

## FORUM

POPULATION REGULATION IN INSECT HERBIVORES -  
TOP-DOWN OR BOTTOM-UP?

S. WRATTEN

Department of Entomology and Animal Ecology  
Lincoln University  
Canterbury  
New Zealand

**Recent evidence points to the plant's being a much more limited resource than previously expected. In addition to the restraints on feeding and population growth imposed by such factors as leaf toughness, the physical environment, plant nutrition, etc., recent work points to the role of feeding-induced chemical changes in the leaves in reducing herbivore 'fitness'. This suggests that population regulation in herbivores may indeed sometimes be from the trophic level below that of the herbivore—the plant itself.**

**Keywords:** trophic levels; herbivores; population regulation; wound-induced changes.

Ecologists have always liked to ask 'big' questions, although historically the resulting debates have often generated more hot air than fact, partly due to vague definitions and too much semantics. Good examples are the discussions of the role and frequency of density dependence in animal populations and the diversity/stability connection, among others. The arguments have often progressed logically, but, as the statistician G.E. Yule pointed out, 'Logic and mathematics are only of service ... once you have found the right track'. The extreme view, articulated by Peters (1991), is that this questioning approach signifies a subject which has lost its way - read the Peters book and see if you agree! A current area in ecology which has certainly enticed ecologists along particular 'tracks' is that of population regulation in herbivorous insects. One track, or paradigm which has attracted considerable support, is the idea that herbivore numbers are regulated (i.e., an upper limit imposed on their growth via density-dependent negative feedback) by the action of natural enemies.

Successful cases of biological control in New

Zealand, Australia and elsewhere point to the fact that this regulation via the trophic level above (i.e., top-down) does occur. However, the opposite mechanism, that of intra-specific competition among the herbivore population, is often dismissed. Thirty years ago, a classic paper by Hairston and colleagues addressed the 'big' question of 'why the world is green'. In other words, why around 95% of plant productivity in natural ecosystems remains largely intact at the end of the growing season, finding its way to the decomposer guilds. Hairston, Smith and Slobodkin (1960) stated that ....

"obvious depletion of green plants by herbivores are exceptions to the general picture, in which the green plants are abundant and largely intact... The (only possible) remaining method of general herbivore control is predation ... including parasitism... Herbivores are seldom food-limited, appear most often to be predator-limited, and therefore are not likely to compete for common resources".

Over twenty years later, an excellent textbook (Strong, Lawton and Southwood, 1984) appeared which covered some aspects of insect-plant ecology. This book, with a strong community ecology emphasis, picked up the Hairston quotation and suggested that it was based on '... stunningly simple logic'; G.E. Yule's ears would have twitched! One of the book's authors, a year later, suggested that '... plant effects upon insect populations are likely to be so trivial that they are swamped by the other processes such as natural enemies affecting the populations' (Fowler and Lawton, 1985).

Both quotations, separated by nearly a quarter of a century of experimental work, enshrine the same belief: that the plant is a super-abundant resource for insect herbivores, and that intra-specific competition among

the grazers is therefore a rare event. This view is supported by the rich community of difference-equation predation models which have had a large effect on the ecological literature (see any ecology textbook) over the last two decades. Most of these have begun with a simple model of a predator's or parasitoid's searching behaviour (incorporating 'attack rate', 'area of discovery', 'handling time', 'interference constants' etc.) and have depended heavily on many of the simple assumptions in the Nicholson-Bailey equations of the 1930s. These models pointed to a host's equilibrium level to which the population returned following perturbation, via density-dependent predation or parasitism as the mechanism.

With the evidence of successful biological control and the pedigree of the models from the 'Hassell and May' school, it would not be surprising to find that the role of the plant has been underplayed. If population studies are carried out regarding the host plant as a static canvas on which to paint the dynamic picture then obviously important host-plant variables could be missed.

Experiments over the last decade, however, have shown that it is often wrong to measure the insects' food simply in terms of kilograms of herbage; we now know that much of this '... super-abundant resource ...' is highly variable in space and time and that much of it is effectively unavailable to the herbivore, which may seem nevertheless to be in a green '... sea of plenty'. There is an obvious range of factors which can influence the herbivore at the individual level; such factors as cuticle thickness, toxins, hairs, amino acid and nitrogen levels, leaf toughness, water status, phloem depth (in the case of sap-feeders), exposure to sun and wind, etc., have all been shown to be important. However, for the 'big' question of regulation to be properly addressed, we would need to show that the herbivore's **populations** are affected by host-plant quality. A whole new category of evidence which supported the view that the plant could indeed be a limiting resource to the herbivore was that a plant could actively defend itself via wound-induced chemical changes. This work includes the important demonstration by Green and Ryan (1972) that tomato and potato plants synthesise powerful proteinase inhibitors when damaged. In trees, Finnish workers (e.g., Haukioja and Neuvonen, 1987) showed that leaves' suitability to insects declined following insect feeding while workers in the U.K. (e.g., Wratten, Edwards and Dunn, 1984) showed in laboratory and field bioassays that the leaves' acceptability to insects also declined, leading to the foliage receiving much less subsequent grazing. Much of this 'palatability' work was carried out in the laboratory, initially on leaf discs (a bad idea) and subsequently on intact leaves, shoots and whole plants. The main 'paradigm' which the

bioassay work suggested was that wound-induced changes are an additional and under-researched aspect of the plant's (un)suitability for herbivores.

