.8x more on cv Dometica than cv Piccolo. In May, this result was almost completely reversed with 2x more on cv Piccolo than cv Dometica.
- On cv Dometica, the numbers of feeding marks were 2.3x greater in February than in May. In contrast, on cv Piccolo, numbers of feeding marks were 1.6x greater in May than in February.
- In February, there were 2.5x more pupae on cv Dometica than cv Piccolo. In May, the numbers were similar on the two cultivars.

The one consistent feature was that all cultivars produced many more pupae in February than May (eg. 8x as many for cv Dometica' and 4x as many for cv Piccolo), suggesting that increases in carbohydrate, fat, total sugar and /or non-combustable minerals (ash) somehow act to deter egg laying.

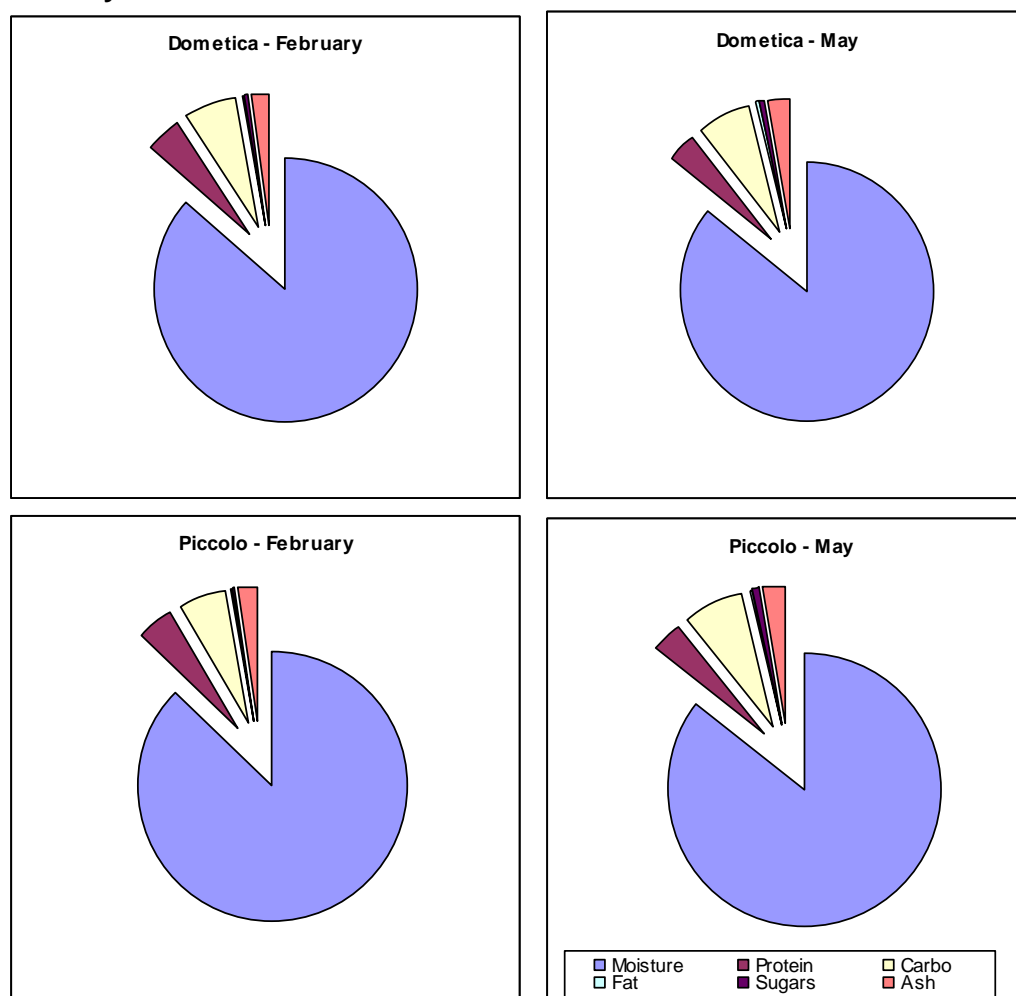
## **PART 6: CORRELATION OF LEAF NUTRIENTS AND LEAFMINER POPULATION GROWTH**

### **Summary of nutrient levels in leaves**

There were quite large differences in the nutrient content of leaves taken from the experimental crops in February and May. Overall, their protein content decreased by 13% between February and May, while their content of carbohydrates, fats, sugars and ash (non-combustable minerals) all increased substantially. The largest percentage increases were in fat (+58%) and sugars (+66%). The energy value stayed approximately the same although it must have come from different nutrients (i.e. more from carbohydrate, fat and sugars and less from protein).

