

RESUMES

THE EFFECT ON SEED GERMINATION OF VOLATILES FROM *Pinus radiata* LITTER

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It is suggested that the observed effects of *P. radiata* litter vapour on ryegrass and clover germination were caused by ethylene and CO₂. If these gases are present at active concentrations in the litter layer, they could play a part in the poor development of undergrowth in *P. radiata* stands in Canterbury

Pinus radiata D. Don is an important tree in New Zealand where it is widely grown for timber and, to a lesser extent, in association with pasture species. In pure stands of *P. radiata* in Canterbury, poor development of undergrowth may in part be caused by volatile inhibitory substances released from the decomposing litter. In previous work it was shown that vapour from incubated *P. radiata* litter inhibited seedling growth. This inhibition was attributed to ethylene which was present in the vapour.

Experiments were carried out to investigate the effects of litter vapour on the germination of *Trifolium repens* (clover) and *Lolium perenne* L. (ryegrass) seed. Clover germination was delayed by litter vapour, but when the vapour was diluted 10-fold a stimulation of germination was observed. Ryegrass germination was delayed by both undiluted vapour and a 10-fold dilution. When ethylene was removed from the litter vapour the stimulatory effect on clover germination was lost, but no change occurred in the inhibitory effect on ryegrass germination. Removing CO₂ from litter vapour capable of inhibiting clover germination removed the inhibition and also greatly reduced the inhibitory effect on ryegrass germination.

These results suggest that ethylene and CO₂ in the litter vapour could be causing the observed effects. Ryegrass germination was inhibited by both ethylene (5 µl/l) and CO₂ (100 µp/p) but a mixture of ethylene and CO₂ caused no additional inhibition. Clover seed treated with six concentrations of ethylene at four concentrations of CO₂ showed stimulated germination both by CO₂ in the absence of ethylene and by ethylene in the absence of CO₂. As the CO₂ concentration increased, the stimulation by ethylene was reduced and at ethylene concentrations above 0.5 µl / l, CO₂ caused a reduction in germination rate. The lowest germination rate observed was in the absence of both ethylene and CO₂.

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MODERN NICHE THEORY AND PLANT ECOLOGY

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According to the competitive exclusion principle, in a community at equilibrium every species must occupy a different niche. Controversy has surrounded this basic hypothesis of niche theory since the limiting resources that define the niche of a species are not known for the great majority of species. The niche is the total physical, chemical, and biological relationship of an organism to its environment, so there are a large number of possible niche characteristics to measure. Plant ecologists find it difficult to explain how the niches of the one-half million vascular plant species differ so markedly, when all plants simply need water, light, carbon dioxide, and minerals. Various explanations have been advanced and have been elaborated on by Grubb (1977) to explain the coexistence of many species in plant communities:

1. There may be variation in life form with each species utilizing different parts of the physical environment.
2. Short-term fluctuations in the environment may favour first one species then another species, resulting in a dynamic equilibrium of species dominance.
3. Species may differ in phenological characters, such as time of growth, flowering, and fruiting.
4. Plant species may vary in their competitive ability with age.

However, all of these theories only consider a limited aspect of the adult niche, without regard to reproduction, fruit dispersal, and establishment, as pointed out by Grubb (1977).

Within the last 15 years, niche theory has under-

gone a tremendous expansion as a result of the work of Robert MacArthur and his colleagues. This approach involves quantification of community structure by measuring the place occupied by each species in a community along a designated resource gradient. The extent to which different species overlap in their niches and the width of niches can be determined using these methods. This approach has been used most effectively in analyzing the community structure of birds and lizards and explaining immigration rates and extinction rates of species on islands. The most recent examples of this approach can be found in *The Ecology and Evolution of Communities*, edited by Cody and Diamond (1975). Multivariate statistics, such as principal component analysis, are frequently used to examine several resource gradients simultaneously. Such statistical analysis is not generally meant to prove anything, but is used mainly to illustrate underlying community structure.

There are many limitations to this mathematical methodology in relation to the study of plant communities. Unlike bird and lizard communities, where feeding ecology is closely related to general morphology, in plants the relevant variables are not easily determined. While certain basic processes such as photosynthesis, respiration, and transpiration are common to all plants, the measurement of these in the field for most plant species is either not possible or difficult with present techniques. Given all of the plant characters related to morphology, anatomy, growth, reproduction, establishment, and dispersal, studying one particular character and ignoring others is an arbitrary decision given our present state of knowledge. Further, many aspects of plant morphology and physiology change in different environments, so there is the further difficulty of deciding which environmental conditions should be chosen for evaluating the characters. It must be emphasized that comparisons of niche width and niche overlap among species or among communities are possible only when the same characters are used.

