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Insect predation of seeds of native New Zealand woody plants in some central South Island localities

JON J. SULLIVAN
COLIN J. BURROWS
Department of Plant and Microbial Sciences
University of Canterbury
Private Bag 4800
Christchurch 1, New Zealand

JOHN S. DUGDALE
Manaaki Whenua - Landcare Research
Private Bag 92170
Auckland, New Zealand

Abstract Samples of fruit collected from woody plants in central South Island lowland forests, showed that nine species were more or less heavily affected by insect seed predation (more than 10% of seeds and up to 63% eaten in some samples). One obligate seed-eater each occurred in seven of these; the rest had two or more. Two were also attacked by facultative seed-eaters. A further eight species of plants were affected to a lesser degree by obligate or facultative seed-eating insects. Moth larvae from nine families and ten genera are the main seed eaters, but weevils are important for some plant species.

Keywords native woody plants; seed predators; pre-dispersal feeding; Lepidoptera; Coleoptera (Curculionidae)

INTRODUCTION

Seed loss through predation by animals is one of the important environmental influences affecting the sizes of seed crops of wild plants (Janzen 1969, 1971; McKey 1975; Jermy 1984; Crawley 1992). In the New Zealand context seed predators of native plants may include native and introduced birds, introduced rodents, and native insects. Seeds may be affected while they are on the parent plant, or after they have been dispersed. This account focuses on insects as seed eaters and on pre-dispersal feeding. Relatively little has been published on the subject in New Zealand. The original descriptions of many of the insects concerned record their habitats, so the entomological systematics literature contains some information (e.g., that summarised by Hudson 1928, 1939).

One of us (J.D.) has been gathering information on the insects in relation to their plant hosts over a long period (cf. Dugdale 1975, 1988). There are also relevant data in ecological papers that describe the plant-predator relationship (e.g., Beveridge 1964; Mark 1965; Molloy 1975; White 1975; Spence 1990; Kelly et al. 1992). Only a few of these deal with predation of the seeds of woody plants.

The present study was undertaken to determine which plant species in some central South Island forests were being affected by seed predators; to identify the insects concerned; to carry out a pilot study on the quantities of fruit and seeds affected; and to record anything relevant on the insect life histories and behaviour. During the summer 1993–94 J.S. undertook some systematic sampling at sites on western Banks Peninsula, while C.B. sampled more widely in forests on Banks Peninsula, in Riccarton Bush (Christchurch), on the Kaikoura coast, and in Westland, when opportunity arose (Fig. 1). Insects were identified by J.D.

The forests that were investigated are all at relatively low altitude (10–500 m) and comprise diverse mixtures of angiosperm and gymnosperm woody species. The tree, shrub, and vine species which were examined included those that were known to be affected by seed predators from previous seed-trapping studies (Burrows 1994) and sampling for seed germination studies (C. J. Burrows unpubl. data). During the study samples were also taken from various other species that were noticed to be affected by insect seed predators. J.D. knew of most of the insect taxa involved in relation to their specific hosts (cf. Dugdale 1975) but this study is one of the first

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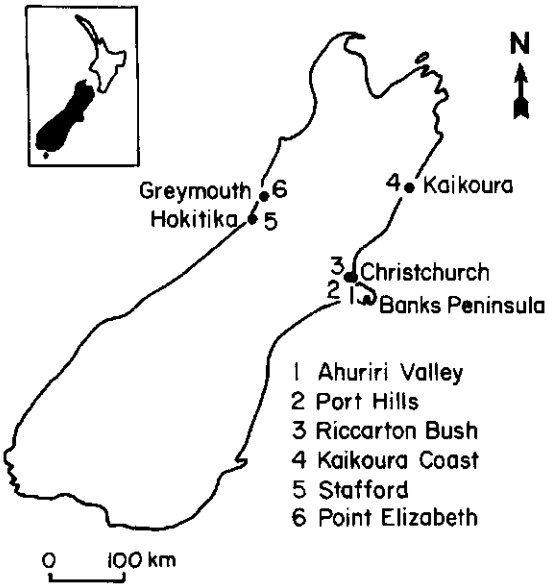

Fig 1 Location of sampling sites.

attempts to estimate the quantities of fruit and seeds affected for native woody plants.

This account mainly concerns insect taxa which appear to be predominantly seed-eaters. In some cases the flowers and the pericarps and other fruit tissues are also eaten. Some generalist herbivore insects that may eat fruit and seeds if they encounter them are also noted.

