FOOD AND OUTBREAKS OF PHYTOPHAGOUS INSECTS

with special reference to Cardiaspina densitexta Taylor, (Psyllidae, Homoptera) on Eucalyptus fasciculosa (Myrtaceae)
in South Australia.

by

T. C. R. WHITE

B.Sc. (N.Z.) ; B.Sc. (For.) Edinb.

Department of Zoology
The University of Adelaide

JUNE, 1966

A thesis submitted for the degree of Doctor of Philosophy
in the University of Adelaide
SUMMARY

LIST OF ILLUSTRATIONS

LIST OF TABLES

DECLARATION

ACKNOWLEDGEMENTS

1. INTRODUCTION
   1.1 The Problem
   1.2 The Host Tree
   1.3 History of Outbreaks
   1.4 Discussion of the approach to the problem: an outline of the main working hypothesis formed during the study, and the theory arising from the study

   2.0 Introduction
   2.1 Field Sampling
      2.11 Preliminary Experiment
      2.12 Design of a Sampling Method
      2.13 Investigation of between-tree variance
      2.14 "Cost-structure" analysis
      2.15 Comparison of a high and a low population of C. densitexta on two adjacent trees

2.2 Laboratory Rearing Techniques
<table>
<thead>
<tr>
<th>Section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.3</td>
<td>The Adult</td>
<td>47</td>
</tr>
<tr>
<td>2.30</td>
<td>Introduction</td>
<td>47</td>
</tr>
<tr>
<td>2.31</td>
<td>Mating behaviour and stridulation</td>
<td>48</td>
</tr>
<tr>
<td>2.32</td>
<td>Dispersal</td>
<td>52</td>
</tr>
<tr>
<td>2.33</td>
<td>Oviposition</td>
<td>59</td>
</tr>
<tr>
<td>2.330</td>
<td>Introduction</td>
<td>59</td>
</tr>
<tr>
<td>2.331</td>
<td>Site of oviposition</td>
<td>60</td>
</tr>
<tr>
<td>2.332</td>
<td>Preferences exhibited</td>
<td>65</td>
</tr>
<tr>
<td>2.333</td>
<td>Discussion of preferences</td>
<td>74</td>
</tr>
<tr>
<td>2.4</td>
<td>Selection of a Host-Plant</td>
<td>77</td>
</tr>
<tr>
<td>2.41</td>
<td>Other species of <em>Eucalyptus</em> on which <em>C. dersitexa</em> has been recorded</td>
<td>77</td>
</tr>
<tr>
<td>2.42</td>
<td>Field and laboratory trials with other species of <em>Eucalyptus</em></td>
<td>79</td>
</tr>
<tr>
<td>2.43</td>
<td>Discussion</td>
<td>80</td>
</tr>
<tr>
<td>2.5</td>
<td>The Egg</td>
<td>84</td>
</tr>
<tr>
<td>2.50</td>
<td>Introduction</td>
<td>84</td>
</tr>
<tr>
<td>2.51</td>
<td>Water Relations</td>
<td>86</td>
</tr>
<tr>
<td>2.510</td>
<td>Introduction</td>
<td>86</td>
</tr>
<tr>
<td>2.511</td>
<td>Experimental demonstration of uptake of water by the eggs</td>
<td>87</td>
</tr>
<tr>
<td>2.512</td>
<td>The survival and development of eggs when removed from the leaf tissue</td>
<td>100</td>
</tr>
<tr>
<td>2.52</td>
<td>Hatching in relation to light and temperature</td>
<td>102</td>
</tr>
<tr>
<td>2.520</td>
<td>Introduction</td>
<td>102</td>
</tr>
<tr>
<td>2.521</td>
<td>Materials and Methods</td>
<td>104</td>
</tr>
<tr>
<td>2.522</td>
<td>Results</td>
<td>105</td>
</tr>
<tr>
<td>2.523</td>
<td>Discussion</td>
<td>110</td>
</tr>
</tbody>
</table>
2.6 The Nymphs

2.60 Introduction

2.61 First-instar Nymphs

2.611 Dispersal

2.612 Effects of crowding

2.613 Selection of a site to settle

2.62 The Lerp

2.63 Development and survival after settling

2.631 Orientation on the leaf

2.632 Effect of aspect

2.633 Effect of crowding

2.64 Feeding

2.641 Mechanism and site of feeding

2.642 Effect of feeding on the tissues of the plant

2.643 Possible causes of damage to the host's tissues

2.65 Food and its influence on abundance

2.7 Parasites and Predators

2.71 Parasites

2.72 Predators

2.721 Invertebrate predators

2.722 Predation by birds

3. THE VIGOUR OF THE PLANT AND INSECT ABUNDANCE

3.0 Introduction

3.1 The Relationship of Soil-moisture to Vigour of the Plant

3.2 The Relationship of Soil-moisture to Insect Abundance

3.3 The Relationship of Soil-moisture to the Nitrogen Content of the Plant
3.4 The Relationship of Nitrogen Changes in the Plant to Insect Abundance 177

