THE ROLE OF NITROGEN IN LIMITING THE ABUNDANCE OF ANIMALS

by

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ABSTRACT

This thesis comprises a review of the impact that my published work has had over the last thirty years on the discipline of Ecology. The essence of this contribution is encompassed in five key papers and a book.

The basis of my work rests in the paradigm that populations of animals are limited by the capacity of their environment to support them. In all but infrequent and brief instances they are limited by a lack of adequate food for breeding females and growing neonates. The principal limiting component of that food is nitrogen that is accessible and in a form which can be readily absorbed and incorporated into body protein. Consequently most breeding is of limited success and most young animals starve.

This proposal is directly opposed to the ruling paradigm that populations are regulated by the action of their predators, or their own intraspecific competition. However, it has been repeatedly demonstrated that predators are largely inefficient, and, anyhow, unable to regulate their prey when that prey has an abundance of nitrogenous food: predators are themselves limited by their food. Competition, on the other hand, is simply the outcome of a shortage of a resource; most usually food. It decides *which* of the many gain access to the limited supply, but not *how many* of them: the supply of available food does that.

Many studies have been specifically designed to test my views. Some have not supported them. But many (along with others not designed to directly test my hypotheses) do support them. In total, they bear witness to the extent to which my ideas have influenced the discipline of Ecology. The impact of this way of explaining the world of nature continues to spread, now having a significant and ongoing influence on population, community, ecosystem and food web studies of terrestrial, marine and freshwater animals ranging from invertebrates to mammals.

STATEMENT

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

T.C.R. White.

January, 1999.

INTRODUCTION

I came to Adelaide University as a student of mature age (I was forty when awarded my PhD) to study Ecology under H.G. Andrewartha. Prior to this, and after completing a degree in science at Auckland University and a forestry degree at Edinburgh University, I had been a forest entomologist at the New Zealand Forest Research Institute. There I established and directed the Forest Biology Survey to monitor pests and diseases in plantations throughout the country (Appendix I:1). But this also involved me in personal research into a number of forest insects, both indigenous and introduced (Appendix I:10;11;13;14). Earlier, as an undergraduate student, I had spent two long vacations working with the Forest Pathologist, G.B. Rawlings, during the massive outbreak of the woodwasp *Sirex noctilio* in New Zealand's plantations (Rawlings and Wilson 1949). All these studies led me to become increasingly unhappy with the then currently accepted hypotheses explaining outbreaks of forest pests. These hypotheses, based upon concepts of "regulation" of populations by predators, parasites or disease (and inextricably intertwined with the theory and practice of biological control of introduced pests) did not fit with my own observations of the changes in abundance of these animals.

During this time I read the now famous book of Andrewartha and Birch (1954). This led me to believe that their approach to ecology could supply a better explanation. So I determined to go to Australia to study under Andrewartha. This eventually became possible when I won a three year Wool Research Trust Fund Fellowship at the Waite Agricultural Research Institute. Upon arrival in Adelaide, I told Andrewartha (very naively, I later realised!) that my aim in the next three years was to develop a better theory to explain outbreaks of forest insects. He was sceptical that I might achieve such a grand ambition in the term of my fellowship. (He was, nevertheless, constantly encouraging of my determination to achieve this goal, not only during my studentship, but subsequently in a working relationship which continued until his death).

Thirty years later I published my own book, "The Inadequate Environment" (Appendix I:23; Appendix II:V), which is a culmination and expansion of my previously published papers, and which proposes, within a now much broader context, just such a "theory". I believe this book, and my prior publications, now comprise a significant and continuing influence upon the theory and practise of animal ecology; not just as it relates to forest insect defoliators, but to all herbivores - and beyond to carnivores. Further, the book continues and consolidates Andrewartha's alternative to the majority-view paradigm of the regulation of populations of animals by "density-dependent factors". This alternative view is now often referred to in the literature as the "bottom up" paradigm - that numbers are controlled by the capacity of their habitat to support them - in contrast to the regulationists' "top down" paradigm of control by the action of predators (McQueen et al. 1986).