The specific identity of some of the animals is uncertain at present, either because the taxonomy is incomplete, or because it is difficult to identify some taxa from larvae or pupae. Authorities for the plant species listed below (cf. Table 1) are Allan (1961) and Connor & Edgar (1987); those for Lepidoptera are as in Dugdale (1988); for Hemiptera and Coleoptera they are as listed in current arrangements in the New Zealand Arthropod Collection (NZAC), Landcare Research, Mt Albert, Auckland, New Zealand.

MATERIALS AND METHODS

Sampling and sample treatment

At each site a search was made for individual trees, shrubs, or vines which were accessible (with the aid of a small ladder and pruning tool) and bore sizeable crops of young, green fruit affected by seed predators. Many of the species sampled are dioecious (see Table 1 for sex distributions). Samples of up to a few hundred fruit were placed in new plastic bags, which were labelled and sealed with rubber bands. Usually one or two adjacent plants were sampled; fruit were gathered as widely over the plants as possible. The samples were subsequently checked for infestation and for most samples a count was made of the numbers of fruit damaged and seeds which had been destroyed by the predators. The samples were then rebagged and sent by Fastpost to J.D. in Auckland. Some isolates were sent in vials. If delays were unavoidable samples were kept in a refrigerator before mailing. In practice most samples were received by J.D. within 5 days of collection.

Insect rearing

Larvae and host material were placed in large plastic pots and either left undisturbed until adults appeared, or pupae were recovered and reared on dampened paper towels in smaller pots. Not all rearing was successful; there were problems with mould and, in one instance, larvae had escaped in the mail. Larvae and reared adults have been placed in the New Zealand Arthropod Collection.

RESULTS

The results are summarised in Table 1 and elaborated on, species-by-species, for host plants and insects.

Alectryon excelsus

The paniculate infructescences of female trees bear up to 20 capsules. They are maintained on the tree for about a year, gradually increasing in size, to c. 1.8 cm diameter. In late summer–autumn the top half of the capsule is shed revealing a single, black, shining seed imbedded in a scarlet aril. Occasional capsules have two seeds.

In December 1993 small numbers of sub-mature, unopened fruit from lower branches of two trees at Ahuriri Valley Bush contained advanced larvae of *Conopomorpha cyanospila* (one per seed) or had been damaged by the larvae. In the capsules with pairs of seeds only one was found to be damaged. Some 30% of freshly fallen, unopened fruit beneath the same trees contained larvae or had similar damage. Apparently some of the damaged fruit, but fewer undamaged fruit, are shed; this high amount of infestation thus may exaggerate the actual amount of damage experienced on the tree.

A sample of mainly unopened capsules from the same trees in mid January contained no living *Conopomorpha* larvae, but 6% of the seeds had been damaged. A canopy sample of opened fruit from another part of Ahuriri Valley Bush, in February 1994, had 9% damaged seeds but no living insects. Similar amounts of damage to seeds were noticed from trees at Akaroa in 1989 and Kaikoura in 1994 (C. J. Burrows unpubl. data). The actual amount of damaged seeds as a proportion of all seeds on the tree may have been lower, as birds (mainly kereru, *Hemiphaga novae-seelandiae*) had been feeding on the opened fruit and may have selectively removed some undamaged seeds; empty capsules were present. The damaged seeds and their fleshy arils are often markedly smaller than those not affected. The points of uncertainty need to be examined by frequent monitoring, in comparison with controls, after bagging fruit to exclude birds.

Conopomorpha larvae enter young *Alectryon* fruit through circular holes drilled in the capsule and seed walls. They tunnel into the contents (mainly the embryo with very large cotyledons) killing the seeds. They emerge to pupate in cocoons spun on the underside of the leaves. Little is known of the duration of pupal and adult phases, but as *A. excelsus* fruits heavily at irregular intervals there may be a long adult life period. Further study is needed of the insect's life history in relation to the fruiting periodicity of the tree.

Calystegia tuguriorum

This suffrutescent vine, with flowers borne singly, and present on the plants Dec–Mar each year, has indehiscent capsules, 1 cm × 0.8 cm, each containing up to four seeds. The seed eaters are the larvae of *Stathmopoda skellonii,* often a plant-detritus feeder. Early-stage larvae feed on the dying calyx, then penetrate the base of developing green capsules often eating all of the seeds. Later-stage larvae attack the mature, hard-walled brown capsules and enter the extremely hard-coated orange seeds at the micropylar region. The insects leave the capsules to pupate by late summer. From one plant in Ahuriri Valley 45% of the mostly green fruit sampled in mid January 1994 were infested with larvae. This contrasts with 57% of fruit with damaged seeds (but no larvae present) in a mid February sample. In February samples from the Port Hills, 45% of mature, brown fruit had similar damage but younger green fruit (n = 11) had none.