In searching for correlations between leaf nutrients and leafminer population growth, it is appropriate to focus on two key cultivars, Dometica and Piccolo. Breakdowns of nutrients per 100g of leaf material for these cultivars in both February and May are illustrated graphically in Figure 2. By studying this figure and the more precise data in Table 5, we can see that for cv Dometica the content of carbohydrate, fat, total sugar and ash (non-combustable minerals) increased by 7%, 78%, 27% and 32% respectively, while the same factors increased by 31%, 45%, 42% and 22% in cv Piccolo.

**Figure 2. Nutrient content of leaves of cv Dometica and Piccolo in February and May 2007.**



### Leafminer feeding activity

Despite these changes in the nutrient content of leaves, there was no consistent correlation between leaf nutrient content and the key factors in leafminer population growth within any of the data sets.

Overall, the numbers of feeding punctures recorded were similar in the two experiments but differed greatly between cultivars. With cv Dometica, the numbers of feeding marks were 2.3x greater in February than in May, while with cv Piccolo, the opposite was true and there were 1.6x more feeding marks in May than in February.

### Leafminer development to pupae

As with leafminer feeding activity, there was no consistent correlation between the nutrient content of leaves and the production of pupae within any of the individual data sets. However, unlike feeding activity, there was a marked difference in the overall number of pupae produced in the two experiments; *i.e.* overall there were almost 6x as many pupae in February than in May.

The ratio of feeding marks to pupae, which presumably gives some indication of the suitability of the host plant, was considerably lower in February than May in all



cultivars, indicating that the pest was generally operating more efficiently in the earlier part of the season (Table 8). The seasonal difference was greatest with the two cultivars that had previously been allocated the highest grades in terms of susceptibility to attack by leafminer (*i.e.* cvs Piccolo and Capri). The experiment did not record the numbers of eggs laid because this would have been too destructive. As a consequence, the excessive leafminer feeding relative to pupal formation in May might have been due to fewer eggs being laid than in February or due to increased mortality of immature stages. An additional specifically designed experiment would be required to answer this question. Alternatively, the effect could have been due to female leafminers requiring more moisture during the warmer conditions.

**Table 8. Ratio of feeding punctures to pupae in five cultivars in February and May 2007**

| Cultivar | Ratio of feeding punctures to pupae in: |      |
|----------|---|------|
|          | February                                | May  |
| Santa    | 3:1                                     | 14:1 |
| Dometica | 3:1                                     | 11:1 |
| Conchita | 3:1                                     | 15:1 |
| Piccolo  | 4:1                                     | 26:1 |
| Capri    | 2:1                                     | 21:1 |

A high ratio of feeding punctures to mines has been observed in commercial crops of cvs Piccolo, Conchita, Capri and Nectar between April and June (*eg.* Figure 3). This has usually occurred with the last flush of adult leafminers before the population has been controlled by *Diglyphus isaea*. The relatively small number of mines produced from these punctures has usually been attributed to “stinging out” by the parasitoid rather than excessive leafminer feeding relative to oviposition.

In some cases, growers have successfully applied “soft chemicals” to the tops of tomato plants to reduce the impact of feeding damage by adult leafminers while the parasitoids are controlling the leafminer larvae lower down the plant.

**Figure 3. Leafminer feeding marks on leaves of a commercial crop of cv Piccolo in May 2006**



### **Provisional conclusions**

The results suggest that leafminer performance was not primarily influenced by leaf nutrients, as measured in these experiments. With the benefit of hindsight, it is evident that the methods used for collection of samples for chemical analysis could have been improved. Samples for analysis were packed in cooled containers but were not frozen immediately and so some chemical components might have changed in response to continuing enzymatic activity. It is also quite possible that leafminer performance was influenced by factors that were not measured in these experiments.

The following mini-review will consider whether other factors, such as plant morphology, the presence of secondary metabolites, plant volatiles, or other biochemical defences might influence the behaviour of leaf miners on speciality tomato cultivars. The review will also consider whether factors of the glasshouse environment might have interacted with the chemical make-up of the plants so as to affect insect behaviour.