However, my work comprises more than several interrelated ecological hypotheses. It presents a body of evidence demonstrating the need for a paradigm shift: from the "Systems Paradigm" to the "Natural History Paradigm" of Den Boer and Reddingius (1996).

So I would contend that my published work has "made an original contribution of distinguished merit adding to the knowledge [and] understanding of [Ecology]" (University of Adelaide Calendar, DSc Regulations 3(a)). Over the last thirty years my work has developed as a major influence upon the thinking and direction of research into the study of Ecology in its broadest sense. And, if the current rate of publication of work testing and citing my ideas is any measure, it shows every sign of continuing to do so.

RESUME OF PUBLISHED WORK

My study of an outbreak of the psyllid *Cardiaspina densitexta* attacking *Eucalyptus fasciculosa* in the southeast of South Australia (Appendix I: 2;3;5;6;7;8;9;12;16) led to the first tentative statement of a hypothesis explaining how outbreaks of psyllids, might be generated by changing patterns of weather stressing their food plants (Appendix I:4).

I continued to broaden the scope of this stress hypothesis, incorporating my earlier work on outbreaks of the defoliating lepidopteran, *Selidosema suavis* in New Zealand, and including outbreaks of a number of other geometrid forest defoliators in different parts of the world, and of the tortricid Spruce Budworm of North America (Appendix I:13). The same hypothesis provided a parsimonious explanation of plagues of locusts in Africa, Asia, North America and Australia (Appendix I:15).

Finally, I broadened the hypothesis still further to include a wide range of herbivorous invertebrates responding to changes in their food plants generated by a variety of environmental stresses other than those imposed by the weather (Appendix I:18). This hypothesis is now commonly referred to in the literature as my "Plant Stress Hypothesis" (Price 1991, 1997; Cobb et al. 1997). Watt (1994) states that it was my work which "focused attention on drought stress" by "drawing together the evidence to support the plant stress hypothesis" and "providing a theoretical basis for it (White 1969, 1974, 1976, 1984)". Some (Koricheva et al. 1998) even avow it has "achieved paradigm status".

The basis of this hypothesis is that when a plant is stressed, it becomes a better source of food. Specifically, more of its total content of nitrogen is converted to a soluble form which is more readily accessible to, and assimilated by, newly-hatched invertebrates when they first attempt to feed. This comes about because, when stressed, a plant is, in effect, induced into a state of hastened senescence. Much of its protein is mobilized into various soluble amino acids, including essential ones which animals cannot synthesise. These provide a more readily available - more easily absorbed - form of protein for these neonates. Specialist senescence-feeders will obviously benefit from this enriched outflow; but so too will the more common flush-feeders if the nutrients are translocated to new growth, rather than just to storage tissues.

A corollary of this interpretation of the causes of changes in abundance of animals is an explanation of the causes of "dieback" or "decline" of trees (Appendix I:21). These declines are not normally, as is commonly proposed, the result of attacks by pathogens or insects. Rather these attacks are symptoms of stress of the trees, induced, usually, by patterns of weather which depart sharply from the "norm". And it is this stress which, by upsetting the root-shoot ratio of the trees, causes their crowns to die back. This dieback is necessarily accompanied by hastened senescence of the trees' foliage, providing the improved source of food for organisms attacking that foliage. The insects and pathogens are effect not cause. This hypothesis has subsequently received increasing support from the results of other studies of this world-wide phenomenon (Akashi and Mueller-Dombois, 1995; Auclair, 1993; Davison, 1997; Huettl and Mueller-Dombois, 1993).