The assumption of mathematical models that all the individuals of a species are equivalent in mortality, fecundity, and competitive ability, is clearly ridiculous in plant species where life history characteristics are directly related to plant size and age. These deterministic models depend on a constant environment, yet yearly variations in the environment and unusual events may be important in maintaining species diversity in many plant communities. To compare species, the shapes of the

resource allocation curves should be identical, yet this is an unjustified assumption. Also, resource gradients may be presented after some type of mathematical transformation has been performed, yet how such transformations colour the final description of plant communities is not known.

While bird and lizard communities may be well defined, there is no clear-cut way to determine which plant species belong to a plant community. Decisions affecting which plant species to include in a community will alter the degree of niche overlap: increasing the number of species in a community under study will increase the amount of niche overlap among those species. Despite these technical difficulties, several research workers, such as Werner and Platt (1976), Parrish and Bazzaz (1976), and Platt and Weis (1977), have utilized these mathematical techniques to analyze simple plant communities. These studies are as interesting for the methodological difficulties that are ignored as the actual results obtained.

The traditional approach to the study of plant communities poses many problems and includes many variables, but gives few answers. Every character of the plant species is considered to be important and worth studying. The communities are merely studied in a comprehensive and exhaustive way. Yet mathematical niche theory is not at present developed sufficiently to provide quantitative approaches to problems of plant competition due to the indeterminant and plastic growth of most plants. We are caught between one approach that amasses details and another approach which produces questionable generalizations. We need an intermediate approach which makes moderate generalizations after careful field and laboratory investigation.

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COMPETITION BETWEEN ALPINE GRASSES IN THE LEWIS
PASS – ARTHURS PASS REGIONS

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Alpine grasslands near Lewis Pass differ from those near Arthurs Pass in the presence of carpet grass, *Chionochloa australis*, and the near absence of curly grass, *C. crassiuscula*. *C. australis* has a complex southern boundary from the Paparoa Range in Westland through the upper Taramakau Valley to the Poulter Valley and Puketeraki Range. An hypothesis of competitive exclusion of *C. crassiuscula* (and interference with other species also) by *C. australis* is examined by:

1. study of patterns at the southern boundary, where *C. australis* is invading other communities;
2. study of vegetation composition in equivalent sites on either side of the *C. australis* boundary and
3. study of distribution patterns of the predominant grasses near Lewis Pass with respect to spatial environmental variation.

Possible competitive mechanisms by which *C. australis* gains advantage over other species include:

1. efficient nutrient cycling on poor soils;
2. cooling of the soil by its thick litter layer;
3. antibiotic properties of its litter.

In the light of field evidence, a mechanism involving competition for nutrients seems worthy of further investigation.

ASPECTS OF THE BIOLOGY OF SOME LUMBRICID
EARTHWORMS IN NEW ZEALAND PASTURES

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Lumbricid earthworms, introduced into New Zealand from Europe, are important beneficial soil animals in New Zealand pastures. Their burrowing and feeding activities improve soil quality by mixing the top soil, thereby preventing the formation of a surface peaty layer and facilitating the penetration

of water, air and fertilisers. Not all species of introduced worms are equally beneficial, so it is important to identify species correctly. Fifteen species are included in the most recent guide to the lumbricid earthworms of New Zealand pasture (Martin, 1977), but other species may be present, so reference specimens of any worms found should be retained.

The present investigation into the biology of earthworms was begun because of concern that some insecticides used on pasture are toxic to earthworms and may affect their populations deleteriously. At the MAP Soldier Fly Research Area at Matangi, near Hamilton, the rate of recovery of populations of two species of earthworms, *Allolobophora caliginosa* Savigny and *Lumbricus rubellus* Hoffmeister, was followed after the numbers and biomass of both species were reduced by more than 80 % by cultivation and carbofuran treatment in April 1975. In the treated plots, the numbers and biomass of both species equalled or exceeded those of the untreated plots within 20 months. The soil moisture conditions in summer 1976 were favourable for earthworm survival; under a drier regime it is probable that the recovery of the worm populations would have taken a further year.

Both species of earthworm feed on decaying organic matter and are active only when the soil is moist, but they differ in their methods of surviving dry, summer weather, in their feeding methods and in their effects on the soil. When the soil starts drying out in the spring *A. caliginosa* ceases activity and coils up in cells, but *L. rubellus* can remain active for up to two months longer and does not construct special cells. Both species gain most weight during winter and early spring. Although some sexually mature worms of both species are found in autumn most are found in the spring, when most of the egg capsules are produced. *A. caliginosa* young hatch from the egg capsules in late spring and early summer. Some *L. rubellus* worms emerge during the spring, but others remain in the egg capsule throughout the summer and do not emerge until after the soil is wetted in the autumn. Moist soil stimulates egg capsules of laboratory-reared *L. rubellus* to hatch. Some mature worms die in the spring if food is scarce, but most mortality occurs with the onset of dry weather. Observations by the author on a dairy farm indicate that under extreme drought conditions *A. caliginosa* and *Allolobophora trapezoides* survive better than do *Lumbricus* species.