## **PART 7: FACTORS OTHER THAN NUTRITION WHICH MAY INFLUENCE INSECT POPULATION GROWTH ON SPECIALITY TOMATOES**

### **Characteristics of Leaves**

#### ***Leaf age, size and position***

The age, position and relative sizes of leaves are clearly correlated. Alonso and Herrera (2000) showed that, in general, the impact of insect herbivores tends to be greatest when the host plant's leaves are young, expanding and at the top of the plant. They also reported that insect growth rates were found to be higher on young leaves, which reflected the higher nitrogen (N) and water content of the former. This was in line with many previous studies (e.g. Coley, 1980; Campos *et al.*, 2003; Coley, *et al.*, 2006). Larval growth is positively correlated with leaf expansion rate, partly because of the higher N and water contents of rapidly growing juvenile leaves (van Emden and Bashford, 1969; Raupp and Denno, 1983; Iwasa and Kybo, 1996). However, *L. trifolii* is known to prefer to feed and oviposit on leaves of a specific age. Although the N content is highest in the uppermost leaves, females seem to ignore them and so must select leaves on some other basis (Minkenbergh and Ottenheim, 1990).

The choice of oviposition location depends on several factors, including leaf size and position on the host (Kimmerer and Potter, 1987; Suomela and Nilson, 1994; Fisher *et al.*, 2000; Faeth *et al.*, 1981; Faeth, 1985; 1987; 1990) and there is an extensive literature on how leaf position affects the concentration of nutrients in growing leaves and consequently on the level of herbivory (e.g. Alonso and Herrera, 2001; 2003).

The within-plant dispersion of *Liriomyza* spp. has been studied by Dove (1985), Srinivasan *et al.* (1995), Hammad and Nemer (2000), and Facknath and Lalljee (2005). The preference for feeding and oviposition on the higher middle region leaves was concluded to be adaptive and there is some evidence that development rate and survival of larvae is better on these leaves than on the top leaves (Minkenbergh, 1988).

There was a positive relationship between leaf area and the number of mines per leaf with *L. huidobrensis* (Hammad and Nemer, 2000; Srinivasan *et al.*, 1995; de Souza *et al.*, 1998). A similar response was shown by *L. trifolii* on potato (Mopper *et al.*, 1995) where there was also significantly lower larval survival on the smaller upper leaves (Facknath and Lalljee, 2005). These responses could be due to competition between larvae (Parrella, 1987a) as larval mass decreases significantly with increasing numbers of larval mines per leaf (Tuomi *et al.*, 1981).

Various aspects of leaf demography and plant-insect interactions have been investigated in *L. trifolii* and *L. bryoniae* (Spencer, 1973; Ledieu and Helyer, 1985; Minkenbergh and van Lenteren, 1986; Leite *et al.*, 2001). Parella *et al.*, (1985) and Parella (1987a) found that the type of mine may vary according to the developmental stage of the leaf and that mine locations in leaves may vary considerably.

## **Leaf Morphology**

The distribution and density of trichomes (modified glandular leaf hairs) play an important role in the acceptance and colonisation of a host by the *Liriomyza* (Fagoonee and Toory, 1983; Metcalf and Kogan, 1987; Minkenberg and Ottenheim, 1990; Wilkens *et al.*, 1996). As the total number of trichomes per leaf remains constant during leaf expansion, fully expanded leaves have a lower density of trichomes than young leaves. The selection behaviour of *Liriomyza* spp on 21 tomato cultivars was negatively correlated with the length and density of surface leaf hairs (Li *et al.*, 2003). The presence of trichomes also affects the behaviour of parasitoids and predators (Kennedy, 2003). All trichomes act as physical barriers impeding the movement of adult insects and interfering with their feeding and oviposition. Furthermore, exudates from some types of trichome form a sticky trap while others show insecticidal effects (Lin *et al.* 1987; Alanerb *et al.*, 1993).