The most recent work has shown that the main response by the herbivore to such changes is to move away from the damaged area (Wratten, Edwards and Winder, 1988; Edwards, Wratten and Parker, 1992). It is the population consequences of this movement which are fascinating, because if the herbivore's mortality increases as a result, there is the possibility of a lower trophic level effect on herbivore numbers. Mortality arising from movement may be a result of increased risk from abiotic factors, such as wind, inter-leaf brushing, attachment to stems and petioles, etc. It is also possible that the herbivore's availability to predators, either on the plant or on the ground, may increase. Edwards *et al.* (1992) showed that larvae of the armyworm *Spodoptera* (Lepidoptera) are forced down the host plant by a strong wound-induced change in the upper leaves of tomato (Fig. 1). So, in addition to being at risk due to their extra movement, the larvae are being driven onto 'throwaway' leaves (*sensu* Grime, 1979) which are of poor nutritional quality for the herbivore and of little value to the plant in terms of photosynthesis and competition for light (Grime, 1979). Recent experiments have shown that larvae under these conditions are more likely to move to the soil surface. Here they have an added host-finding problem; in addition, they are at risk from non-climbing, epigeal predators.

When these results are added to the battery of evidence that plants offer severe impediments to

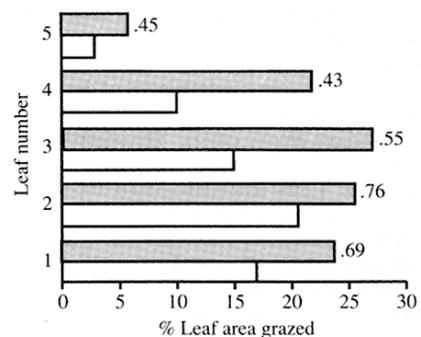


Figure 1: The extent of grazing damage by larvae of *Spodoptera littoralis* to leaves of tomato plants grown in mixtures with and without previous artificial damage to foliage. Mean values (% leaf area grazed) are shown for five trays each with 20 plants. The ratio of leaf area grazed in artificially damaged plants and control leaves is also given. Leaves have been numbered from the base of the plant. Control (undamaged) plants = shaded histograms (from Edwards *et al.*, 1992).

herbivores apart from wound-induced changes, the idea that competition for a resource which **appears** to be superabundant is actually taking place at quite low herbivore population levels becomes attractive. A recent review by Ohgushi (1992) supports this. More experimental work is needed and as Dempster (1991) said in his Presidential Address to the Royal Entomological Society of London, '... our studies of insect population ecology have reached a particularly interesting stage, where experimental entomology must take the driver's seat. At the moment, natural history may have more to offer the subject than computer science'. This is certainly true in the area of resource limitation on insect herbivore populations; a whole range of experiments based on relatively simple protocols awaits the experimental ecologist.

## Acknowledgements

Figure 1 is copyright of Springer-Verlag and is reproduced with kind permission.

## References

- Dempster, J.P. (1991). The role of intra-specific competition in determining insect abundance. *Antenna* 15: 105-109.
- Edwards, P.J.; Wratten, S.D.; Parker, L. (1992). The ecological significance of rapid wound-induced changes in plants: insect grazing and plant competition. *Oecologia* 91: 266-272.
- Fowler, S.V.; Lawton, I.H. (1985). Rapidly induced defences and talking trees: the Devil's Advocate position. *American Naturalist* 126: 181-195.
- Green, T.R.; Ryan, C.A. (1972). Wound-induced proteinase inhibitor in plant leaves: a possible defence mechanism against insects. *Science* 175: 776-777.
- Grime, J.P. ((1979). *Plant strategies and vegetation processes*. Wiley, Cambridge, U.K. 222 pp.
- Hairston, N.G.; Smith, F.E.; Siobodkin, L.B. (1960). Community structure, population control and competition. *American Naturalist* 44: 421-425.
- Haukioja, E.; Neuvonen, S. (1987). Insect population dynamics and the induction of plant resistance: the testing of hypotheses. In: Barbosa, P.; Schulz, J.C. (Editors), *Insect outbreaks*. pp. 411-432. Academic Press, New York, U.S.A.
- Ohgushi, T. (1992). Resource limitation on insect herbivore populations. In: Hunter, M.D.; Ohgushi, T.; Price, P.W. (Editors), *Effects of resource distribution on animal-plant interactions*. pp. 199-241. Academic Press, San Diego, U.S.A. 505 pp.
- Peters, R.H. (1991). *A critique for ecology*. Cambridge University Press, Cambridge, U.K. 366 pp.
- Strong, D.R.; Lawton, D.H.; Southwood, T.R.E. (1984). *Insects on plants*. Blackwell Scientific Publications, Oxford, U.K. 324 pp.
- Wratten, S.D.; Edwards, P.J.; Dunn, I. (1984). Wound-induced changes in the palatability of *Betula pubescens* and *B. pendula*. *Oecologia* 61: 372-375.
- Wratten, S.D.; Edwards, P.J.; Winder, L. (1988). Insect herbivory in relation to dynamic changes in host plant quality. *Biological Journal of the Linnean Society* 35: 339-350.