A. caliginosa burrows extensively in the topsoil where it feeds on decaying plant roots. It also feeds on surface litter and old animal dung. In contrast, *L. rubellus* is a less active burrower and feeds more

on surface litter and fresher animal dung. Because its burrowing mixes the top soil *A. caliginosa* has a more beneficial effect on pastures than does *L. rubellus*.

The fecundity of both *A. caliginosa* and *L. rubellus* was estimated both for the treated and untreated plots at Matangi by dividing the number of egg capsules and newly-hatched worms found in early December by the number of mature (clitellate) worms present in the early spring. Only 4 capsules per clitellate *A. caliginosa* were produced in the untreated plots, compared to 20 egg capsules per clitellate worm in the treated plots. This latter figure is much closer to levels of fecundity achieved in the laboratory. The large differences in fecundity between the two treatments may reflect the amount of food available per worm in the over-populated untreated plots and under-populated treated plots. The number of egg capsules per clitellate *L. rubellus* was about 10 in both treatments, a level well below that achieved in the laboratory but which is about twice as high as *A. caliginosa* in the untreated plots. This low fecundity in both treatments may be because *L. rubellus* is not well-adapted to sheep-grazed pasture.

Preliminary laboratory experiments showed that the rate of growth of juvenile worms was directly related to the amount of organic matter in the soil, though some forms of organic additives were preferred to others, e.g., grass meal to lucerne meal or ground sheep dung. Newly-hatched worms grew on a more restricted range of media than the larger worms. There appeared to be differences between species in their reaction to the type and concentration of organic matter. These problems are now being investigated.

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AGE-SPECIFIC SURVIVAL PATTERNS IN PLANTS

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Survival schedules are summaries of events which happen to individuals. If survival patterns are to be explained in terms of natural selection, they should be viewed as manifestations of life history strategies rather than primarily as phenomena of population

dynamics, the usual approach of plant ecologists. Age-specific survival processes operating at different post-germination stages in the life histories of plants can be related to some general selective forces and to constraints imposed by the nature of the morphology of diverse plants.

The principal units used in the analysis of plant survival are "vegets", the minimum self-sufficient units capable of carrying out all processes that occur in germinated plants. In species with vegetative propagation, vegets correspond to the ramets of Sarukhan and Harper (1973). Non-propagating species also exist as vegets, which in this case are coextensive with the genetical units or genets (all cells with the same genotype). Two broad classes of vegets can be distinguished by their growth habit. In "accumulating" vegets, some or all axial tissues are retained throughout the life of the veget, whereas in "non-accumulating" vegets all tissues are continually replaced and the axial tissues do not become progressively older throughout the life of a veget.

The three types of survivorship curves recognised by Deevey (1947) and many subsequent authors have limited usefulness because:

1. they have been used in widely varying senses and therefore lack precision,
2. the conditions they represent are often characteristic of only a limited portion of the lifespan,
3. they are not sensitive indicators of short-term changes in survival since they are based on cumulative data.

An examination of changes with time in survival probabilities (for a constant time interval) is often superior to survivorship curves for revealing age-specific survival patterns.

Three elementary conditions of age-specific survival, which often relate to only part of the life cycle, are recognised. (Any of these conditions may have fluctuations of greater or lesser magnitude superimposed upon them by unique or repeating events):

1. *Maturescence-* an overall increase in survival probability preceding the period of maximum probability of survival. Maturescence is a near-universal characteristic of vegets originating from seed. Vegets originating by propagation usually do not exhibit matuscence.
2. *Age-independent survival-* the absence of any persistent and regular change in the probability of survival over a part or all of the lifespan. Age-independent survival appears to be associated with vegets that maintain a constant

ecological status as time progresses, and in particular it is characteristic of DOD-accumulating vegets.

3. *Senescence*-an overall decrease in survival probability after the period of maximum probability of survival. The theory of Williams (1966) predicts that senescence is universally expected in organisms with a soma that is essential to reproductive success but is not directly transmitted to either sexual or asexual offspring. According to this theory, genes with favourable early effects and unfavourable later effects are advantageous overall but bring about senescence as a secondary consequence. Accumulating vegets have a soma of the type specified by Williams, and indeed some accumulating vegets (particularly those which are monocarpic) do show senescence. But the limited data available suggest that some polycarpic accumulating vegets not only lack senescence but show maturescence up to the oldest observable age classes (e.g., balsam fir and hemlock trees, Hett and Loucks, 1976). In these cases, an improving ecological status associated with increasing dominance may override selection which results in senescence.

A number of species which have been investigated show phases of both maturescence and senescence. The survivorship curves of such species have in the past been misleadingly interpreted as either Deevey Type I curves (when most deaths occur during the final phase of senescence, e.g., *Bouteloua iliformis* interpreted by Sarukhan and Harper, 1973) or as Deevey Type III curves (when the initial phase of maturescence predominates, e.g., *Sedum smallii* and *Minuartia uniflora*, Sharitz and McCormick, 1973).