Some damage is caused to *Calystegia* capsules by mining of their walls by the small larvae of the moth *Bedellia somnulentella*. It is not known whether this has adverse effects on seeds. This animal may, in fact, assist in seed dispersal by weakening the capsule walls, which eventually collapse. Seed dispersal otherwise is slow, as the tough-walled capsules often remain on the parent plant for up to a year.

Hoheria angustifolia

The flowers of this tree are borne in clusters of from two to at least five. Ovules in each flower develop into five free, winged single-seeded fruit, dispersed by wind in autumn. The seeds, at one end of the fruit, are tightly enclosed by the pericarp (i.e., are achene-like) and set in a circle around the receptacle. The "achene" is c. 2 mm long. Flowering tends to be episodic, with a heavy flowering year being followed by several years when flowering does not occur or is meagre (C. J. Burrows unpubl. data). In Ahuriri Valley, where flowers and fruit develop about a month earlier than on the summit ridge of the Port Hills, a mid February sample of full-sized but green seeds contained the larvae of *Anisoplaca achyrota*. Late February samples from the Port Hills, with immature green seeds, contained small larvae of two moth species, *Anisoplaca* sp. and *Heterocrossa* sp. cf. "*morbida*", and also three species of weevil, *Peristoreus* spp. The *Anisoplaca* larvae eat their way through the pericarp and seed coat of one seed and devour its contents, then progressively work their way around the entire circle of seeds. It is not clear what type of seed damage, or how much, is contributed by the other animals.

Prior experience from seed trap results (Burrows 1994) shows that up to 40% of the trapped seeds from isolated *H. angustifolia* trees in forest may be destroyed by insects. In several years prior to 1993–94, during attempts to collect ripe seeds for germination tests from heavily-fruiting *H. angustifolia* trees at forest margins on the Port Hills and in Riccarton Bush, it was found that none had escaped predation. A Riccarton Bush sample in April 1994 was similarly affected. The *Hoheria* seed predator complex warrants further, more intensive and long-term study, to determine the full ecological implications.

Ileostylus micranthus

This is a common hemi-parasite on *Sophora microphylla*, *Coprosma* spp., *Hoheria angustifolia*, and other species, at Ahuriri Valley Bush. Its bisexual flowers are borne in panicles of up to 10. Green fruit (6 mm × 4 mm) are present from January to April. In one sample the Loranthaceae-spe-

Table 1 Samples of fruit and seeds eaten by insects, from central South Island lowland forest localities. Most insect identifications are from larvae; a few are from pupae or (weevils, Hemiptera) adults. 1, obligate seed-eater; 2, obligate fruit-eater which also eats some seeds; 3, specific (monophagous) herbivore which may eat host fruit; 4, generalist (polyphagous) herbivore which may eat host fruit; 5, generalist detritivore (on dying/dead host tissue) which may eat host seeds. Collection sites: A, lower branches; B, upper branches: C, ground. * (*Calystegia tuguriorum*) minimum estimate. Seven damaged fruit had lost all of their seeds so that the number eaten is unknown.