## **Leaf Structure**

Leaf thickness, tissue structure (Jones *et al.*, 1993; Wei *et al.*, 2000), mechanical barriers on or within the leaf, as well as qualitative barriers such as the composition of leaf cuticles (Jackson *et al.*, 1986; 1991) and phenological changes (Kimmerer and Potter, 1987; Suomela and Nilson, 1994; Fisher *et al.*, 2000; Faeth *et al.*, 1981; Faeth, 1985; 1987; 1990) all appear to have a role in herbivory. Young leaves are softer and easier to pierce and mine but, as leaf thickness increases with leaf age, older leaves may confer a survival advantage by providing more resources of food and space while rendering larvae less exposed to parasitoids (Hartnett and Bazzaz, 1986; Facknath and Lalljee, 2005). Lipids within the leaf cuticle can act as attractants to insects and some improve the survival of beneficial insects.

## **Secondary metabolites**

Plant secondary metabolites comprise i) invertebrate attractants, such as colour pigments and scents, ii) invertebrate repellents, such as antifeedants, and iii) toxins that can affect the growth and development of both herbivores and their natural enemies. However, herbivorous insects can sometimes employ plant-synthesised compounds to their own advantage, *eg.* as signals for feeding and oviposition and the location of prey (Dicke and Hilker, 2003).

Plant secondary metabolites together with nutrients frequently dictate herbivore growth rates and hence herbivore susceptibility (Visser and Piron, 1994; 1997; 1998; Visser *et al.*, 1996; Coley *et al.*, 2006). The production of plant secondary metabolites has been comprehensively reviewed by Collinge (1986) and Bourgaud *et al.* (2001), as has their impact on herbivorous insect behaviour (Awmack and Leather, 2002).

The availability of N and other nutrients influence the allocation of resources to secondary metabolism (Coley *et al.*, 1985; Mole and Waterman, 1987; Reichardt *et al.*, 1991; Herms and Mattson, 1992). However, allocation is also influenced by ecological demands for defence, especially the demand that is signalled by herbivore attack (Lerdau *et al.*, 1994; Theis and Lerdau, 2003). Feeding by herbivores initiates qualitative and quantitative changes in secondary metabolism (Tallamy and Raupp, 1991; Karban and Baldwin, 1997). Such induced changes in phytochemistry can extend beyond the damaged tissues, are often rapid (occurring within hours) and are often correlated with systemic increases in resistance to subsequent herbivory (Tallamy and Raupp, 1991; Karban and Baldwin, 1997; Cipollini and Redman, 2007; Redman *et al.*, 2001).

## **Phenolics and Polyphenolic Compounds**

Changing fertiliser regimens can affect the levels of foliar N, terpenes, and phenolics in host plants and hence their impact on insects (McNeill and Southwood, 1978; Mattson, 1980; Letourneau *et al.*, 1996; Jauset *et al.*, 1998; Facknath and Lalljee, 2005; Facknath and Wright, 2007). The concentration of phenols generally increases with the protein content of the food (Kennedy, 2003).

Defence in tomato plants results from mechanisms that involve the production of tomatine, catecholic phenolics and phenol oxidases, proteinase inhibitors, and lipoxygenase. The catalytic role of plant oxidative enzymes in activating a variety of defense mechanisms has been reviewed by Timmerman *et al.* (1999) from the view of digestibility reducer, toxin, and nutrients.

The foliage and fruit of the tomato plant (*Lycopersicon esculentum*) contains polyphenol oxidases (PPO) and peroxidases (POD) compartmentally separated from orthodihydroxyphenolic substrates in situ. When insects such as the tomato fruitworm or the beet army-worm feed on tomato foliage and damage the leaf tissue, the enzyme and phenolic substrates come in contact, resulting in the rapid oxidation of phenolics to orthoquinones (Felton *et al.*, 1989a, b). A substantial amount of the ingested chlorogenic acid is oxidized to chlorogenoquinone by PPO in the insects' gut. The relative growth rate of the fruitworm was negatively correlated with PPO activity. Phenolic chlorogenic acid could act as an insect antifeedant.

## **Alkylating Agents**

Phytochemicals that are ingested with protein may negatively impact protein utilisation (Bernays, 1986). There is a wide distribution of secondary metabolites, such as alkylating agents, found in plants that form covalent bonds with nucleophilic side chains of proteins (eg. -SH, -NH, -NH<sub>2</sub>) and may limit the availability of amino acids to herbivores (Felton *et al.*, 1992; Felton, 1996; 2005; Johnson and Felton, 1999).