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THE POTENTIAL ROLE OF CHEMOSTERILANTS IN VERTEBRATE PEST CONTROL

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The use of chemosterilants for effecting control of vertebrate pest species, particularly the European rabbit (*Oryctolagus cuniculus*) was investigated between 1973 and 1976 as part of a Ph.D. programme. Four compounds that had shown long-term activity from a single oral dose in other species were evaluated, but even at doses of up to 100 mg/kg body weight their effect on rabbit reproduction was limited. The longest effective duration achieved was six months, with most animals breeding successfully within three months. Simulated field trials with the most effective compound were inconclusive, with no significant effect on the growth of the treated populations.

The utilization of chemosterilants in the control of vertebrate pest species is still in its infancy, although the potential benefits to be derived are considerable. Some of the most significant theoretical benefits are that the reproduction of non-treated animals may be restricted by their mating with sterile individuals; that there is unlikely to be a compensatory breeding response following treatment; that non-reproductive animals occupy space and tend to restrict immigration, and that the effect of the treatment is prolonged. However, compounds currently available have been developed, almost without exception, for use in human contraceptives and lack many of the properties required for use in wild animals. Conversely, compounds known to have desirable properties have usually been found to have undesirable side effects, particularly teratogenic or mutagenic properties, and pharmaceutical companies have been very reluctant to develop them when their commercial viability is doubtful. In fact, for most compounds even registration could be unlikely.

Current research into the development of long-acting, single-dose contraceptives for use in wild animal control is very limited. The likelihood of significant developments in the use of chemical means of artificially controlling the reproduction of wild or feral vertebrate pest populations is small. Further, the cost of these materials in the quantities required is currently very considerable and would make large operations prohibitively expensive when compared with the cost of the more conventional poisoning operations.

The development of a chemical suitable for field

use is possible if the economic viability of such a programme could be guaranteed, or if sufficient public demand for alternative control methods to the use of toxic materials arose.

FIORDLAND SAND DUNE VEGETATION AND ITS MANAGEMENT FOR CONSERVATION

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Botanical studies of sand dunes in Fiordland National Park were prompted by the lodging of mineral prospecting warrant applications for some of the dune areas. It became apparent that dunes in Fiordland, because of the absence of agricultural modification and their isolation from weed sources, still hold good examples of native dune vegetation, this having largely disappeared in many other parts of the South Island. Consequently a wider botanical survey has been initiated, aimed at documenting the dune vegetation and its condition, identifying threats to the vegetation, and advising the Park Board on management.

The larger dune systems in Fiordland are those at Martins Bay, Transit Beach, Sutherland Sound, Catseye Bay, Coal River and in Preservation Inlet at Te Whara Beach, and there are about 30 smaller dune systems. The flora is quite variable: 14 typical sand dune species occur on average at less than half of the 13 dunes studied so far. A typical vegetation sequence is as follows:

1. foredune with *Desmoschoenus spiralis*, *Poa tridoides* and *Calystegia soldanella*,
2. dune crests with scattered low scrub (e.g., *Olearia avicenniaeefolia*, *Cortaderia richardii*, *Phormium tenax*), older dune surfaces with low forest of broadleaved tree species (e.g., *Hedycarya arborea*, *Myrsine australis*, *Griselinia littoralis*),
4. oldest dunes with taller forest, mainly *Metrosideros umbellata* and *Weinmannia racemosa*.

Twenty-four weed species have been recorded from sand dunes, the most troublesome being marram grass, gorse and Californian thistle. In addition to these weeds, other threats to the dune vegetation are fire, browsing by deer, mineral prospecting and mining.

ASPECTS OF THE ECOLOGY OF BELLBIRDS ON TIRITIRI ISLAND

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Research on the social organization, behaviour, and feeding ecology of the New Zealand bellbird *Anthornis melanura*, is being carried out as part of a programme testing a model which relates social organization to the predictability of resources, especially food. The study is being undertaken on Tiritiri Matangi Island near Auckland and is concentrated in a 4 ha area of forest which has a continuous canopy of kohekohe, mahoe, pohutakawa, taraire, mapou, manuka and kanuka. The understorey is open, but some areas have dense growths of *Coprosma rhamnoides*. A puriri tree, centrally located in this forest and the largest of two on the island, is an important nectar source for much of the year. The forest is gridded at 15 m intervals so that birds may be accurately located on maps. Most bellbirds using the study forest are banded and their position and activity are recorded whenever they are sighted. Feeding records outside the puriri tree are taken at 5 sec intervals.

Bellbirds are sexually dimorphic, although young males have the same facial stripe as females. Bellbirds are one of the three New Zealand honeyeaters, but in addition to nectar they take considerable numbers of insects and soft fruits. Feeding records, excluding those from the puriri tree during autumn and winter, indicate that nectar and fruit comprise approximately 50% of the female diet but more than 60% of the male diet. Inclusion of feeding records from the puriri would increase the significance of these foods further. For the remainder of the feeding observations, bellbirds were seen to take insects or to be foraging in trees lacking both flowers and fruit. Foraging occurs in the canopy, subcanopy and shrub layer, but rarely on the ground.