I also extended this concept of limitation "from below" by demonstrating (Appendix I:17,20) that a shortage of available nitrogen in the food of the very young is not confined to invertebrates but is, in fact, at the base of the limitation of very many animals, both herbivore and carnivore. The crux of this hypothesis (the "nitrogen limitation hypothesis"; Schetter et al. 1998) is that for breeding females to successfully produce young, and for any fast-growing young animal to subsequently survive, a high level of readily available and easily absorbed and digested nitrogen is essential. And of all essential nutrients it is this nitrogen which tends first to become limiting in the environment of most animals, be they herbivores or carnivores. Energy, the currency usually considered critical, is not normally in short supply.

In my book (Appendix I:23; Appendix: V) I attempted to further consolidate and integrate these hypotheses, showing that they all stem from the fact that the abundance of animals is constrained by their access to limited resources - their environment is inadequate - rather than by the depredations of their predators.

But the book goes much further than this. It indicates the need for a reassessment of many ecological "axioms": the role of competition; the efficiency of predators; the regulation of populations around equilibria; self-regulating mechanisms; the "balance" of nature; apparent and unapparent plants; competitive exclusion; r and K strategies; optimal foraging. It shows how a wide variety of structural, physiological and behavioural adaptations of animals operate to eliminate individuals unable to cope with this shortage of available nitrogen, and to channel what is accessible to only a limited number of breeding females and neonates in a population. It shows how this interpretation of the processes limiting the numbers of animals leads to a more parsimonious explanation of such apparently disparate phenomena as cyclic populations, territoriality, philopatry and cannibalism. In herbivores, it similarly explains leaf-mining, gall-forming, gut microbes, coprophagy, carnivory and selective feeding (including the important distinction between flush- and senescence-feeders). It shows how sudden large increases in abundance - outbreaks - of every sort of animal, from rabbits and voles to insect defoliators of forests, are the result of the temporary alleviation of the inadequacy of their environment; an increase in the availablity of nitrogen for the successful production and survival of young.

RECOGNITION OF THE WORK.

a) The breadth of the influence of my work: disciplines.

At the time that I was completing my work on the psyllids in South Australia, my conclusions as to the causes of outbreaks of these insects were contradicted by the published work of L.R. Clark who had worked under the leadership of A.J. Nicholson in CSIRO Division of Entomology. He had studied outbreaks of a closely related psyllid on red gums in and around Canberra. He concluded that their populations were regulated by their predators and parasitoids (Clark 1964). However, he later conceded that "Finally, it is necessary to mention that White (1969, 1971) was correct in drawing attention to soil moisture as affecting the food supply and hence abundance of *C.albitextura*, ..." (Clark and Dallwitz 1975).

More recent work by a new generation of CSIRO entomologists (studying renewed outbreaks of the same species of psyllid with which Clark had worked), has demonstrated that it is, indeed, the physiology of the trees, influenced by changing patterns of weather, which determines the abundance of these herbivores; their predators and parasitoids have no significant influence in preventing or ending outbreaks (Farrow and Floyd 1996). Additionally, recent work by botanical ecologists (Marsh and Adams 1995) and by non-ecological specialists (Crawford and Wilkens 1996) in Australia supports my hypothesis. Thirty years on, psyllid ecologists still cite my general psyllid papers (eg. Luft and Paine 1997; Purcell et al. 1997).

Beyond this "local" influence, however, my ideas have had a significant impact throughout the world in my original field of entomology (eg. Louda and Collinge 1992; Price 1997; Price et al. 1990), and today the debate and testing of them continue unabated (eg. Cobb et al. 1997; Joern and Behmer 1997; Karhu and Neuvonen 1998 [& Appendix I:24]; Koricheva et al. 1998; Schetter et al. 1998; Schowalter et al. 1999).

Many of the studies so influenced are of other Homoptera (eg. Brodbeck et al. 1995; McClure 1985; Washburn et al. 1987), but also embrace many works on Lepidoptera (eg. Bloem and Duffy 1990; Brewer et al. 1987; Thomas and Hodkinson 1991; Myer and Post 1981; Stoszek et al. 1981), as well as ones with Coleoptera (eg. Dijk 1996; Ohmart et al. 1987; McQuate and Connor 1990), Diptera (eg. Collinge and Loude 1988; Minkenberg and Ottenheim 1990), Hymenoptera (eg. Marchisio et al. 1994; Niemela et al. 1987; Price and Ohgushi 1995; Vasconcelos and Cherrett 1996), Orthoptera (eg. Joern and Behmer 1997; Simpson and Abisgold 1986) and Trichoptera (eg. Becker 1990; Hart 1987).