3.5 The Relationship of Nutrition of the Plant to Insect Abundance 179

3.6 Previous Work Relating Water-stress, Nitrogen Changes in the Plant and Insect Abundance 181

3.7 Watering Experiment 183
   3.7.1 Materials and Methods 183
   3.7.2 Results 186
   3.7.3 Discussion 187

3.8 Summarized Hypothesis Erected on the Evidence presented in this Section 189

4. CORRELATION OF OUTBREAKS OF PHYTOPHAGOUS INSECTS WITH STRESS CAUSED BY WATER-LOGGING OR DROUGHT 191

4.1 The Stress Index 191

4.2 Outbreaks of Psyllids 194
   4.2.1 In South Australia 194
      4.2.11 C. densitexta on E. fasciculosa 194
      4.2.12 C. densitexta on E. cornuta 197
      4.2.13 C. albitexture on E. camaldulensis 198
      4.2.14 C. retator on E. camaldulensis 199
      4.2.15 C. fraxinella sp. on E. glacioflexus 201
      4.2.16 Other psyllids in South Australia 201
      4.2.17 Response to "frilling" of trees 202

4.22 In other states of Australia 202
   4.221 C. albitexture on E. blakelyi in A.C.T. and N.S.W. 202
   4.222 Glycaspis spp. on Eucalyptus spp. in N.S.W. 204
   4.223 Cardiaspina spp. on Eucalyptus spp. in Victoria 204
   4.224 C. periculosa on E. rufa in Western Australia 204
4.23 In America - *Paratricosa cockerelli* on potatoes 205
4.24 Discussion 207

4.3 Outbreaks of other Phytophagous Insects 209
4.31 Other Australian insects 209
4.32 Two examples from New Zealand 210
   4.321 *S. suavis* on *P. radiata* 210
   4.322 *S. noctilio* in *P. radiata* 214
4.33 Spruce budworm in Canada 216
4.34 Bark beetles 219
4.35 Aphids, mites, thrips, miscellaneous species, and forest defoliators in Europe 220
4.36 An example of the recorded effects of a drought in British Columbia 221

5. AN INTERPRETATION OF THE CHANGES OF ABUNDANCE OF PHYTOPHAGOUS INSECTS 224

5.0 Introduction 224

5.1 The Role of Food in Changes of Abundance of Phytophagous insects 225
5.2 The Role of Predators in Changes of Abundance of Phytophagous insects 231

BIBLIOGRAPHY 238
SUMMARY

Major outbreaks of *C. denticula* on *E. fasciculosa* occurred in 1914-20 and 1956-62. Nymphs kill the leaf-tissue on which they feed so high numbers defoliate and sometimes kill trees. Adults disperse widely in the spring but not in the summer and autumn. Aerial dispersal of first-instar nymphs is unimportant. There is a well defined mating "dance" and the males stridulate. Females lay their eggs on recently mature leaves, rejecting young and old leaves. They lay more eggs on north than south facing leaves; they strongly prefer the base of the leaf; but because of a tactile response to irregularities on leaf surfaces, they lay some eggs near other irregularities on other parts of the leaf.

The eggs replace water lost by transpiration by taking up water from the leaf. The rate of water movement varies with the age of the eggs, and in older eggs there is an "inner compartment" - presumably the embryo - which has a slower rate of flow than the rest of the egg. Eggs develop and hatch normally when removed from the leaf to distilled water. Time of hatching is determined by the periodicity of light and darkness, the frequency of the peak depending on the stimulus of "light on", and its amplitude on the duration of the preceding dark period. The time taken to respond to the "light on" stimulus increases with decreasing temperature.

Newly hatched nymphs become more active as their density increases. The proportion settling is inversely proportional to the number already established. Survival and growth rate increase with increasing density, increased light on leaf discs, and
on northern aspects of tree crowns - i.e. in response to improved nutrition.

Field samples were collected at random with the aid of a special six-sided die. In the laboratory psyllids were reared on discs of leaf floated on distilled water under fluorescent lights. Later refinement enabled isolation of the psyllids on one side of the discs from the water on the other.

Outbreaks of C. densitexta and of many other psyllids on Eucalyptus in Australia are associated with periods when wet winters are followed by dry summers. In an experiment in which C. densitexta were raised on E. fasciculosa that received different amounts of water more nymphs survived on the moderately watered trees than on those receiving too little or too much. This relationship between soil-moisture and outbreaks of psyllids is due to water-stress in the plants increasing the soluble nitrogenous food available to the nymphs. This same correlation of outbreaks with rainfall was found to hold for a number of different phytophagous insects in different parts of the world. As a result a general theory is proposed: that the abundance of many phytophagous insects is determined by a shortage of food - absolute when the plant is rare relative to the insect - relative when the insect is rare relative to the plant; and that those of the latter which erupt to outbreaks do so in response to the seasonal rainfall pattern stressing the plant and increasing the amount of nitrogenous food, and thus alleviating the relative shortage of food for the insects.

There is no competition for food when it is scarce, and predators have negligible influence on the prey's abundance when food becomes plentiful.