Mapping all sightings of the 12 resident male and female bellbirds produces home ranges which, although localized in different parts of the forest, extend to the puriri. Home ranges overlap considerably. In mid-winter, when highly localized patches of kohekohe flower were present, bellbird ranges centred on these rather than on the puriri.

In the puriri, bellbirds feed mainly on the side of the tree which is directed towards their home range. Within the tree, there is a linear hierarchy amongst the males and all females are subordinate to any male. When there are low flower numbers in the

puriri, females are excluded from the tree. At such times few other flowers are available in the forest and this may explain why insects form a greater proportion of the females' diet. In addition to the residents of the study forest, more than 30 other birds are known to feed in the puriri.

Both male and female bellbirds sing distinct songs which are used in countercalling against members of either sex. This may be a means of regulating the use of areas of overlap. Songs are given while feeding in all forest tiers. As expected for species singing within forest areas (Morton, 1975), all songs have a preponderance of pure frequency notes and are of relatively low frequencies (1000-4000 Hz).

Bellbird behaviour contrasts with that of the tui (a second honeyeater on the island) which appears to be highly territorial. Song is predominantly by the male, is sung from canopy posts or in flight and is of mixed and pure notes with high and low frequencies (1000-13 000 Hz). Research on both species is continuing.

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PROGRESS AND TECHNIQUES IN THE MANAGEMENT OF THE NEW ZEALAND FALCON(*Falco novaeseelandiae*)

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A captive breeding project was undertaken for two reasons: (a) to assess the practicability of breeding New Zealand falcons in captivity using techniques developed overseas, and (b) to observe the courtship behaviour of this species.

In selecting birds for captive breeding, individuals which are imprinted on their own species must be chosen, otherwise they will not form a pair bond. Additionally, there is mounting evidence that falcons imprint, at least partially, on the nest site in which they were reared, so that it is necessary to provide at least one nest site of the correct type. If possible, both parents should have originated from the same basic type of nest; this avoids disagreement during nest site selection in late courtship.

The diet fed to the falcons was mainly chunks of whole brown hares (*Lepus europeaus*), rabbit

(*Oryctolagus cuniculus*) or dead domestic turkey chicks from a commercial hatchery. Wild birds were fed to the falcons infrequently because of the danger of pesticide contamination. During spring, food was fed in 10-20 g lots, 4-12 times a day, to promote courtship feeding.

The aviary was constructed of untreated pine poles and measured 15.2 x 17.6 x 3.2 m. Two of the side walls were of corrugated iron and the other two were a dense laurel hedge lined with chicken netting. The roof was of chicken netting suspended by wires from above. The aviary contained six fruit trees and a row of young pine trees. Ten assorted nest sites, mostly earth-filled ledges, were provided. A concrete bath was made in a tractor tyre and kept filled by a hose from outside. Two observation hides were used and were equipped with observation slits, camera ports and food ports so that once the falcons were placed in the aviary they saw no human beings.

An average aviary, with a volume of about 300 m³, is only about 0.001 % of the size of the nesting territory of a pair of wild New Zealand falcons. Three factors may prevent breeding in small aviaries:

1. If a falcon is placed inside an aviary which is smaller than its normal psychological territory and it sees an intruder within that territory, the falcon is unable to sally out and may therefore be stressed. This stress causes overproduction of adrenalin, which is antagonistic to follicle-stimulating hormone and thus inhibits breeding. This problem is overcome by providing opaque-walled aviaries.

2. Stimulating courtship flights require a certain amount of fast flying. A New Zealand falcon requires about a 7-8 m circle to turn at speed. Aviaries with a diameter of less than this hamper courtship, lowering stimulation and the likelihood of breeding.

3. The individual distance of two unpaired wild falcons is about 2-5 m. Thus, if two strange falcons are placed in an aviary smaller than 5 m in diameter one may dominate the other too much for breeding to take place.

During the 1975 season a wild-caught adult female falcon and a juvenile male obtained as a nestling, courted and scraped a nest but did not lay, presumably because the male was still immature and the female not fully acclimated to captive conditions. A nestling falcon placed in the aviary in December 1975 was adopted and raised by the male but not by the female. In November 1976 the female laid three eggs; one disappeared and the other two were removed and artificially incubated at 37.5°C egg-top temperature and 50-60% relative humidity, and turned 3-8 times daily in a forced-air incubator. One

egg embryo died just before pipping. The other egg hatched and the chick was hand-raised on small pieces of meat. Although the chick appeared healthy and doubled in weight it died suddenly at nine days old of unknown causes.