However, the influence of my work has not stopped with entomology. It has spread well beyond to encompass the broader field of animal ecology. Other studies which have been influenced by, and have produced experimental and observational results in support of my hypotheses, include those investigating the ecology of nematodes (eg.

Bongers et al. 1997; Yeates 1982), mites (eg. English-Loeb 1990), scorpions (Pollis and McCormick 1987), isopods (Rushton and Hassall 1983), spiders (Greenstone, 1989), crabs (eg. Kennish 1997; Wolcott and Wolcott 1987), molluscs (eg. Osenberg 1989; Zamora and Gomez 1996), fish (eg. Horn et al. 1995), reptiles (eg. Troyer 1984), birds (eg. Gardarsson and Einarsson 1994), and many mammals (eg. Bergeron et al. 1990; Goldingay and Kavanagh 1990; Hobbs et al. 1982; Lochmiller et al. 1995; Schetter et al. 1998). They also include studies in marine (Fleming 1995) and freshwater (Pinder 1992) environments. Nor are they confined to studies in population ecology. Those working as community (Faeth 1987) and food web (Polis and Strong 1996) or food chain (Fretwell 1987) ecologists, as well as botanical ecologists (Marsh and Adams 1995), have been influenced by my ideas. The most recent spread of the impact of my work has been to the field of evolutionary biology (Parsons 1996).

Furthermore, I have encountered reference (some of it extensive) to my work in more than two dozen textbooks including ones on ecology (Andrewartha and Birch 1984; Begon et al. 1996; Colinvaux 1988; Crawley 1983; Den Boer and Reddingius 1996; Krebs 1985), entomology (Berryman 1986; Hodkinson and Hughes 1982; Price 1997; Schoonhoven et al. 1998; Speight and Wainhouse 1989), forestry (Spurr and Barnes 1980), pest management (Horn 1988) animal physiology (Langer 1988), and evolutionary biology (Hoffman and Parsons 1997).

b) The depth of the influence of my work: citations.

Not only has my work impinged upon many fields within animal ecology, it has also influenced the direction of thinking and experimentation of many workers in those fields. This depth is perhaps best illustrated by reference to the citation history of my publications.

I know of 1534 citations of my relevant publications since 1970. However, prior to the publication of my book in 1993, the core of my contribution to ecological theory was contained in only five key papers (Appendix II;IV). These five have received 1284 of those total citations, the book (Appendix II;V) 79.

But the number of citations that a publication receives varies greatly from discipline to discipline, so some measure other than raw numbers is needed to truly highlight the impact of the work.

One such widely accepted measure is the Institute for Scientific Information's (ISI) identification of papers which have had a major influence in their field. My 1978 paper (Appendix I:17) was one of these. Nine years after its publication, with 125 citations, it was an ISI "Citation Classic" (Appendix I:22; Appendix III). The 1984 paper (Appendix I:18) was another. Eleven years after publication and with 181 citations, it was the fifth of ISI's ten most cited papers in the field of Environmental Sciences (Moore 1995, Appendix III). Both continue to be highly cited with, currently, 354 and 337 citations respectively.

Another objective measure would be a comparison of the number of citations of the papers in Appendix II with the ISI's "Journal Impact Factors" of the journals in which they were published. This factor, calculated annually, is the average of all citations of all papers published in a journal in the previous two years. The average of citations of my 1969 paper (Appendix I:4) over 28 years is 6.6. The annual Impact Factor of "Ecology", the journal in which it was published, has averaged 2.5 over the last five years.