## **Semiochemicals**

“Semiochemical” is a generic term for a chemical compound that is produced by one organism but then influences the behaviour of another organism. The chemicals can act as attractants, repellents, or allelochemicals (Jones and Finch, 1987; Naranjo and Gibson, 1996; Coll, 1996, 1997; Coll and Izraylevich, 1997; Coll and Guershon, 2002) and the term includes pheromones, allomones, and kairomones. Semiochemicals are generally volatile chemical signals. They include simple compounds, such as methyl salicylate which acts as a promoter of plant-defence signalling (Pettersson *et al.*, 2000), induced resistance (Shulalev *et al.*, 1997) and a host-leaving stimulus, as well as more complex compounds (Pettersson, 1970; 1971; Price *et al.*, 1980; Bengtsson *et al.*, 2006). The chemical constituents of plants also provide stimuli which play a major role in host-plant identification and location (Renwick, 1989; Phelan *et al.*, 1991; Vet and Dicke, 1992; Vet, 1999; Ryan, 2002; Derksen *et al.*, 2007) as this involves a complex interaction of chemical, visual, and nutritional cues (Renwick, 1989; Vet and Dicke, 1992; Vet, 1999; Derksen *et al.*, 2007; Phelan *et al.*, 1991; Ryan, 2002). Specialist herbivores appear to integrate information from many different cues and the outcome is more than a simple summation. The systemic production of insect-induced volatiles by plants and their impact on predator behaviour has been reviewed by Pickett (1992); Ochieng *et al.* (2002); Pickett and Glinwood (2007).

### **Attractants**

Facknath and Lalljee (2005); Derksen *et al.* (2007), and Pickett and Glinwood (2007) have all focused on the molecular basis of host-plant attractants. The approach of foraging insects to prospective host plants is thought to increase the plants' detectable semiochemical profile and chemical complexity (*i.e.* detectability) (Miller and Strickler, 1984; Schoonhoven, 1982; Visser, 1986). Infestation itself may induce local and systemic plant responses (Stout *et al.*, 1998a, b, c; Türyakü, 2004).

### **Deterrents**

Plants also produce chemicals with repellent properties or signal to natural enemies that *Lyriomyza* is present. Host selection can depend on a lack of deterrents. Ohmart *et al.* (1985), Taylor (1989) and Berenbaum (1980, 1983, 1995) have all investigated chemicals that deterred herbivory and acted principally as 'antifeedants'. There is a considerable literature on the anti-nutritive and toxic components of plant defence against insects (e.g. Städler and Schöni, 1990; Duffey and Stout, 1996). Amino acids and proteases in leaves often act as deterrents for mining insects by reducing the digestibility of the leaf material (Felton *et al.*, 1989a, b; Felton and Duffey, 1991; Felton and Summers, 1993; Felton, 2005).

Studies of induced direct defences have included proteinase inhibitors in Solanaceous plants as these interfere with insect digestive systems, and retard larval growth and development. In feeding experiments, herbivory increased when protease inhibitors were eliminated from artificial diets (Felton *et al.*, 1989a, b; Türyakü, 2004.) but phytophagous insects appear able to alter the nature of protease inhibitors expressed in host plants (Felton and Summers, 1993; Felton, 1996). Tomato plants respond according to the type of insect which causes the tissue damage. When attacked by leaf miners, cv Castlemart, increased the activity of peroxidase and also produced four foliar proteins. These actions rendered the leaves unpalatable and the oxidised phenolics were toxic to the leaf miner (Stout *et al.* 1994, 1998a, b, c; Stout *et al.*, 2001; Appel, 1993). The presence of pyrrolizidine alkaloids acts as an antifeedant (Van Darn, 1983).

### **Feeding Stimulants and Antifeedants**

Factors such as feeding stimulants and antifeedants and protective ingredients are important as they may be viewed as 'anti-nutrients'. Experiments to investigate the defence mechanisms interrupting protein synthesis of *Solanum lycopersicum* proteins (arginine and threonine) that accumulate in the midgut of *Manduca sexta* larvae reared on the plant showed that jasmonate-inducible proteins thwart insect attack by disrupting digestive processes by catabolising the essential amino acids in the insect gut (Chen *et al.*, 2005). Hormone signalling pathway strongly influences the midgut protein content of phytophagous insects which supports the hypothesis that catabolism of amino acids in the insect digestive tract by host enzymes plays a role in plant protection against herbivores (Chen *et al.*, 2005).