BREEDING OF THE GREY WARBLER AT
KOWHAI BUSH, KAIKOURA

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Breeding of the grey warbler (*Gerygone igata*, Muscicapidae: Malurinae) was studied at Kowhai Bush near Kaikoura (South Island). The sexes look alike, but were distinguished behaviourally since only the male sings, and only the female builds nests, incubates eggs and broods young. Observation of colour-banded birds showed adults to be highly sedentary, remaining during winter in much the same area that was defended against conspecifics in the breeding season. The species is monogamous and solitary-nesting, the nest being enclosed and pensile. In the simply-structured, low-diversity habitats dominated by kanuka (*Leptospermum ericoides*), territories were 0.6 ha on average.

Examination of 38 occupied nests during the summer of 1976-77 indicated a breeding strategy different from that regarded as typical for small song-birds of the north temperate zone.

Length of breeding cycle. Females took at least 10 days, and up to 3 weeks, to build the first nest, and there was a delay of about 6 days before laying. Laying in the population began asynchronously over about five weeks from early September. The incubation and nestling periods were long (respectively 19.3 and 16.5 days on average; ranges 17-21 and 15-18 days). Fledged juveniles were fed for up to five weeks, mostly by the male in the case of first broods, while the female built the second nest. The delay between fledging of the first brood and laying of the second clutch was two to six weeks. Given the average breeding cycle of 42 days from laying to fledging, the initial asynchrony and the delay between broods, pairs probably cannot raise more than 2 broods in a season, even though it extends from August to January.

Laying interval. Eggs were laid every second day so that it took seven days to complete a clutch, which was nearly always four. Except in the grey warbler

and some of its Australian close relatives, laying at 48-hour intervals is unknown among small song-birds (sub-Order Oscines), which typically lay on consecutive days.

Weight of nestlings. Unusually for a passerine, the average adult weight (6.4 g) was consistently exceeded, by up to about 30%, during the growth of each nestling. There was a recession in weight before fledging.

The grey warbler's breeding strategy is different from that of most other song-birds. For example, in raising a *small* family slowly, the warbler is unlike the species with safe nests in the north temperate zone which raise *large* families slowly. However, in looking beyond passersines, there are four factors which the warbler shares with swifts and procellariiform seabirds. Namely, the safe nest (on two scores for the warbler, which, as well as having a covered nest, has evolved in recent isolation from snakes and mammalian predators), the small clutch-size, the long nestling period and the high weight of nestlings relative to that of adults.

Ornithologists debate two opposing views on the evolution of the reproductive rate of birds. One school of thought holds that reproduction is always maintained by natural selection at the maximum level which produces adequately nourished young (e.g., Lack, 1966). On this view the warbler's strategy can be explained, as for swifts and seabirds, as a response to a scarcity of food. The small clutch-size is an adaptation to the few young which can be successfully reared on the available food, and young must develop slowly. An extended life in the nest is only possible because of safety from predators, and nestlings acquire reserves as an adaptation to likely periods of starvation.

Shortage of food for an insectivore in New Zealand's mild and equable conditions seems incongruous. However, Ashmole (in Lack, 1968) suggested that in the tropics seasonal changes in the food supply are not marked, and that the adult population of birds may always remain close to the limit set by food. Hence there is difficulty in finding the extra food needed to raise young. I believe that similar conditions may exist for the warbler at Kowhai Bush.

The observations are just as plausibly explained, however, by contrary arguments that the reproductive rate of birds is adjusted to balance mortality (e.g., Skutch, 1967). In these terms the warbler's strategy could be interpreted as a series of adaptive restraints to reproduction. The building of an elaborate nest, and incubation by the female alone, the small clutch-size, and the overall slowness of breeding could be "deliberate" devices to prevent over

population in a mild and stable environment with ample food.

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ECOPHYSIOLOGY -- LEAF ELONGATION AND
PHOTOSYNTHESIS --IN SOME ALPINE SNOW
TUSSOCKS FROM CENTRAL OTAGO

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In 1960, reciprocal transplants were established for snow tussocks from low (910 m), mid (1220 m) and high (1590 m) altitude sites on the Old Man Range, Central Otago. Mature tussocks of *Chionochloa rigidula* (low, mid) and *C. macra* (high altitude) were subdivided and clone members (ramets) reciprocally transplanted to "gardens" at each of the three altitudes. Marks' (1965) data on

growth and flowering behaviour clearly established that the three populations were genetically differentiated (*C. macra* was not formally recognized as distinct until 1970). One aim of the present study was to investigate the extent to which residence for a long period (14 years) at two alternative sites may have modified the response of the different clone members to further reciprocal transplanting. In December 1974, clone members of six original plants from each population at each of the three sites were quartered and distributed among the three mountain sites and the Botany Department garden in Dunedin (an operation involving 216 ramets in total-12 for each of the original transplants).