Plant species	Family	Sex distribution	No. of seeds per fruit	Collection site	Date of collection	Percentage of fruit affected	Percentage of seeds damaged	Insects feeding on fruit and seeds (Order : Family)
Ahuriri Valley Bush, western Banks Peninsula								
Alectryon excelsus	Sapindaceae	dioecious	1	A	Dec 1993		1 (n = 100)	*Conopomorpha cyanospila* [1]
				C	Dec 1993		30 (n = 100)	(Lepidoptera : Gracillariidae)
				A	Jan 1994		2 (n = 102)	
				A	Jan 1994		6 (n = 90)	
				B	Feb 1993		9 (n = 400)	
Calystegia tuguriorum	Convolvulaceae	bisexual	4	A&B	Jan 1994	45 (n = 41)	not counted	*Stathmopoda skellonii* [5]
				A&B	Feb 1994	57 (n = 42)	47 (n = 70)	(Lepidoptera: Oecophoridae)
				A&B	Jan 1994	23 (n = 48)		*Bedellia somnulentella* [3]
								(Lepidoptera: Lyonetidae)
Hoheria angustifolia	Malvaceae	bisexual	5	B	Feb 1994	50 (n = 26)	41 (n = 124)	*Anisoplaca achyrota* [1]
				B	Feb 1994	80 (n = 44)	63 (n = 197)	(Lepidoptera : Gelechiidae)
Ileostylus micranthus	Loranthaceae	bisexual	1	A&B	Jan 1994		6 (n = 231)	*Zelleria sphenota* [3]
								(Lepidoptera : Yponomeutidae)
Melicytus ramiflorus	Violaceae	dioecious	8	A&B	Dec 1993	1 (n = 100)	not counted	*Dipterina imbriferana* [1]
				A&B	Jan 1994	38 (n = 97)	not counted	(Lepidoptera : Tortricidae)
				A&B	Jan 1994	not counted		*Pyrgotis plagiatana* [4]
								(Lepidoptera : Tortricidae)
Myrsine australis	Myrsinaceae	dioecious	1	A&B	Jan 1994		1 (n = 300)	*Microcolona limodes* [1]
				A&B	Feb 1994		1 (n = 104)	(Lepidoptera : Elachistidae)
Plagianthus regius	Malvaceae	Mainly dioecious –a few flowers of opposite sex present	1	B	Jan 1994		2 (n = 450)	*Anisoplaca* sp. (cf. *acrodactyla*) [1]
				B	Jan 1994			(Lepidoptera : Gelechiidae)
				B	Jan 1994	not counted		*Peristoreus* sp.
								(Coleoptera : Curculionidae) [1]
Prumnopitys taxifolia	Podocarpaceae	dioecious	1	C	Dec 1993	not counted		*Heterocrossa iophaea* [1]
				C	Jan 1994	not counted		(Lepidoptera : Carposinidae)
				C	Feb 1994		24 (n = 105)	
				B	Feb 1994		11 (n = 71)	
				B	Feb 1994	not counted		unidentified larva [4]?
								(Lepidoptera : Tortricidae)
Sophora microphylla	Papilionaceae	bisexual	4	B	Feb 1994	22 (n = 62)	11 (n = 250)	*Stathmopoda aposema* [1]
								(Lepidoptera : Oecophoridae)
Port Hills, western Banks Peninsula								
Calystegia tuguriorum	–	–	–	B	Feb 1994	45 (n = 47)	23 (n = 103)*	*Stathmopoda skellonii* [5]

Clematis foetida	Ranunculaceae	dioecious		A	Feb 1994	3 (n = 150)		no animals seen
Coprosma linariifolia	Rubiaceae	dioecious	2	B	Feb 1994	not counted		*Praolepra* sp. [1] (Coleoptera : Curculionidae)
Griselinia littoralis	Griseliniaceae	dioecious	1	B	Jan 1994		1 (n = 110)	*Heterocrossa* sp. (*gonosemana* [1]
				B	Feb 1994		2 (n = 199)	group) (Lepidoptera : Carposinidae)
				B	Mar 1994		4 (n = 250)	
Hoheria angustifolia	–	–	–	B	Feb 1994		35 (n = 150)	*Anisoplaca achyrota* [1] (Lepidoptera : Gelechiidae)
								Heterocrossa sp. (cf. "*morbida*" auct.) [3] (Lepidoptera : Carposinidae)
								Peristoreus australis [1] (Coleoptera : Curculionidae)
								P. stramineus [1]
								P. sp. K2 (undescribed) [1]
Myrsine australis	–	–	–	A	Feb 1994		3 (n= 90)	*Microcolona limodes* [1]
Solanum laciniatum	Solanaceae	bisexual	c. 250	B	Feb 1994	83 (n = 40)	22 (n = 550)	*Sceliodes cordalis* [2] (Lepidoptera : Crambidae)
Riccarton Bush, Christchurch								
Pittosporum eugenioides	Pittosporaceae	bisexual	6	A	Feb 1994	not counted		*Montiethiella humeralis* (Hemiptera : Pentatomidae)
								Stephanorhynchus crassus [1] (Coleoptera : Curculionidae)
								Ctenopseustis sp. [4] (Lepidoptera : Tortricidae)
Kaikoura Coast								
Myrsine australis	–	–	–	A	Mar 1994		7 (n = 50)	*Stathmopoda horticola* [5] (Lepidoptera : Oecophoridae)
Stafford Cemetery, near Hokitika								
Myrsine salicina	Myrsinaceae	dioecious	1	B	Feb 1994		5 (n = 50)	*Microcolona limodes* [1]
							22 (n = 200)	*Heterocrossa* sp. (cf. "*epomiana*") [1] (Lepidoptera : Carposinidae)
Point Elizabeth Walkway, near Greymouth								
Griselinia lucida	Griseliniaceae	dioecious	1	B	Mar 1994		6 (n = 50)	*Heterocrossa gonosemana.* [1] (Lepidoptera : Carposinidae)
Rhopalostylis sapida	Arecaceae	monoecious	1	B	Feb 1994		23 (n = 200)	*Doxophyrtis hydrocosma* [1] (Lepidoptera : Yponomeutidae)