The other four papers (Appendix I:13,15,17,18) were all published in "Oecologia". That journal's average annual Impact Factor over the last five years is 1.5. But these four papers have average citations of, respectively, 10.2 over 23 years, 7.7 over 21 years, 18.3 over 19 years and 24.7 over 13 years.

The annual Impact Factors of both "Ecology" and "Oecologia" lie in the first twenty of some seventy ecology journals, immediately behind the review journals which are always more highly cited than other journals.

Finally, some indication of how my work ranks alongside that of others in my own field can be gained by a comparison of the rate of citation of my papers with those of A.J. Nicholson, the "father" of density dependence (Nicholson 1933), and one of the most quoted earlier workers in ecology. From 1970 to 1994, 25 of his papers were cited 1170 times (CSIRO unpublished records). In the same period 21 of my relevant papers received 1189 citations.

There is no doubt that some ecologists' disagreement with my views has accounted in part for the extensive citations my work has received. But their citations are far outnumbered by those of the ecologists who support my hypotheses. Either way, they demonstrate the extent of the influence of my work on the discipline.

c) General.

Since the mid 1970s I have been an invited speaker and consultant on plant-herbivore relations at various laboratories in Australia, North America, the United Kingdom, Europe and South Africa. In 1984 I was an Australian Academy of Science visiting lecturer to China. In 1989 I was an invited lead speaker at the Gordon Conference on the Chemistry of Plant-Herbivore Interactions, in Oxnard, California. Most recently (1998) I was an invited consultant in the Department of Biological Sciences of Northern Arizona University, Flagstaff, and one of two annual Visiting Professors at the University of Padova, Italy, delivering a series of lectures to senior students at the University's Instituto di Entomologia Agraria.

Last year I resigned after 15 years as the Australian zoological editor of "Oecologia", a job I was appointed to when Prof. Charles Birch retired. Eleven years after retiring I still receive manuscripts from colleagues and journals for comment and refereeing, and maintain an extensive correspondence with colleagues around the world.

d) Some comments about "The Inadequate Environment".

The most pleasing (and unsolicited) opinions of my book that I have received are those of three ecologists of world stature.

The late Prof. Dr. H. Remmert, Philipps-Universitat, Marburg, Germany.

"This is definitely a great book and I'm very proud that I managed to persuade you! To publish in one book, one unifying theory on the abundance of animals and plants including the famous lemming cycles is a job almost equalling Darwin"

Dr P.J. den Boer, University of Wageningen, The Netherlands.

"I repeat that you succeeded to formulate and support with sufficient examples one of the very few `general rules' that dominate ecology. My congratulations with that, for there are not many other `general rules' possible in ecology."

Prof. J.D. Shorthouse, Laurentian University, Ontario, Canada.

"Once I started reading it, I could not put it down! Your arguments are very convincing and indeed, have provided me with a whole new perspective on insect-plant relationships. I am anxious to change my lecture notes in principles of ecology and general and forest entomology!"

"Furthermore, your book will be standard reading for my graduate students ... All biologists owe you a world of thanks for synthesizing such a vast amount of literature. Can't believe how much I learned from this book, especially about concepts I had not even thought of previously. And you have written it in such a wonderful, relaxing style! Again congratulations and a sincere, Thank You!"

CONCLUSION.

The basis of my work is an essentially very simple proposition, yet a very far-reaching one in its implications for the direction of ecological research. It stems from the discovery that there is a common pattern of limitation of populations of animals by a shortage of nitrogenous food available in their environment, and that, in all animals, a wide range of anatomical, physiological and behavioural adaptations has evolved to counter this shortage.

It says that animals do not increase without limit because the capacity of their environment to support them is variably finite, not because they are regulated around an equilibrium by density-dependent factors impinging upon their populations. Their numbers fluctuate as the capacity of their environment fluctuates. In turn this carrying capacity is largely influenced by the weather experienced in that environment. And this explanation is equally as true for predators as it is for their prey. All are limited "from below"; not "from above". The key resource contributing to the finite carrying capacity of their environments is the limited availability of nitrogenous food for breeding females and growing young. The influence of other factors which can and do impinge upon the distribution and abundance of animals, is, for most of the time, subsumed by this usually chronic shortage of accessible nitrogen in a form that can be readily absorbed and incorporated into body protein. The truth of this view is unambiguously illustrated on the relatively rare occasions when the numbers in a population increase explosively to outbreak levels. This happens because the environment becomes temporarily less inadequate.