New leaf production, flowering behaviour and leaf elongation were measured for two seasons, 1975-76 and 1976-77. The seasonal course of photosynthesis was determined throughout one season for whole plants randomly chosen from within the resident snow tussock population at each site. These plants had been established in plastic buckets so they could be transferred with minimum disturbance to and from Dunedin for short periods for the gas exchange measurements. The photosynthetic capacity of the same eight tillers in each of two plants from each site was determined monthly under constant conditions (15°C, PAR > 400 E m⁻² s⁻¹, > 70% R.H.). For four plants of *C. rigidula* (two from each site), the response of photosynthesis to variation in temperature (-5°C to 35°C) was measured in May 1977 to determine their optimum photosynthetic temperature.

TABLE 1. Mean seasonal cumulated leaf elongation (cm) averaged over two seasons 1975-76 and 1976-77.

Origin	Pretreatment	1960-74 Site		1974-77 Site		Means	
		High	Mid	Low	DN	Origin ¹	Pretreatment ²
1590 m	High	19.8	30.9	34.4	97.6	38.0 ^a	49.4 ^c
	Mid	19.9	21.8	25.8	63.7		
	Low	19.1	35.6	30.4	67.3		
1220 m	High	23.2	40.2	42.8	82.8	42.58 ^{a,b}	36.5 ^d
	Mid	21.7	22.9	32.7	68.2		
	Low	23.9	38.9	38.1	74.1		
910m	High	29.2	55.6	57.5	88.4	50.8 ^b	45.4 ^c
	Mid	20.7	28.3	38.1	74.5		
	Low	28.2	46.3	47.7	95.4		
1974.77 Site Mean ³		22.8 ^e	35.6 ^f	38.6 ^f	78.0 ^g		

1. Mean of 12 values from within each origin.

2. Mean of 12 values from within each pretreatment

3. Duncan's New Multiple Range Test. Letters in common indicate non-significant differences (P = 0.05) between means within each of the three groups (origin, pretreatments, sites).

Results for mean seasonal leaf elongation (Table 1) show that differences associated with clone origin were highly significant, with clinal variation apparent. These genetic differences show that initial differences in performance (1961-63) could not have been due to differences in food reserves as tentatively suggested by Mark (1965).

Comparison of leaf elongation of snow tussock ramets at the four sites revealed to what extent environment controlled growth. Differences were highly significant, some being due to changes in length of the growing season (Mark, 1965).

Clones pre-treated at the mid-altitude site between 1960 and 1974 showed a modified response to further transplanting. There was no significant effect of pre-treatment at either the high- or low-altitude site. These data suggest that when snow tussocks which have been resident for a long time in a different environment are grown alongside plants which have not previously been shifted, there is no significant difference in the response to transplanting of the two groups.

Seasonal photosynthesis followed the course of seasonal leaf elongation. The photosynthetic capacity reached a maximum of c. 7.0 mg dm⁻² hr⁻¹ by December and varied little between sites. This value comes within the reported range for herbs from shaded rather than sunny habitats (Sestak *et al.*, 1971) but exceeds those so far reported for *Chionochloa* species (Scott and Menalda, 1966, 1970; Mark, 1975). This is, however, the first report of photosynthesis measured in snow tussocks recently transferred from the field.

Winter photosynthetic rates varied between sites. Negligible photosynthesis was detected in high-altitude site plants (*C. macra*) between July and August, but for mid- and low-altitude site plants (*C. rigida*) the rate ranged between 1.0-1.5 mg dm⁻² hr⁻¹.

Temperature optima for photosynthesis varied between 10-15°C with a flattened peak. This is slightly higher than that reported by Mark (1975) and Scott and Menalda (1970) for several *Chionochloa* species, but is below the optima reported by Mooney *et al.* (1964) for several Northern Hemisphere plants from a greater range of elevation.

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STREAM INVERTEBRATE COMMUNITIES IN A WEST COAST BEECH FOREST CATCHMENT

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Since early 1976 I have been studying stream invertebrate communities in the Devils Creek and Oriental Creek catchments south of Reefton on the West Coast of the South Island (NZMSI, S38 ca. 337234). The headwater streams drain predominantly silver beech-podocarp forest and have hard, slightly acidic waters. Benthic sampling has been carried out monthly at four sites, two in forested first and second order streams, and two in a larger, open third order stream, Devils Creek, which is a tributary of the Inangahua River.

Gut contents of the more abundant insects are being examined to determine the trophic relationships of the fauna. Stream invertebrates can be assigned to four functional categories on the basis of their feeding methods: (1) shredders, or coarse-particle detritivores, (2) collectors, or fine-particle feeders, which include filterers and browsers, (3) scrapers, which remove diatoms and organic debris from rocks, and (4) predators (Cummins, 1974). These categories are not mutually exclusive and some species can be included under two or more headings. A high proportion of the species examined in this study feed primarily as collectors, whereas shredders are scarce even at the forested sites. This is particularly interesting as large-particle detritivores

are often abundant in small forested streams in the Northern Hemisphere.