cific foliivorous larvae of the moth *Zelleria sphenota* were found to be eating these immature fruit. Related species have been reared by J.D. from fruit, leaves, and shoots of this and other Loranthaceae. A related Indian species is also specific to Loranthaceae (Zhang 1994).

Melicytus ramiflorus

A tree with fascicles of up to 20 flowers borne in large numbers along the young stems, *M. ramiflorus* has a periodic flowering system with two or three peaks in one year, beginning in early summer (Powlesland et al. 1985). On female trees the immature green fruit begin to turn purple in January. The maturing fruit (3 mm × 4 mm) are attacked by the larvae of the moth *Dipterina imbriferana*, which often eat all the seeds of any affected fruit. Dugdale (1966) recorded this species as an obligate seed-eater in *M. ramiflorus*. In one sample from Ahuriri Valley in mid January 1994, 38% of fruit were damaged. Adjacent affected fruit tend to adhere to one another and most are eventually shed from the tree. Burrows (1994) reported 17% (1985) and 88% (1986) of fruit caught in seed traps at a site on the Port Hills to be damaged by moth larvae, presumed to be *D. imbriferana*. The larvae leave the fruit in late summer to pupate in chambers chewed in dead wood.

M. ramiflorus in the central South Island flowers in most years, but the fruit crops are variable in size. Further study is needed to ascertain how the *D. imbriferana* population dynamics are co-ordinated in relation both to these year-to-year fluctuations and the within-year flowering periodicity of the host plant.

Myrsine australis

Individual female trees flower through the summer, autumn, or winter. Fruiting is episodic, with gaps of several years with no or few fruit between the heavy fruiting years. The fruit (c. 5 mm × 4 mm) are borne in fascicles of up to five, arranged densely on young branches. In a January 1994 sample of unripe fruit from Ahuriri Valley, 1% were affected by the very small larvae of a moth, *Microcolona limodes*. A February 1994 sample from the Port Hills contained 3% of affected seeds. Similar damage was found in casual samples of *M. australis* fruit from Ahuriri Valley in March 1994, and at Lake Wahapo in Westland where more than 90% of the seeds on one tree were damaged (December 1993) (C. J. Burrows unpubl. data).

Some 7% of a sample of green *M. australis* fruit from Omihi Reserve near Kaikoura in March 1994 had been chewed by larvae of a moth *Stathmopoda* sp. cf. *horticola* and damage to the fruit in this sample was also being caused by the larvae of a leaf tyer moth *Pyrgotis plagiatana* (Tortricidae). Both of these are generalist herbivores.

Plagianthus regius

The large cymose inflorescences of this tree resemble panicles. Fruiting is somewhat episodic, with lean years between the years with abundant fruit. The fruit (2.5 mm × 2 mm) are achene-like. In a sample from Ahuriri Valley Bush in mid December 1993 an *Anisoplaca* sp. and a few *Peristoreus* weevils were present. A mid January 1994 sample had 2% of fruit affected by the larvae of *Anisoplaca* cf. *acrodactyla*. *Heterocrossa* sp. cf. "*morbida*" was also raised from this sample.

Seed collections of *Plagianthus* from the Port Hills in 1989 contained moth larvae presumed to be *Anisoplaca* sp. and numerous small weevils. Although counts were not made, the proportions of damaged fruit were clearly much more than in the 1994 samples. Further study of the seed predator complex is needed, in comparison with that of *Hoheria*.

Prumnopitys taxifolia

At two year intervals female trees have spicate structures each carrying up to 12 seeds, but years with abundant seeds occur sporadically. The ovules are pollinated in Nov-Dec and the seeds then slowly mature over the next 14–16 months. In autumn the ripe seeds (8 mm × 8 mm) have a fleshy outer covering and a very thick, hard inner wall.