My explanation for the observed distribution and abundance of animals is thus the antithesis of the paradigm that emanated from Nicholson's work, and which has held sway for more than fifty years as the "received wisdom" in Ecology (eg. Begon et al 1996). This entrenched view has it that the numbers of animals - especially herbivores - must be "regulated" by competition or other "density-dependent factors" (ie. factors whose influence on the survival of animals in a population varies as the number of animals in that population varies). This regulation tends always to return that number to a pre-ordained mean - an equilibrium point; it is a negative feed-back mechanism. If this did not happen, its proponents maintain, populations of animals would increase "without limit". They take no cognisance of the power of the environment to prevent this from happening for other than infrequent and brief periods in the history of any population of animals.

The most commonly invoked regulating factor is the action of predators. But it has been repeatedly demonstrated that predators are largely inefficient; and totally unable to regulate their prey when that prey has an abundance of nitrogenous food. Predators are themselves limited by their food.

The other is intraspecific competition. However, competition is simply the outcome of a shortage of a resource; most usually food. Competition decides *which* few of the many gain access to the limited supply of resource. But it does not determine *how many* of them do; the supply of available food does that.

Once the reality of the universal limitation of the numbers of animals by their environment's capacity to support them becomes fully understood, the regulationists' view will continue to fade. My influence on the discipline of Ecology will then extend further than it has to date. I will have contributed to a "paradigm shift" in Ecology, a major achievement in any science (Den Boer and Reddingius 1996; Krebs 1995; Wilson 1994, page 320), and far more than I ever imagined I could do when I first came to study with Andrewartha.

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APPENDIX I

RELEVANT PUBLICATIONS, T.C.R. WHITE.
(All single author papers)

1. Forest Biology Survey in New Zealand. N Z Timber J 4(3):38-40. 1957.

2. Uptake of water by eggs of *Cardiaspina densitexta* (Homoptera; Psyllidae) from leaf of host plant. J Insect Physiol 14(11):1669-1683. 1968a.

[And see "Trends and Discoveries" New Scientist 40:683 1968]

3. Hatching of eggs of *Cardiaspina densitexta* (Homoptera; Psyllidae) in relation to light and temperature. J Insect Physiol 14(12):1847-1859. 1968b.

4. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. Ecology 50(5):905-909. 1969.

5. Some aspects of the life history, host selection, dispersal and oviposition of adult *Cardiaspina densitexta* (Homoptera: Psyllidae). Aust J Zool 18(1):105-117. 1970a.

6. The nymphal stages of *Cardiaspina densitexta* (Homoptera: Psyllidae) on leaves of *Eucalyptus fasciculosa*. Aust J Zool 18(3):273-293. 1970b.

7. The distribution and abundance of pink gum in Australia. Aust Forestry 34(1):11-18. 1970c.

8. Lerp insects (Homoptera; Psyllidae) on red gum (*E. camaldulensis*) in South Australia. Sth Aust Nat 46(2):20-23. 1971.

9. The production of amylose in the faeces of psyllid larvae with special reference to the lerps of *Cardiaspina densitexta*. J Insect Physiol 18(12):2359-2367.1972.

10. The distribution, dispersal and host range of *Antheraea eucalypti* (Lepidoptera: Saturnidae) in New Zealand. Pacific Insects 14(4):669-673. 1973a.

11. The establishment, spread and host range of *Paropsis charybdis* Stal (Chrysomelidae) in New Zealand. Pacific Insects 15(1):59-66. 1973b.