### **Elicitors**

Elicitors were once defined as substances of biotic origin which induced a defence response but the term now includes signalling substances, such as jasmonates,

salicylic acid, and ethylene. There are many direct and indirect plant defences elicited by insect attack and which differ from that elicited by mechanical wounding. The signal components are employed by elicitors to induce the accumulation of plant secondary metabolites (Ryan, 1983; Rainier *et al.*, 1992; Hadacek, 2002, Türyakü, 2004; Zhao *et al.*, 2005). Plants may also protect themselves either directly by expressing biochemical and morphological traits that interfere with herbivore development or behaviour, or indirectly, by encouraging the herbivore's natural enemies. These resistance mechanisms are not always expressed at maximal levels by plants but can be induced to higher levels by a variety of stimuli, notably prior herbivory.

### **Jasmonates**

There is a considerable recent literature on jasmonates (Thompson, 1988; Thompson and Dahlman, 1998; Agrawal *et al.*, 1999; Rodriguez-Saona and Thaler, 2005; Chen *et al.*, 2005).

Jasmonates are plant hormones which are lipid-derived compounds with signal functions produced in response to abiotic and biotic stresses, as well as having a role in normal plant growth and development. The jasmonic acid activates host defence responses against a broad spectrum of herbivores and it controls the expression of a large set of target genes in response to tissue damage and impairs herbivore performance (Chen *et al.*, 2005). The jasmonate pathway regulates the induction of resistance against herbivores and jasmonic acid acts as an oviposition deterrent (Thaler *et al.*, 2001; Kennedy, 2003; Halitschke and Baldwin, 2004; Rodriguez-Saona and Thaler, 2005; Tebayshi *et al.*, 2007; Wasternack, 2007). Jasmonate signalling plays a critical role in plant development by protecting them from pathogens and insects and in limiting damage from abiotic agents (Türyakü, 2004).

Mechanical damage and wounding induces biochemical changes (Mooney and Gulmon, 1982; Edwards and Wratten, 1983; 1985; Edwards *et al.*, 1991; Redman *et al.*, 2001; Lankau, 2007; Wasternack, 2007) that are mimicked by treating tomato plants with jasmonic acid (Cipollini and Redman, 1999; Redman *et al.*, 2001). Stout *et al.* (1994) studied the effects of mechanical and chemical damage and three types of biotic damage on the activities of four foliar proteins of the tomato plant (*Lycopersicon esculentum* Mill var. Castlemart). Damaged leaflets were assayed and a proteinase inhibitor, polyphenol oxidase, peroxidase, and lipoxygenase activities were identified and concluded to be a defensive response by tomato plants.

### **Volatiles**

Plant volatiles can directly reduce fecundity or induce responses in neighbouring plants. They may also have inhibitory or repellent effects that interrupt insect responses to pheromones and attract predators and parasitoids to the attacking species after herbivory injury. The role of volatiles at the leaf surface in guiding oviposition has been well established, though less is known of the non-volatile leaf

chemicals that might determine host plant selection (Bernays and Chapman, 1984; Harborne, 1997). Larval feeding also elicits the release of volatile compounds within the plant (Röse *et al.*, 1996). Heath and Manukian (1994) have described an automated system for collecting volatiles released from plants.

Trans- $\alpha$ -farnesene and linalool accumulate in the volatile emission from young leaves and together they appear to function as a “young-leaf” signal (Phelan and Miller, 1982). Different odours ( $\alpha$ -thujene, methyl salicylate) accumulate in older leaves and appear to function as mild deterrents, steering the ovipositing female away towards the younger leaves. Sugar esters, such as acyl esters, have a defensive role against insects (Mutschler *et al.*, 1996). Various reviews discuss the role of plant volatiles (e.g. Bromley and Anderson, 1982; Pickett, 1992; Visser and Piron, 1994; 1997; 1998; Visser *et al.*, 1996; Park and Hardie, 2003, 2004).