Samples of the seeds were difficult to obtain from the canopies of parent trees, so the samples from Ahuriri Valley Bush in December 1993 and January and February 1994 were all fallen, green, immature seeds, collected from the ground. Up to 24% of these were infested by the larvae of *Heterocrossa iophaea*, one per seed. In a February 1994 sample from a *P. taxifolia* canopy 11% had been attacked by *H. iophaea*.

It is known from seed trap contents from Ahuriri Valley (C. J. Burrows unpubl. data) that, in the late spring of the year following fertilisation, the contents of many immature seeds of *P. taxifolia* are eaten by a moth caterpillar, presumed to be *H. iophaea*, and these seeds fall to the ground. As the seeds remaining on the tree increase in size, predation and shedding of damaged seeds continue. By February of the following year, just before the outer tissues of the

remaining seeds turn black and juicy, the *H. iophaea* larvae cease eating their way into the seeds, presumably because the maturing inner coats are too thick and hard. They then eat the sugar-rich outer wall tissues before pupating. Further study of the long-term periodicity of *P. taxifolia* seeding in relation to this seed predator is needed. Beveridge (1964) noted fallen *P. taxifolia* seeds in a North Island forest that had been eaten by an unknown insect. *Heterocrossa iophaea* may have caused this damage.

Prumnopitys taxifolia seeds are affected by at least one other insect predator. Morvan (1980) recorded attack on small seeds from a South Island location by larvae of a tiny dipteran (Cecidomyidae) which modifies the form of the developing ovule and kills it. Distorted small ovules occur at Ahuriri Valley so this insect may occur there. J.D. has found a generalist seed-eating moth larva, *Cryptaspasma querula* (Tortricidae), feeding on miro *(P. ferruginea)* seeds in North Island localities. It may also affect *P. taxifolia.*

Sophora microphylla

The mature fruit of this tree is a long pod (up to 12 cm) borne in clusters of up to 10, and each containing up to eight seeds. In a February 1994 sample of mature fruit from Ahuriri Valley, 22% of the fruit had been attacked by the larvae of *Stathmopoda aposema* which had destroyed 52% of the seeds in those pods (but only 11% of seeds in the whole sample). Some seeds in individual pods escaped predation because they were in separate "chambers" created by constrictions of the pod. *S. aposema* is well known as a seed-eater in *Sophora* spp. A detailed study of the mode of attack and damage caused by its larvae was done by Webb (1993).

Clematis foetida

The panicles of female plants of this vine bear up to about 12 flowers. Each flower has about 20 achenes surrounding its receptacle. Each achene has a long, plumed tail and the tails curl over into a ball-like form. These seed heads remain on the plant through the autumn and winter, as the individual achenes are gradually shed. No animals were found in seed heads collected on the Port Hills, near Christchurch, during summer 1994, although chewed achenes were present. A moderate proportion of trapped achenes are also chewed (Burrows 1994). From previous experience J.D. suggests that larvae of a species of *Stathmopoda* (Lepidoptera:Oecophoridae) may be involved.

Coprosma linariifolia

Green fruit on this shrub in a site on the Port Hills were damaged by oviposition and eating of the seeds by larvae of a weevil, *Praolepra* sp. (February 1994). Similar oviposition damage and seed-eating of *Coprosma robusta* has been seen on the Port Hills and at Riccarton Bush but no animals were found. Further study of the predators and their effects is needed.

Griselinia littoralis

The females of this tree bear small flower panicles in early summer. Green fruit are on the tree through the summer and ripen in autumn (to 7.5 mm × 5 mm). The seed coat and pericarp are both thin. Samples gathered through the summer at Ahuriri Valley and on the Port Hills showed signs of damage, but the only definite identification was a single larva of *Heterocrossa* sp. (cf. *gonosemana*) from a Port Hills collection in January 1994. Ripe fruit collected in March 1994 from the same tree were more heavily infested (4%) with the same species. At this time the larvae (one per seed) had eaten most of the seed contents and filled about two thirds of the space inside the seed coat. Rearing was unsuccessful.

Solanum laciniatum

The flowers of this shrub are borne in small panicles of up to six. They develop into large green berries (3 cm × 2.2 cm) during summer. These are attacked by the larvae of the moth *Sceliodes cordalis*, which eats the flesh and some of the unripe seeds. Feeding continues up to the orange ripe-fruit stage, when heavily attacked fruit often are shed. Affected fruit are noticeably tunnelled and have brown blotches. A February 1994 sample from the Port Hills had 83% damaged fruit and 22% damaged seeds (whole sample).