12. Aerial dispersal of adult *Cardiaspina densitexta* (Homoptera: Psyllidae) in South Australia. Trans Roy Soc Sth Aust 97(1):29-31. 1973c.

13. A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in plantations of *Pinus radiata* in New Zealand. Oecologia 16(2):279-301. 1974.

14. A quantitative method for sampling larval stages of *Selidosema suavis* in exotic plantations in New Zealand. Canad Entomol 107(4):403-412. 1975.

15. Weather, food and plagues of locusts. Oecologia 22(2):119-134. 1976.

16. A method of sampling populations of psyllids living on the leaves of *Eucalyptus* trees. Pacific Insects 19(1-2):39-44. 1978a.

17. The importance of a relative shortage of food in animal ecology. Oecologia 33(1):71-86. 1978b.

[and see 22. Citation Classic 1987].

18. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63(1):90-105. 1984.

[and see Moore PD (1995) How plants deal with what's eating them. Hot Papers in Research: environmental health. Current Contents AB&ES 26(22):3-5, May 1995; Science Watch 6(4):7-8, April 1995]

19. Green islands - nutrition not predation - an alternative hypothesis. Oecologia 67(3):455-456. 1985a.

20. When is a herbivore not a herbivore? Oecologia 67(4):596-597. 1985b.

21. Weather, *Eucalyptus* dieback in New England, and a general hypothesis of the cause of the dieback. Pac Sci 40(1-4):58-78. 1986.

22. The importance of a relative shortage of food in animal ecology - ISI Citation Classic. Current Contents (AB&ES) 18(34):14. 1987.

23. The Inadequate Environment. Nitrogen and the Abundance of Animals. Springer-Verlag, Heidelberg New York London Paris Tokyo Hong Kong Barcelona Budapest. 41 figures, XIX + 425pp. 1993.

24. Green islands still not explained. Oecologia 113(4):517-518. 1998

APPENDIX II

CITATIONS OF FIVE KEY PAPERS AND "THE INADEQUATE ENVIRONMENT"

	4	13	15	17	18	23		
	1969	1974	1976	1978	1984	1993	Total	Mean
1970	1						1	
1971	2						2	
1972	2						2	
1973	3						3	
1974	2						2	
1975	1	1					2	
1976	2	2					4	
1997	2	6	2				10	3.4
1978	3	7	4				14	4.6
1979	6	5	3	5			19	4.8
1980	8	12	5	13			38	9.5
1981	8	10	8	18			44	11.0
1982	2	5	7	14			28	7.0
1983	12	16	15	22			65	16.3
1984	10	12	6	27			55	13.8
1985	5	8	11	21	7		52	10.4
1986	5	10	7	25	19		66	13.2
1987	15	26	16	35	34		126	25.2
1988	12	15	16	23	35		101	20.2
1989	11	14	7	14	25		71	14.2
1990	11	7	9	21	46		94	18.8
1991	14	16	8	16	35		89	17.8
1992	8	8	5	21	18		60	12.0
1993	9	11	6	13	14		53	10.6
1994	8	13	8	16	22	4	71	11.8
1995	14	17	11	19	30	16	107	17.8
1996	5	6	4	12	18	22	67	11.2
1997	5	7	4	13	18	24	71	11.8
Total	186	234	162	348	321	66	1317	(to 9.98)
Mean	6.6	10.2	7.7	18.3	24.7	16.5	47.0	
Years	28	23	21	19	13	4	28	
1998	6	4	1	6	16	13	46	
Total	192	238	163	354	337	79	1363	(to 9.98)

APPENDIX III

I.S.I. "CITATION CLASSICS" OF TWO OF THE KEY PAPERS.

The importance of a relative shortage of food in animal ecology. Oecologia 33:71-86. 1978.

The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63:90-105. 1984.

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APPENDIX IV

THE FIVE KEY PAPERS

1) An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. Ecology 50:905-909. 1969.

2) A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in plantations of *Pinus radiata* in New Zealand. Oecologia 16:279-301. 1974.

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