The majority of reviews of leaf volatiles as olfactory stimuli have focused on the responses of aphids (Metcalf and Kogan, 1987; van Giessen *et al.*, 1992; Park and Hardie, 2003, 2004). However, leafminers also respond to the odours of host and non-host plants (Metcalf and Kogan, 1987; Cooper and Goggin, 2005; Hanson *et al.*, 2004; Visser, 1986; Zhao and Kang, 2003; Facknath and Lalljee, 2005; Facknath *et al.*, unpublished). Olfactory sensitivity to host plant location by *Lyriomyza* species has been investigated using both electroantennograms and behavioural assays in olfactometers (Zhao and Kang, 2003). *Lyriomyza* selectively responded to host plant odours from tomato plants but non-host plants in the vicinity could provide camouflage, diversionary or repellent components (Uvah and Coaker, 1984). Terpenes released from the trichomes of *Lycopersicon hirsutum*, provide resistance against arthropod herbivores (Harborne, 1997). Nearly 20 monoterpenes are found in the leaves of cultivated tomatoes (Buttery *et al.*, 1987). Nitrate-limited plants are better able to defend their leaves against insect herbivores because they produce more volatile leaf terpenes and these inhibit feeding (Mihaliak *et al.*, 1987; Joseph *et al.*, 1993).

### **Non-volatile Chemical Signals**

Non volatiles may be released as deterrents as a host-plant response to herbivory (Powell and Hardie, 2001; Powell *et al.*, 2006; Pettersson *et al.*, 2000; Pickett, 1992; Park and Hardie, 2002, 2004). The steroidal glycoalkaloid  $\alpha$ -tomatine is toxic to the parasitoids of the tomato fruitworm, *Heliothis zea*, feeding on tomato plants (Campbell and Duffey, 1981). The same material is also involved in the host-plant resistance of tomato to the Colorado potato beetle, *Leptinotarsa decemlineate* (Barbour and Kennedy, 1991).



## **Stimulants**

Tyramine acts as an oviposition stimulant and various amino acids induce significant feeding stimulation in sugar-cane-infesting scarabaeids Allsopp (1992). Some glucosinolates increase feeding of cabbage stem flea beetle (Bartlett *et al.*, 1994).

## **Environmental Influences**

### **Seasonal Variation**

There are clear seasonal patterns in the size of herbivorous insect populations, and close relationships between season and variation in both the quantity and quality of available food (Coley and Barone, 1998; 2001; Ottosson and Anderson, 1983; Price 1991; Dudt and Shure, 1994). Seasonal peaks of insect abundance often coincide with the relatively short periods when plants are producing flushes of new leaves. Seasonal variation in leaf characteristics (notably nutrient concentrations) and food selection patterns by herbivores have been well documented (e.g. Alonso and Herrera, 2000, 2001, 2003). Although glasshouse-grown tomatoes do not produce flushes of leaves, their leaf characteristics could be influenced by season.

### **Temperature**

Temperature has a pronounced effect on plant-herbivore interactions (Atwal, 1955; Patel and Schuster, 1983; Leibe, 1984; Niesenbaum and Kluger, 2006) and strongly influences biocontrol agents such as *Diglyphus* spp. (Bazzocchi *et al.*, 2003). The influences of temperature and photoperiod on the speed of development, longevity, and fecundity of insects have been well documented (e.g. Atwal, 1955; Leibe, 1984; Minkenberg, 1988). In a study of 477 greenhouses used for vegetable cultivation in Tunisia, 33% of those which were heated were infested with leaf miners whereas only 15.8% of the unheated ones were infested Gahbiche *et al.* (2003). Temperature also affects the emission of leaf phenolics and volatiles (Tingey and Laubgayer, 1981; Tingey and Sinden, 1982; Tingey, 1985; Loreto *et al.*, 1996). In general, herbivory is inversely related to emissions of foliar phenolics.

### **Light**

Light influences the movement of larvae within the leaf canopy (Dudt and Shure, 1994; Alonso and Herrera, 2000) and emergent *L. trifolii* larvae seek areas of low light and low humidity which are more suited to their survival during pupation (Leibe, 1984). However, the effects of light (including daylength) on the behaviour of leaf miners have not been fully investigated. The concentrations of foliar phenolics and tannins increased under bright light (Dudt and Shure, 1994) but the relevance to the UK is unclear.

### **Carbon Dioxide**

Cultivating plants in a raised CO<sub>2</sub> concentration increases the carbon supply to leaves resulting in a reduction in leaf nutrient concentrations and an increase in herbivore food intake (Lincoln *et al.*, 1986; Bezemer and Jones, 1998). The increased consumption is more likely due to a reduction in leaf N rather than any increase in carbon-based defensive metabolites (Lincoln *et al.*, 1986). In general, herbivorous insects simply increase their consumption rates to compensate for lower quality leaves (high C: low N) (Kause *et al.*, 1999). Stiling and Cornelissen (2007) reported that more herbivores die on plants growing in elevated CO<sub>2</sub> concentrations, perhaps because the insects feed for longer and so are more exposed to natural

enemies. Plants grown at higher CO<sub>2</sub> concentrations contain more tannins and other phenolics in their leaves (Stiling and Cornelissen, 2007). Elevated CO<sub>2</sub> concentrations affected leaf-miner performance and plant growth in dock, *Rumex* spp. (Salt *et al.*, 1995).