The fruit of *S. laciniatum* contain soft pulp, seeds, and hard, oblate, seed-like objects, which are clusters of stone cells. The possibility that the stone cell clusters act as decoys or repellents, deflecting attention of the *Sceliodes* larvae from the seeds proper, warrants investigation.

Pittosporum eugenioides

This tree flowers in early summer. The paniculate infructescences bear up to 20 fruit. The fruit (8 mm × 6 mm) may remain green for about a year. Through the autumn to the following summer the capsules darken and open, revealing the mucilage-covered black seeds. Little insect damage is evident in the

green fruit, except oviposition scars and some feeding by larvae of at least one generalist herbivore, the tortricid moth *Ctenopseustis* sp. However, after the capsules open some seeds are eaten. Insects present in open capsules of *P. eugenioides* in Riccarton Bush, Christchurch, in January and February 1994 included two host-specific herbivores, the pentatomid bug *Montiethiella humeralis*, and the weevil *Stephanorhynchus crassus*. Some closed capsules yielded *S. crassus*. More study is required of the quantitative aspects of the herbivore-plant relationship.

Myrsine salicina

Females of this tree bear fascicles each with up to 10 flowers along the young branches in early summer. The fruit (6 mm × 5 mm) mature over about a year. In a February 1994 sample of green fruit from Stafford, Westland, 22% contained larvae of the moth *Heterocrossa* sp. cf. *epomiana*. The affected fruit were brown, drying off, and beginning to be shed. Many were tied together with larval silk and much frass was evident. A further 5% of the sample contained larvae of *Microcolona limodes*.

Griselinia lucida

Females of this epiphytic vine, or tree, bear panicles of flowers in summer. The fruit ripen during winter. Relatively few (6%) of a February 1994 sample of green fruit from Point Elizabeth near Greymouth were affected by the larvae of a moth, *Heterocrossa gonosemana*.

Rhopalostylis sapida

The unisexual flowers of this palm species are borne (males and females mixed) on large branched spadices. Different individuals flower at intervals through the summer. The sessile fruit, arranged densely along the spadix arms, ripen slowly over about a year and ripe fruit (1.2 cm × 0.8 cm) may be present for several months before removal by birds. The unripe and ripe fruit (and the spadix stems) are attacked by the larvae of a moth, *Doxophyrtis hydrocosma*. The larvae drill into the hard ripe seeds, creating large amounts of frass. In a February 1994 sample from Point Elizabeth, 23% of seeds were affected. As seeds are present for many months, a high degree of infestation is likely over the whole year.

In studies of *Rhopalostylis* near Auckland, Enright & Watson (1992) noted that 15% of seeds had been eaten by unidentified insects. It is likely that *Doxophyrtis* was involved, as J.D. has observed its presence from North Cape to Westland.

DISCUSSION

Five categories of insects on fruits were recognized (Table 1):

1. *Obligate seed-eaters, usually on the developing seed.* Virtually all species recorded are monophagous, restricted either to a genus (e.g., the weevil *Stephanorhynchus crassus* to *Pittosporum* spp.) or to a species (e.g., the moth *Heterocrossa iophaea* to *Prumnopitys taxifolia*). The only known polyphagous obligate seed-eater is the microcorsine tortricid moth *Cryptaspasma querula*, feeding on the large seeds in fallen fruit of *Beilschmiedia*, other drupe-like fruit, and seeds of *Prumnopitys ferruginea* (NZAC records).
2. *Obligate fruit-eaters which also eat seeds.* The fruit-eaters may be monophagous (e.g., *Sceliodes cordalis* on various Solanaceae) or possibly polyphagous (some *Heterocrossa* species). Rearing and distinguishing between *Heterocrossa* species is often difficult; several species appear to be fruit-eaters.
3. *Specific (monophagous) herbivores which may eat host fruit.* These herbivores can attack any growing part of the plant, depending on what is available: green shoots, buds, leaves, flowers, fruit. The moth *Zelleria sphenota* on leafy Loranthaceae is an example, where larvae can be found overwintering in green fruit.
4. *Generalist (polyphagous) herbivores which may eat host fruit.* Larval feeding (chewing or sucking) includes developing fruit and, usually, foliage, and is recognised by pitting or erosion (chewing) or lesions (sucking). Feeding is opportunistic, and the 'predator' is usually a successful polyphage, e.g., the abundant (and commercially significant) leaf rollers *Ctenopseustis* spp. and *Pyrgotis plagiatana*.
5. *Generalist detritivores, feeding on arboreal dying or dead plant parts.* Caterpillars of several moth groups feed on accumulations of dead plant parts in leaf axils or branch forks, especially on plants with crowded or tufted leaves, and on persistent dying bracts and calyces of inflorescences. In particular, larval feeding will also include contiguous live tissue, including seeds. One moth group for which this mode of feeding is characteristic is the genus *Stathmopoda* and its allies.