Hynes (1975) has asserted that shredder feeding "lies at the base of almost all the biotic activity in the water", and by this activity leaves are broken down into the fine particles upon which collectors are assumed to feed. If the shredder pathway is relatively unimportant in New Zealand streams, other energy flow pathways must have greater significance. Gut content analyses suggest that some collectors and scrapers remove organic material, including fine particles and leaf fragments, from the surfaces of rocks. Relatively few diatoms are ingested by most species, although they do make some contribution to the diet of stoneflies especially at the open, downstream sites. Another pathway by which organic matter could become available to collectors is through the uptake of dissolved and colloidal organic matter by microflora associated with bottom sediments (Lock and Hynes, 1975, 1976). Dissolved organic matter can comprise a major portion of the energy input into forested streams (Fisher and Likens, 1973) and enters both in groundwater flows and as leachate from wetted leaves.

Although the headwater streams being studied are in beech-podocarp forest, the riparian (streambank) vegetation is dominated by fuchsia (*Fuchsia excorticata*) trees. Autumn-falling fuchsia leaves contribute a large proportion of the annual leaf fall entering the forested tributaries. Leached organic compounds from these and other leaves are probably taken up by micro-organisms which form part of the organic layer on stones and other surfaces (Madsen, 1972). These bacteria and fungi are then ingested by collector and scraper organisms. This is probably an important food pathway in many New Zealand forest streams as low shredder densities are not uncommon (D. Cowie, M. J. Winterbourn, unpublished surveys). Our fauna lacks several Northern Hemisphere families in which shredders are common (Winterbourn, 1976), and many of the species whose larvae can act as shredders, although widely distributed, are not often abundant. These include the trichopterans, *Triplectides obsoleta*, and several species of Oeconesidae, as well as some of the larger stoneflies (*Zelandoperla feneustrata*, *Megaleptoperla grandis*, *Austroperla cyrene*). Establishing the nature and possible origin of the food utilized by stream invertebrates is a principal objective of the present study.

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THE ALLELOPATHIC POTENTIAL OF KAHIKATEA
A PROGRESS REPORT

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Experiments were begun in 1973 to determine whether or not mature native conifers were capable of suppressing their own progeny by producing toxic chemical substances. Such allelopathic self-inhibition is known as autotoxicity. A secondary aim is to see if one conifer species will suppress by similar means the progeny of another within the same plant community; an apparently widespread allelopathic phenomenon. These experiments were initiated to help explain one of the anomalies in New Zealand conifer-hardwood forests, namely, the scarcity of conifer seedlings, saplings and pole-size individuals, and the predominance of mature and veteran trees; the so-called regeneration gap.

From the twenty species of New Zealand conifers we chose kahikatea or white pine (*Dacrycarpus dacrydioides*; also known as *Podocarpus dacrydioides*) to begin with, as this widely distributed species shows the above regeneration pattern as well as any other, and there are accessible local populations to study. In addition, kahikatea flowers fairly regularly,

sets abundant seed in the same season, and this seed germinates readily the following spring, thus giving a plentiful supply of seedlings for experiments. In nature these seedlings may occur in great numbers on the forest floor following good seed years, so that germination is no barrier to regeneration. However, in undisturbed forest most of these seedlings die in the first year or two. From time to time a few will be recruited to fill canopy gaps caused by the death and/or windthrow of older trees, but vigorous regeneration seems to take place only when large areas of forest are destroyed by fire, felling, or other large-scale site disturbances.

To test the presence of toxic substances, water-soluble extracts were made of the fresh green leaves, bark, roots, litter, and soil associated with mature kahikatea trees. These were obtained by soaking 300 g of material overnight in 600 ml of distilled water. The effect of the supernatant of each extract and of the combined extracts was compared with that of distilled water and a nutrient solution on first-year kahikatea seedlings growing in natural daylength and at room temperature. Almost 50% of the seedlings died in the litter and combined extracts, and 100 % died in the fresh green leaf extract. This experiment was repeated and similar results were obtained. The green leaf extract in

particular proved to be very toxic; in this extract seedling leaves turned brown, roots failed to grow, and death occurred within 30 days.

First-year kahikatea seedlings were then tested in autoclaved and non-autoclaved solutions of the fresh green leaf extract, with and without an added nutrient solution. This was followed by tests on first-year and older seedlings with fresh green leaf extract, and leaf extract that had been stored at cold temperature for 20 months. Again the leaf extract proved to be very toxic to all seedlings, irrespective of added nutrients, and its activity did not diminish with cold storage.

In a further line of experiments, kahikatea seedlings were grown in water-soluble extracts of fresh green leaves, bark, roots, litter and soil associated with mature trees of matai or black pine (*Podocarpus spicatus*) and totara (*Podocarpus totara*). Once again the leaf extracts proved to be highly toxic and most of the seedlings died.

So far, partitioning of the green leaf extract of kahikatea with Butanol has not succeeded in further separating the toxic factor, although phenolic substances are probably implicated. Further work along these lines is proceeding with kahikatea and other native conifers.