### ***Drought***

The water content of host plants is important (Awmack and Leather, 2002; Joern and Mole, 2005) because water is essential for the survival of herbivores (Johnson and Felton, 1999). However, as presently cultivated, glasshouse-grown tomatoes are unlikely to suffer drought stress.

## PART 8: OVERALL SUMMARY

More than 400 references have been consulted in the course of this project but no obvious explanation for the susceptibility of speciality tomato cultivars has emerged. The original hypothesis that differences in leaf nutrients, especially nitrogen, were the underlying cause has not yet been rejected. There is sufficient published evidence to show that leaf nutrients can influence the behaviour, development and survival of insects in many varied ways and it is possible that a subtle mechanism exists but has not yet been detected. It is also possible that more sophisticated analytical tests may be required to detect differences in leaf nutrients.

The review of literature in Part 7 of this report suggests there are numerous other factors that could make cultivars such as Piccolo and Capri more susceptible to attack by leafminers. These factors might also account for many fewer pupae being produced in May than February on all the speciality cultivars tested here and for the adult leafminers having to make more leaf punctures per pupa produced. The latter observation suggests that the adults have to feed more to obtain adequate nutrients and / or moisture to be able to lay eggs although it might also mean that more larvae die. In addition, cv Piccolo always caused leafminers to make more feeding punctures per pupa than cv Dometica, which implies that cv Piccolo is less palatable or produces more deterrents, even though, in commerce, it is regarded as more susceptible.

The most obvious factors that might account for the seasonal differences in behaviour would be effects of 'season' on biochemical and physical characteristics of plant leaves. In this context, 'season' could mean increases in light quantity per day, daylength or temperature, each alone or in combination. Such seasonal changes could alter leaf size, affect light penetration into the leaf canopy producing micro-environments that were more or less suitable to leafminers, and increase leaf thickness making leaves tougher and less digestible.

Even more likely, perhaps, might be effects of season on the biochemical composition of leaves. Trichomes and their exudates are unlikely to be factors as *Liriomyza bryoniae* injects its eggs into the upper leaf surface and the trichomes are mainly on the lower leaf surface. Differences between cultivars could be due to differences in the lipid composition of their cuticles, or in the production of secondary metabolites, such as phenols, alkylating agents, terpenes, or other volatiles. It is also noteworthy that in the commercial production of tomato, average concentrations of CO<sub>2</sub> would be higher in February than May which might increase the carbon supply to leaves resulting in a reduction in leaf nutrient concentrations and an increase in herbivore food intake in summer. However, in general, herbivorous insects simply increase their consumption rates to compensate for lower quality leaves.

In the absence of data it is tempting to invoke differences in semiochemicals as these are involved in inducing plant defences, in attracting or repelling insects and in reducing the digestibility of leaf material. The results obtained in this project suggest that leafminers produce more pupae per feeding visit in February than in May and they always make twice as many feeding attempts on cv Piccolo than cv Dometica for a given number of larvae produced. The review of literature revealed that when leaf miners attack tomato plants, the plants increase peroxidase activity and produce four foliar proteins. The combined effect was to render the leaves unpalatable and the oxidised phenolics were toxic to the leaf miner. The proportions and mix of amino acids and proteases also act as deterrents to mining insects and those investigated appear to reduce the digestibility of leaf material. Oviposition stimulants,

such as tyramine, could be different in different cultivars. Elicitors of defence responses, such as jasmonates, might be involved so that attack by a leafminer induces the tomato's natural defences to operate at a higher level or even deters oviposition by the leaf miner. Of the non-volatiles produced by plants, the steroidal glycoalkaloid  $\alpha$ -tomatine has a toxic effect on insects and would be ingested by them from tomato tissues.

It should also be noted that the performance of natural parasitoids of *Lyriomyza* is also affected by seasonal and cultivar-based differences.

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