The following discussion refers mainly to insect species which are obligate seed eaters. Moths and certain weevil groups appear to be the most important obligate and facultative insect seed predators in New Zealand forests. The weevil groups concerned are monophagous at family-, tribe-, or genus-level. Specimens in NZAC include groups monophagous on Asteraceae (*Celmisia*, *Olearia*), Cupressaceae (*Libocedrus*), Papilionaceae (*Carmichaelia*), Elaeocarpaceae (*Elaeocarpus*), Fagaceae (*Nothofagus*), Oleaceae (*Nestegis*), and Podocarpaceae (*Phyllocladus*), as well as those reported here. Most of the moths reported here are similarly monophagous, but obligate fruit/seed-eating is a minor category of herbivory in New Zealand Lepidoptera (28 known or suspected species out of 1222 herbivorous (live-tissue) feeders, or about 2.3%).

Certain genera and families of moths are relatively prominent among the obligate seed-eaters noted in the present study (*Anisoplaca*, Gelechiidae; *Heterocrossa*, Carposinidae; *Stathmopoda*, Oecophoridae); nine plant species were affected relatively severely by insect species from 10 genera and nine families. Seven of the nine affected plant species are subject to seed predation by only one insect species; the rest have two or more seed-predators. Fruit/seed eating can be a family trait; for instance only one of our 18 indigenous gracillariids (leaf miners) is an obligate seed-eater, but nine of our carposinids (bud moths) are known or strongly suspected to be fruit/seed eaters.

The temporal pattern of attack of moths which are obligate seed-eaters varies from species to species. Larvae may penetrate developing seeds at various times after flowering. Usually one larva eats the contents of a seed. At least in some instances (e.g., *Griselinia littoralis*, *Myrsine australis*) only one seed appears to be eaten by one individual, but in other cases (e.g., *Prumnopitys taxifolia*, *Hoheria angustifolia*) the same individual may eat several seeds. While it is possible in the case of the *Anisoplaca* species which eat *Hoheria* seeds that more than one generation of moths occurs during the same seed year, too little is known of the insect life histories for this to be more than speculation.

Although this study makes some progress in knowledge of the seed predators of native woody plants, it is clear that sampling programmes which examine plant populations, seed populations, and insect populations, over periods of several to many years, are needed to explore the plant/seed predator relationship fully. Seed trap results (Burrows 1994, and unpublished longer-term data), though having inherent biases, suggest that flowering and fruiting periodicity, and fruit and seed productivity of most native woody species, as well as the degree of infestation of fruit by predators, are all quite variable from year to year. Therefore the present results must be regarded as indicative, rather than very representative. More rigorous sampling procedures are required in future seed predation studies, with repeated sampling in the canopies of larger numbers of individual plants. Such work was undertaken by Webb (1993) in his one-year study of the seed biology of *Sophora microphylla*. When studies are made of species with bird-dispersed seeds, bagging of fruit and comparisons with unbagged controls may be necessary. Full investigations of the life histories of the seed-eating insects are necessary especially in relation to variations in plant phenology due to weather variability and the periodicity of seeding in those species which produce fruit at irregular intervals or in highly variable amounts.

Little is known of the interactions between different insect species, in the instances where several seed predators affect the same host. The interactions between birds feeding on fruit and the seed predators are virtually unknown in New Zealand, although some studies have been made on them elsewhere (e.g., Herrera 1984). Kereru (*Hemiphaga novaeseelandiae*) are known to eat green fruit of some plants (Burrows 1994), including *Myrsine australis* and *Prumnopitys taxifolia*; they may remove some insect seed-eaters at the same time. Whether any predominantly insectivorous birds such as grey warbler (*Gerygone igata*), whitehead (*Mohoua albicilla*), tomtit (*Petroica macrocephala*), or rifleman (*Acanthisitta chloris*) eat seed-eating insects is unknown.

It is our hope that this pilot study will encourage plant scientists and entomologists to take a greater interest in this area of plant-animal interaction in New Zealand. Although various studies have been made on herbaceous plants and their dependent insects in this respect, especially *Chionochloa* (Mark 1965; White 1975; Kelly et al. 1992) and *Celmisia* (Molloy 1975; Spence 1990), the forest seed-eating fauna is relatively neglected.

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